STUDIES IN THE BORAGINACEAE, XXV
A REVALUATION OF SOME GENERA OF THE LITHOSPERMEAE

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AS A BACKGROUND for a study of *Lithospermum* and its immediate relatives it has been necessary to investigate and determine the characters of some of the other genera included in the Lithospermeae. It has been surprising to discover that most of these latter genera have a variety of interesting features that have gone unmentioned in published accounts of them. So much of interest was found that it has seemed desirable to prepare new and more complete descriptions of these genera and also to discuss their characters and relations. Six genera, all confined to the Old World, are so treated in the present paper.

The general affinities of the genera treated are well indicated by their pollen morphology. *Lithodora* appears to be a highly specialized derivative of the *Lithospermum*-complex, notable chiefly for its frutescent habit and aberrant nutlets. Its pollen has eight pores and a form duplicated also in *Lithospermum* and its close allies. The remaining five genera discussed appear to be more closely related to one another than to *Lithospermum* or its close allies. Except in one section of *Moltkia* their pollen is 3-pored and hence of a type different from that in *Lithospermum* and its immediate allies. As a group the five genera are also notable for the frequent development of bent nutlets and for the recurring manifestations of bilateral symmetry in their corolla and androecium.

The six genera discussed may be distinguished by the following key:

Nutlets circumscissile above the base, their major seminiferous portion falling away, leaving the true base persisting as a usually cupulate appendage permanently affixed to the gynobase; corolla without annulus or appendages; pollen ellipsoidal or somewhat ovoid, pores usually 8, borne at or slightly below the middle of the grain; body of nutlet straight. ..... 1. *Lithodora*.

Nutlets detaching completely from the gynobase.

Corolla without annulus; stamens all affixed at the same height on the corolla; pollen globose or globose-ellipsoid, pores 3–8, equatorial; body of nutlet somewhat bent.

Corolla without appendages; lobes short, broadly imbricate in the bud, becoming erect; style exserted only after the corolla is fully developed; anthers not ciliate; pollen with 3–8 pores. ..... 2. *Moltkia*.

Corolla with squamate appendages between the base of the filaments; corolla-lobes elongate, very narrowly imbricate in the bud; style precociously exserted, protruding from the incompletely developed corolla; anthers having the margins of the theca ciliate with crowded stout hairs; pollen with 3 pores. ..... 3. *Halacsya*.

Corolla with annulus developed; stamens usually affixed at unequal heights on the corolla; pollen usually conic-ovoid with the sides straight and convergent above the broad rounded base, pores 3, borne above base of the grain.

Nutlets very strongly and conspicuously bent, attachment small and substipitate; stamens deeply included, never exserted from the corolla, sometimes all affixed at the same height on the corolla but usually with the 2 adaxial ones affixed lower than the other 3; filaments very short; anthers with a narrow connective to which the filament is directly affixed, lacking a pit in the connective; corolla usually with appendages at the base of the deep throat or near the middle of the tube, these appendages alternating with the stamens and borne near or somewhat above the level of the filament-attachments; corolla usually glanduliferous inside; style deeply included, usually less than half the length of the corolla. ..... 4. *Alkanna.*

Nutlets straight or rarely weakly bent, attachment sessile and usually broad; stamens some or all usually exserted from the corolla-throat, sometimes affixed at the same altitude on the corolla but usually with the 2 adaxial members highest or the abaxial one lowest on the corolla; filaments usually very elongate; filaments affixed to the anthers in the depths of a pit located near the middle of the relatively broad connective; corolla without any appendages alternating with the stamens and never glanduliferous inside; style usually elongated and usually exserted at least beyond the throat of the corolla.

Annulus composed of a minute collar or of a ring of 5–10 minute sparingly hairy lobes, borne very close to (less than 1 mm. above) the corolla-base; style almost always 2-lobed; corolla facing backwards over the curved top of the cyme and more or less distinctly resupinate. . . .. 5. *Echium.*

Annulus developed well above (1.5–6 mm. above) the corolla base and represented by 5 evident, densely villous swellings or 5 squamose appendages borne one below the attachment of each stamen; style always simple; corolla usually erect, rarely resupinate; South Africa. ..... 6. *Lobostemon.*

1. **Lithodora** Griseb. Spicileg. Fl. Rumel. **2**: 85 (1844); Reichenb. Icon. Fl. Germ. **18**: 66, t. 1315 (1858); Johnston, Contr. Gray Herb. **73**: 55 (1924); G. Stroh, Beih. Bot. Centralbl. **58**^{B}: 211 (1938). Type species *L. fruticosum* L.

Lithospermum § *Lithodora* Boiss. Fl. Orient. **4**: 219 (1879).

Plant perennial, fruticose. Leaves veinless or nearly so. Cymes small, lax, 1–10-flowered, not scorpioid. Calyx 5-parted, lobes narrow, subequal, slightly accrescent at maturity. Flowers heterostylic or monomorphic. Corolla blue or purple, funnelform, with a cylindric tube and a short ob-

conic throat, outside glabrous or hairy; lobes ascending or spreading, rounded ovate or suborbicular, imbricate in the bud; throat without appendages, glabrous or bearing stipitate glands or sometimes villose; tube glabrous inside, lacking a basal annulus [1] or vestiges of it. Stamens affixed low in the throat and all borne at the same level, or the stamens affixed at unequal heights in the throat of the individual corolla. Filaments filiform, much shorter than the anthers or nearly as long or even longer, in heterostylic species short filaments associated with long-styled flowers and long filaments with short-styled ones, in species having stamens borne at unequal heights on the throat the lower stamen usually with the shortest filament. Anther oblong, usually several times longer than broad, affixed medially or slightly submedially, included or slightly exserted only in some short-styled flowers, base emarginate, apex obtuse or retuse, thecae usually united almost to the base but in one species these more or less separate below their middle. Style filiform and frequently somewhat laterally compressed, usually either shorter than the calyx or about twice as long, simple or somewhat forked at the summit, included or shortly exserted from the throat; stigmas 2, terminal and juxtaposed on the tip of the simple style or one terminating each of the short stout lobes of the apically forked style. Pollen small, 18–25 × 15–23 μ, ellipsoidal or somewhat ovoid; pores usually 8, borne in a single row around the grain at or slightly below the equator. Nutlets straight, ovoid or ovoid-cylindric, commonly only one maturing, smooth or very abundantly and minutely muriculate, turberculate or rugulose, with a prominent ventral keel (ventral suture fused, obscure), at maturity developing a circumscissile abscission above the base, the major seminiferous portion of the nutlet detaching and falling away, leaving the short sterile basal section to form a usually cupulate appendage permanently affixed to the low pyramidal gynobase; attachment scar of detached nutlets basal, horizontal, or slightly oblique, nearly as broad as long, bearing a projecting indurate appendage; appendage usually peg-like and nearly central but in one species angulate, somewhat pyramidal, and occupying most of the dorsal half of the scar.

The genus *Lithodora* has been recognized by few authors. Its species have been almost universally assigned to *Lithospermum,* and because of general similarities in fruticose habit even associated with species referable

[1] The term **annulus** is applied to the usually minute appendages borne inside the corolla-tube usually just above its very base. Though in some species and genera it is never developed, in most Boraginoideae it is usually represented either by a tumid ring, a narrow annular ridge, or a collar-like structure, or, perhaps more commonly, by a ring of 5–10 small equidistant lobes borne just above the corolla-base. When present the annulus is usually appressed against the base of the ovary and apparently functions in limiting access to the nectary beneath the ovary. Only in a few genera, such as *Onosma*, are the lobes of the annulus themselves apparently nectariferous. Because of this it seems desirable to substitute the appellation *annulus* for "tube-nectary," which I have used in several previous papers of this series. The annulus is a structure that has been generally ignored by students of the Boraginaceae, although its usefulness in classification was long ago indicated by Bunge, Heliocarya 10–11 (1871). For some recent notes on its function see H. Schaefer, Bot. Jahrb. 72: 319 (1942).

to *Moltkia* and *Buglossoides*. As a matter of fact the genus is probably not very closely related to the genera mentioned. Actually it is one of the very distinct members of the *Lithospermeae*. It has nutlets of a type that is unique in the whole Boraginaceae. Only in a group of plants that has had no over-all critical re-examination for over a hundred years, such as the *Lithospermeae*, could the unusual features of this genus have gone so long unrecognized.

The species of *Lithodora* are low shrubs which frequent cliffs and other exposed rocky places. One species ranges in western France (north to Brittany) and in western portions of the Iberian peninsula and Morocco. The six other congeners occur in restricted areas scattered in the Mediterranean region as far east as coastal Anatolia.

The distinctive features of the fruits of *Lithodora* are all associated with the fact that the nutlets are freed from the gynobase not by a basal, but a suprabasal abscission. In all *Boraginoideae* other than *Lithodora* the abscission is developed at the very base of the nutlet at the level where the latter becomes differentiated from the gynobase. In such genera as *Lithospermum*, which may agree with *Lithodora* in having erect basally affixed nutlets, the abscission, usually plane, is exactly basal, and as a result the complete nutlet is freed from the gynobase. In *Lithodora*, however, a basal section of the nutlet never becomes detached from the gynobase. The abscission freeing the major seminiferous portion of the nutlet develops not at the morphological base of the nutlet but distinctly (0.5–1 mm.) above it. As a result, when the fertile upper section of the nutlet detaches, a short basal section of it remains as a persisting saucer-shaped or cup-shaped appendage on the gynobase. The condition is unique. It distinguishes *Lithodora* from all other genera of the Boraginaceae.

Since the attachment end of the freed nutlets is not the morphological base of the nutlet, it is not surprising that its attachment scar should have peculiarities. The scar may be horizontal or slightly oblique but is never plane, as is prevalent with the nutlets of genera related to *Lithospermum*. In six of the seven species of *Lithodora*, the attachment surface bears near its center a vertical peg-like appendage 1–2 mm. long. This appendage is composed of indurate tissue that surrounds the tubular canal through which the ovule was formerly supplied by a vascular strand arising from the gynobase. On the detached nutlets of *L. rosmarinifolia*, *L. moroccana*, *L. oleaefolia* and *L. diffusa*, the canal within the appendage is usually empty. The section of the funicular strand which formerly occupied it remains attached to the basal section of the nutlet, and like a bristle arises from the center of that cup-like structure. In *L. fruticosa* the base of the detached nutlet has different features. The dorsal half of the base is occupied by a solid, irregular, somewhat pyramidal mass of salient indurate tissue. An angular excavation may occupy most of the ventral half of the base. The projecting rough pyramidal mass contains two embedded vascular strands but no tubular canal. This appendage on the detached nutlets of *L. fruticosa* not only has a more dorsal position on the base, it has a structure that is different from the peg-like appendage on the nutlets of the

other species of the genus. In the latter the appendage is made up of hardly more than the bony walls of the funicular canal. In *L. fruticosa* the funicular canal is not included in the appendage. The canal for the funicle has a course paralleling and just inside the ventral keel of the nutlet and continues so downward to just below the abscission. In the portion of the nutlet remaining affixed to the gynobase, its lower course is apparently marked by a ridge sloping downward and inward towards the middle of the cup-like structure. The canal remains close to the ventral wall of the nutlet and joined to it.

The prominences on the base of the detached nutlets of *Lithodora* have a superficial similarity to the strophiolate outgrowths on the attachment surface of the nutlets of the *Anchuseae*. They are, however, morphologically very different structures. The nutlets of the *Anchuseae* detach completely from the gynobase. Their prominent, rounded, plug-like attachment surface is oily and parenchymatous (an elaiosome) and is seated in a socket in the gynobase, cf. Bacin, Bul. Fac. de Ştilnţe, Cernauţi 9: 123–169 (1935). The prominences on the attachment scar of nutlets in *Lithodora* are bony tissue formerly filling a basal section of the nutlet that never becomes freed from the gynobase.

The androecium of *Lithodora* shows considerable diversity and presents some unusual developments. Heterostyly is well developed in five of the seven species. In flowers with long styles the stamens are borne low in the corolla-throat on filaments much shorter than the anthers (usually about a quarter as long) while in short-styled flowers the stamens are borne slightly higher in the throat on filaments equaling or even slightly longer than the anthers. The dimorphism here involves not merely differences in style length and the height at which stamens are affixed in the throat, but also length of filaments. Among the Boraginaceae I know of only one other example with this particular type of dimorphism, viz., *Lithospermum hispidissimum*, cf. Jour. Arnold Arb. 33: 325 (1952). Unlike that species, however, the five members of *Lithodora* show no dimorphism in pollen. In *Lithodora* the pollen of long- and short-styled flowers is indistingishable. Illustrations of the dissected corollas of *L. hispidula*, *L. oleaefolia*, *L. Zahnii*, and *L. rosmarinifolia* are given by Spengler, Oesterr. Bot. Zeitschr. 68: 115, t. 1, f. 18, 20, 21 and 22 (1919), but by coincidence only the short-styled corollas of all these species were selected for illustration.

Lithodora fruticosa presents a very simple form of heterostyly. As in the species previously described, the flowers have either a short style, reaching about half way up the corolla-tube, or a long one which may equal the corolla-tube or become shortly exserted from it. In *L. fruticosa*, however, there is no concomitant dimorphy in the androecium. The stamens always have short filaments and are always borne in the same relative position low in the corolla-throat, cf. Spengler l.c., t. 1, f. 17. Heterostyly in this species appears to be reduced to its simplest expression, dimorphy of style only.

In *L. diffusa* the androecium deviates in organization from that in all other species of the genus. The flowers are not at all heterostylic. The

stamens are not equal nor verticillate. The five stamens within a flower differ in length of filament and in the altitude at which each is attached above the corolla-base. There are three uppermost stamens borne at nearly the same level. Below these there is a fourth stamen attached at middle height and below that a fifth, obviously affixed lowest down in the corolla-throat. The distance between the attachment points of the highest and lowest stamens may be 1.5–3 mm. Associated with the varying heights above the corolla-base at which the stamens are attached is also a variation in the length of the filaments. The higher the position of the stamen the longer its filament. The lowest stamen, accordingly, is distinguishable not merely by its low attachment but by the shortness of its filament as well. Its position on the corolla relative to the axis of the cyme (whether axial or abaxial) I have been unable to determine with certainty. The anthers in most species of *Lithodora* are elongate, usually several times as long as broad. In *L. diffusa* they are proportionately shorter, usually less than twice as long as broad, and instead of having merely emarginate bases usually tend to be distinctly lobed below their middle. Plants of *L. diffusa* have either a long style in the flower or a short one. From the collections examined I can find no evidence that individual plants differing only in style length grow together in one locality. Interestingly, all the plants seen from northern portions of the geographic range of the species have long styles only, whereas those from the south have oniy short styles. The indications are that in *L. diffusa* style length varies only as a character of geographic races.

The pollen of *Lithodora* is small, 18–25 × 15–23 μ, and usually ellipsoidal or ovoid. It is circular in polar profile. The eight pores are inconspicuous and are arranged around the grain in a single row on the equator or slightly below it. None of the species of the genus have distinctive pollen, and there is no difference in the grains of long- and short-styled flowers of heterostylic species. In some species individual plants producing somewhat ovoid grains with submedial pores appear to be more common than those producing ellipsoidal grains with equatorial pores. In other species the reverse condition prevails. In varying degrees, however, the variation from ellipsoidal to ovoid is observable among individuals in all the species.

The bracted inflorescence is short, loose, and few-flowered, and not at all markedly differentiated from the leafy mass of the plant. It commonly bears three to seven flowers (rarely as many as ten), and even at maturity is not at all scorpioid.

When he established *Lithodora,* Grisebach gave a generic description and listed six species of *Lithospermum* referable to the proposed genus, viz., *Lithospermum fruticosum* L. ("cum forma brevistyla: *L. rosmarinifolio* Ten."), *L. hispidulum* Sm., *L. calabrum* Ten. (known only from description), *L. oleaefolium* Lois. (no flowers seen) and as "parum a ceteris aberrant," also *L. prostratum* Lois., and *L. graminifolium* Viv. Of the six species mentioned *L. calabrum* belongs to *Buglossoides* and *L. graminifolium* to *Moltkia.* Two species, *L. prostratum* and *L. graminifolium,*

Grisebach considered aberrrant, for as he states, they have characters not in accord with his diagnosis of *Lithodora*. Grisebach knew *L. calabrum* only from the literature and had only incomplete specimens of *L. oleaefolium*. His concept of *Lithodora*, accordingly, must have been founded primarily upon *L. fruticosum* and *L. hispidulum*. Of these two the former is selected as type of the genus. It is to be noted that at the time he founded the genus *Lithodora*, Grisebach made no new binomials under that genus. He merely listed species of *Lithospermum* referable to it. Five new combinations (for all the species mentioned except *L. rosmarinifolium*) are, however, legitimately published in the index concluding the volume. The two volumes of Grisebach's "Spicilegium Florae rumelicae et bithynicae" were published in six fascicles issued over a period of three years. The description of *Lithodora*, vol. 2, p. 85, was included in Heft 5 (pp. 1–160) issued in mid-1844, cf. Flora **1844**[2]: 526, Aug. 14, 1844. The index concluding volume 2 was included in the Double Heft, 5–6 (pp. 161–548) issued early in 1846, cf. Flora **1846**: 96, Feb. 14, 1846, and Bot. Zeit. **4**: 226, March 27, 1846. Although published in the same volume, Grisebach's genus bears the date 1844, whereas his binomials under that genus date from 1846.

Gymnoleima Decne. (1844) has been treated as a synonym of *Lithodora*, but I have typified it by *Lithospermum graminifolium* Viv. and placed it as a synonym of *Moltkia*.

Section **Allostema**, sect. nov.

Flores evidenter dimorphi. Stamina sub altitudinibus aequalibus inserta; eis in flores stylum longiorem gerente basim versus faucium orientibus, filamentis quam antheris brevioribus donatis; eis in flore stylum breviorem gerente supra medium faucium orientibus, filamentis antheris aequilongis vel longioribus donatis. Antherae elongatae basi emarginatae. Nuculae laeves vel (ea L. hispidulae) muriculatae cicatrice appendiculam erectam gracilem elongatam canale funiculari inclusam proferente donatae.

Lithodora rosmarinifolia (Ten.) Johnston, Contr. Gray Herb. **73**: 56 (1924).

Lithospermum rosmarinifolium Ten. Fl. Neap. Prodr., Suppl. **2**: 66 (1811–13) and Fl. Neap. **3**: t. 114 (1811–15).

Known only from southern Italy, Sicily, and northeastern Algeria. Shrub to 6 dm. tall; stem and narrow elongate leaves strigose (hairs usually less than 1 mm. long, closely appressed, all antrorse); corolla evidently hairy outside, throat sparsely glanduliferous inside; calyx short, base becoming distinctly thickened and ribbed at maturity; nutlets smooth.

Lithodora moroccana, sp. nov.

Lithospermum diffusum var. *micranthum* Faure & Maire in Maire, Bull. Soc. d'Hist. Nat. Afr. du Nord **22**: 56 (1931).

Known only from Morocco. Shrubby with prostrate stems, plant less than 1.5 dm. tall; stems and narrow elongate leaves clothed with slender loosely appressed hairs (0.8–2 mm. long) which are partly antrorse and partly retrorse; corolla evidently hairy outside, inside with sparsely glanduliferous throat; calyx short, the base becoming thickened and ribbed at maturity; nutlets smooth.

Frutex depressa 5–15 cm. alta cinerea; caulibus prostratis lignosis ramosis vetustiore decorticatis, ramulis foliatis 1–10 cm. longis erectis vel adscendentibus dense hispido-villosis pilos gracillimos rigidulos 1.5–2.5 mm. longos juventate adscendentes mox erectos deinde retrorsos gerentibus; foliis oblanceolatis 1–2.5 cm. longis 2–6 mm. latis margine saepe revolutis, facie superiore pilos gracillimos 0.8–2 (saepe ca. 1) mm. longos laxe antrorseque adpressos e basi bulbosa vel rariter discoidea orientes gerentibus, facie inferiore pilis albis abundantibus gracillimis laxe appressis alii antrorsis alii retrorsis gestis indumento denso albo laxe appresso praeditis; calyce 5–6 mm. longo tubo corollae conspicue breviore sessili maturitate basi evidenter incrassato, lobis cuneatis; corolla 15–18 mm. longa, extus pilis numerosis gracilibus antrorsis gesta, limba ca. 1 cm. diametro, lobis rotundis 3–3.5 mm. longis 2.5–3 mm. latis ascendentibus, faucibus inconspicue glanduliferis, tubo 12–16 mm. longo intus glabro; antheris elongatis 1.5–2 mm. longis; filamentis aequalibus, in floribus stylum longum gerentibus supra medium tubi corollae (6–9 mm. supra basim tubi) affixis brevis ca. 0.5 mm. longis, in floribus stylum longum gerentibus longioribus 1.5–2 mm. longis apice tubo corollae affixis; stylo 6–7 mm. longo et paulo supra medium tubi corollae attingente vel 12–17 mm. longo et tubo aequilongo vel longiore; nuculis erectis albis laevibus 2.7–3.7 mm. longis.

MOROCCO: env. de Debdou, rocailles et rochers dominant le Camp Roumons, 100–1200 m., Apr. 4, 1928, *Briquet 227* (G); Debdou, ad rupes supra Castra Roumens, ca. 1300 m., Apr. 10, 1928, *Wilczek & Dutoit 294* (Kew); Monte Bu-Ibdiren (Beni-bu-Yahi), coteaux calcaires, Jan. 23, 1931, *Mauricio 7946* (G); Monte Bu-Ibdiren, Apr. 22, 1934, *Mauricio & Sennen 7946* (TYPE, Brit. Museum); Beni Snassen, Taforalt, broussailles du Djebel Metchick, 1050 m., 1930, *A. Faure* (G); above Xauen in El Rif, 4500–5500 ft., limestone, April 14, 1939, *Peter Davis 462* and *468* (Kew).

Although confused with *L. diffusa,* this plant is actually very much more closely related to *L. rosmarinifolia.* From the latter it differs in its depressed habit and its indument of much longer, more loosely appressed hairs. In *L. rosmarinifolia* the indument is distinctly strigose, the hairs being much shorter than those of *L. moroccana* and very much more closely appressed. Furthermore they are always antrorse. In the short-styled flowers of *L. moroccana* the filament and anthers are about equal in length. In comparable flowers of *L. rosmarinifolia* the filaments are longer than the anthers.

Lithodora oleaefolia (Lapeyr.) Griseb. Spicileg. Fl. Rumel. 2: 531 (1846).

Lithospermum oleaefolium Lapeyr. Hist. Abr. Pl. Pyr., Suppl. 28 (1813); Stapf, Bot. Mag. **149:** t. 8994 (1924).

Local in the eastern Pyrenees. Plant shrubby, with slender, loosely decumbent stems; larger leaves 7–13 mm. broad, margins obscurely if at all revolute, lower surface with a dense white indument of abundant slender appressed hairs; corolla evidently hairy outside, inside with the throat sparingly glanduliferous; calyx at maturity divided into slender elongate lobes, base not thickened; nutlets smooth and shiny.

Lithodora Zahnii (Heldr.) Johnston, Contr. Gray Herb. 73: 56 (1924).

Lithospermum Zahnii Heldr. in Halacsy, Verh. Zool.-Bot. Ges. Wien **49:** 190 (1899).

Lithospermum fruticosum sensu Sibth. & Sm. Fl. Graecae **11:** 52, t. 161 (1813).

Mountains of Greece. Low shrub becoming 4 dm. tall, branches ascending and more or less regularly dichotomous. Leaves *Lavendula*-like, narrow, elongate and strongly revolute, 2–4 cm. long; corolla glabrous inside and out, throat not glanduliferous; calyx divided at maturity, the lobes not rigid, 8–11 mm. long, base not thickened; nutlets smooth, lustrous.

In this species the cupulate base of the nutlet, remaining joined to the gynobase, is well developed, commonly 1 mm. high. In *L. rosmarinifolia, L. moroccana, L. oleaefolia,* and *L. diffusa* a section of the funicular strand normally remains affixed in the depth of the persisting cup and arises bristle-like from within it. This section of strand is that formerly occupying the tubular canal in the appendage on the lower end of the detached nutlet. In *L. Zahnii* the strand remains within the canal of the detached nutlet, and there is, accordingly, no bristle-like section of it arising inside of the cupule.

Lithodora hispidula (Sibth. & Sm.) Griseb. Spicileg. Fl. Rumel. 2: 531 (1846).

Lithospermum hispidulum Sibth. & Sm. Prodr. Fl. Graecae **1:** 114 (1806) and Fl. Graec. **2:** 53, t. 162 (1813).

A low, twiggy, stiffly much branched shrub 1–3 dm. tall, restricted to islands and coastal regions of the eastern Mediterranean (Crete to southwest Turkey). Corolla glabrous inside and out, throat not glanduliferous; leaves small, spathulate to oblanceolate, less than 15 mm. long, usually ciliate with stout pungent hairs; calyx at maturity with a thick base and a short but distinct tube 1.5–2 mm. long; lobes rigid, 5–6 mm. long; nutlets dull, abundantly and minutely muriculate.

The most mature fruiting structures seen of this species are some with practically mature nutlets still firmly affixed. In these the basal section of the nutlet (that affixed to the gynobase), unlike that in other species of the genus, is longer than thick, and short-cylindric rather than cupulate in form. In collections of other species with a little search one can usually find some old calyces still persisting on the plant after the nutlets have

been matured and freed. In such old calyces the persisting base of the nutlet is studied to best advantage. Although eight collections of *L. hispidula* have been examined, in none of them have old calyces been found persisting.

Section **Eulithodora.**

Flowers not truly heterostylic; style long or short, but the stamens (all borne at the same level) constant as to position on the corolla and as to length of filaments. Corolla glabrous or with some hairs on the outer surface of the lobes; throat glabrous, not glanduliferous. Nutlets minutely and longitudinally striate, strongly constricted just above the base, attachment scar bearing a somewhat pyramidal angulate projection.

Lithodora fruticosa (L.) Griseb. Spicileg. Fl. Rumel. **2:** 531 (1846).

Lithospermum fruticosum L. Sp. Pl. 133 (1753).
Lithospermum consobrinum Pomel, Nouv. Mat. Fl. Atlant. 296 (1874).
Lithodora consobrina (Pomel) Johnston, Contr. Gray Herb. **73:** 56 (1924).

A species native to southeastern (Mediterranean) France, middle and eastern Spain, and the coast of Algeria. In vegetative condition sometimes confused with the very different *L. diffusa*, but readily distinguished by having short, more closely appressed hairs on the herbage, usually more revolute leaf-margins, and lower leaf surface distinctly pallid from minute (0.2–0.3 mm. long), very closely appressed white hairs.

Section **Lasioglottis,** sect. nov.

Flores monomorphi. Stamina sub altitudinibus inaequalibus inserta; filamentis inaequalibus. Corollae extus saepe strigosae; faucibus intus antrorse villoso-strigosis et non rariter glanduliferis. Nuculae minute abundanterque tuberculatae opacae cicatrice appendiculam erectam gracilem elongatam canale funiculari inclusam proferente donatae.

Lithodora diffusa (Lag.) Johnston, Contr. Gray Herb. **73:** 56 (1924).

Lithospermum diffusum Lag. Varied. Cienc. **4**[4]**:** 39 (1805).
Lithospermum prostratum Lois. Fl. Gall. 105 (1806).
Lithodora prostrata (Lois.) Griseb. Spicileg. Fl. Rumel. **2:** 531 (1846).

As here accepted, the species is given the very broad definition almost universally accepted by past authors. It includes a very variable group of plants ranging in western France (north to Finistère), in western and southern Spain, and in Portugal and Morocco. The species needs a detailed study. A number of varieties have been published, but these are based on rather intangible differences in gross habit. No attention has been given to characters revealed only by the dissection of the corolla. Some of these appear to be geographically correlated, and when properly studied will probably be useful in defining really significant varieties (and possibly segregates) of the species. Between northern and southern forms of *L. diffusa* I have noted differences in length of style, size of anthers,

lobing of anthers, and abundance of hairs and glands in the corolla-throat.

In having the filaments unequal and affixed at unequal heights on the corolla-throat, and in having the corolla-throat usually conspicuously hairy, *L. diffusa* is not merely distinguished from its congenera — it has features unusual in the Boraginaceae. The irregular distribution of stamens in the throat seems most like that characteristic of two species of *Lithospermum*, cf. Jour. Arnold Arb. 33: 303 (1952). In those species, however, the filaments are equal and do not vary in length according to their high or low position in the throat, as in *L. diffusa*. The irregular androecia of all these species no doubt have a fixed orientation within the corolla, but this can be determined with certainty only by someone with a supply of fresh flowers for dissection. From my observations, the odd stamen, that affixed lowest down in the throat, seems to be located on the abaxial side of the flower. Possibly it alternates with the two anterior lobes of the corolla, which, in all the species mentioned, frequently seem to be more spreading than the three posterior lobes. The hairy corolla-throat of *L. diffusa* is also noteworthy. In some southern forms of the species the throat may be sparingly hairy or rarely nearly glabrous, but in the common forms of the plant the throat is densely clothed with evident slender, antrorsely appressed hairs. The stamens emerge from among the abundant hairs. This condition is found elsewhere in the *Boraginoideae* only in *Ancistrocarya, Sericostoma,* and *Echiochilon.*

2. **Moltkia** Lehm. N. Schrift. Naturfor. Ges. Halle 3^2: (1817); Lehm. Asperif. 2: 339 (1818); Lehm. Icones 26, t. 43–44 (1821). — based on *M. punctata* Lehm. and *M. caerulea* Lehm.

Gymnoleima Decne. in Jacquemont, Voy. Ind. 4^2: 122 (1844). Type species *Lithospermum graminifolium* Viv.

Lithospermum § *Gymnoleima* [Decne.] Endl. Gen. Pl. Suppl. 3: 77 (1843).

Plants perennial. Stems herbaceous or more or less fruticose, strigose. Leaves alternate, veinless. Cymes evidently bracted, solitary or clustered at the ends of the stems or branches, becoming elongate and evidently unilateral at maturity. Calyx 5-parted, the lobes firm, linear, equal or nearly so. Corolla blue, purple or yellow, elongate and gradually ampliate or with a differentiated tube and swollen throat, glabrous inside and out or with some coarse hairs on the inner face of the lobes and on the adjacent throat; lobes imbricate, becoming erect, rounded, longer than broad to broader than long, equal or practically so; throat without glands or appendages; tube not developing an annulus, smooth and glabrous. Stamens affixed at equal heights above the middle of the corolla; filaments linear, with an evident midvein, equal or unequal, usually longer than the anther, short to very elongate; anthers included or more or less exserted, oblong to lanceolate, straight to strongly recurved, affixed at or near the middle or distinctly below the middle, apex obtuse or emarginate or somewhat apiculate, theca more or less distinct at the base. Pollen sphaeric or slightly longer than broad, small (16–31 μ), pores 3–8, equatorial. Style very slender, filiform, eventually exserted beyond the corolla-

lobes, terminated by a very small entire or weakly lobed stigma. Nutlets smooth and lustrous or minutely tuberculate or papillate and opaque, bent ventrally above the base; ventral keel usually prominent, bearing a closed more or less fused suture; attachment scar large, morphologically basal but because of the bend in the nutlet body appearing to be obliquely basal or suprabasal, ovate or ovate-triangular, flat or concave. Embryo more or less curved or bent, tip of cotyledons directly above the nutlet attachment. Gynobase pyramidal when bearing four nutlets, flat when only a single nutlet is matured.

The six species of *Moltkia* are equally divided between two well-marked sections, one confined to southern Europe from northern Italy to northern Greece, the other to western Asia from Anatolia to Transcaucasia and northwestern Iran. The genus has been confused with *Lithospermum* and some of its species have been persistently referred to it, particularly by gardeners. *Moltkia,* however, differs from *Lithospermum* in having a corolla with erect lobes, glabrous outer surface, and an unappendaged non-glanduliferous throat, as well as a very slender, eventually long-exserted style, a very small entire or only weakly lobed stigma, and not straight, but distinctly bent nutlets. In its fruit *Moltkia* is most like *Halacsya* and *Alkanna,* and its relations are probably closer with these genera than with *Lithospermum.*

The most recent treatment of the genus is by Wettstein, Oesterr. Bot. Zeitschr. 67: 361–69, f. 1–6, t. 3 (1918), who discussed its characters and illustrated the flowers and fruit of most of the species. Among the eight species he admitted to the genus, however, two must be excluded. The plant he accepted as *Moltkia callosa* (Vahl) Wettst. represents the recently proposed monotypic genus *Moltkiopsis,* cf. Jour. Arnold Arb. 34: 3 (1953). His *Moltkia parviflora* (Decne.) Wettst. belongs with the Himalayan representatives of *Mertensia,* with which it agrees in having sparingly bracted inflorescence and very distinctive nutlets. Neither of these two excluded species has any close affinity with *Moltkia.*

Although the nutlets of *Moltkia* appear to have an attachment that is obliquely basal or even suprabasally lateral, the attachment is, in a morphological sense, truly basal. A medio-longitudinal section of the nutlet reveals that the embryo is curved but has the distal portion of its cotyledons located inside the pericarp directly above the attachment scar and in a plane vertical to it, the relation in all basifixed nutlets. The longitudinal section shows further that the nutlet body is bent, at or distinctly below the middle, 45°–90° inward towards the center of the flower. It is because of this distortion of the nutlet body that the attachment has the appearance of being oblique or suprabasal when actually it is basal on the only portion (the lower third to a half) of the body which is morphologically erect. When only one of these nutlets is matured in a flower, and, as a result, the gynobase is not elevated, the nutlet body is more or less horizontal or obliquely ascending. In flowers which mature four nutlets, the gynobase does elevate and is pyramidal and about as broad as high. Straight basifixed nutlets, such as those of *Lithospermum,*

if borne on this pyramidal gynobase, would be very strongly divergent. Since the basifixed nutlets of *Moltkia* are bent, when they are affixed on the pyramidal gynobase their bent form corrects any tendency to divergence, and their tips become connivent and their long axes seem parallel.

The behavior of the androecium in the maturing corolla of *Moltkia* has interesting diversity and some puzzling aspects. Two of the species (*M. Dörfleri* and *M. suffruticosa*) have included stamens with short filaments that have reached their maximum length as the corolla opens. In the four other species of the genus, however, the filaments elongate conspicuously after the corolla opens and eventually become evidently exserted beyond the corolla-lobes. The filaments of the five stamens within a flower do not elongate simultaneously. In *M. caerulea* and *M. longiflora* the individual stamens elongate according to an obvious pattern. The filament of the median forward stamen elongates first, then the filaments of the posterior lateral pair of stamens, and finally those of the anterior lateral pair. Those elongating last never become as long as the other three. As a result, the androecium has evident bilateral symmetry. In *M. aurea* and particularly in *M. petraea* the androecium has no such pattern. Although the filaments eventually become about equally elongate, the rate of elongation and the time of its initiation may differ for each of the five stamens. Indeed, for an interval between the time that the corolla opens and the time the stamens are fully exserted, the filaments of a given flower may all have different lengths. On some plants of *M. petraea* the sequence of elongation seems possibly even in accord with a 2/5 phyllotaxy. The matter deserves attention from someone who has fresh flowers available for observation.

As in other genera of this relationship, the anthers of *Moltkia* dehisce and spill out much of their pollen just before the corolla opens. At this time the style usually surpasses the anthers, and the stigma has a position at the top of the bud above the anthers. Only in some (not all) flowers of *M. caerulea* have I found the style shorter at this stage, i.e., with the stigma borne between and not above the anthers. In *M. Dörfleri* and *M. petraea,* indeed, the style is so elongate that it is accommodated within the closed corolla only by becoming contorted or by having its apex appressed against and even decurved against the still tightly folded corolla-lobes. After the corolla opens the style elongates. In the species having exserted stamens, although the style reaches maximum extension promptly, the elongating filaments eventually raise the anthers to the same height as the stigma or nearly so. What purpose and interrelation the described sequences of changes may have in effecting pollinization is obscure. Since the anthers dehisce and lose much if not all of their pollen while still included in the corolla, their subsequent extrusion would seem to have little purpose.

The generic name *Gymnoleima* was published rather casually by Decaisne in a brief very general discussion of the affinities of the Himalayan species now referred to *Mertensia.* As a proposed segregate of *Lithospermum* it was launched as follows: "Je désignerais par le nom de *Gymnoleima*

les *Lith. graminifolium, oleifolium, rosmarinifolium* et *fruticulosum*, dont la gorge de la corolla n'offre aucun appendice, dont le stigmate est plus ou moins échancré, . . ." Of the species mentioned, the first belongs to *Moltkia* and the remaining three to *Lithodora*. The genus has never been accepted. The only binomials under the genus are the four attributed to Decaisne, which appear in print for the first and only time in the Index Kewensis. Since Decaisne's brief characterization of *Gymnoleima* applies equally well to all the species he lists, I have accepted the first mentioned, *Lithospermum graminifolium*, as the type of the genus. *Gymnoleima* accordingly becomes a synonym of *Moltkia*. This is desirable, for any other typification would bring *Gymnoleima* (1844) into competition with the later *Lithodora* (1845).

Section **Eumoltkia.**

Nutlets with roughened opaque surface, very abundantly and minutely tuberculate or papillate and also coarsely warted, rugose, or pitted, apex of nutlet rounded. Attachment surface of the nutlets and faces of the gynobase green. Corolla with a well-differentiated, more or less swollen throat. Filaments arising from 5 weak invaginations at the base of the corolla throat, elongate, equal or nearly so or 2 distinctly shorter than the other 3. Anthers affixed between the base and middle, becoming conspicuously recurved. Pollen sphaeric or nearly so, polar profile circular or somewhat 3-sided, lateral profile circular or nearly so, pores remaining obscure, apparently 3 and equatorial.

Moltkia caerulea (Willd.) Lehm. N. Schrift. Naturf. Ges. Halle 3^2: 6 (1817).

Onosma caerulea Willd. Sp. Pl. 1^2: 775 (1798).
Moltkia punctata Lehm. N. Schrift. Naturf. Ges. Halle 3^2: 5 (1817).
Cynoglossum rugosum Willd. ex R. & S. **4:** 764 (1819); Cham. **Linnaea 4:** 447 (1829).
Lithospermum rugosum (Willd.) DC. Prodr. **10:** 83 (1846).
Moltkia anatolica Boiss. Diag. ser. 1, **11:** 114 (1849).

Ranging from western Anatolia into Transcaucasia and northwestern Iran. Corolla elongate, 11–19 mm. long, with blue lobes and throat, bearing scattered straight, stiff, antrorsely and loosely appressed hairs on the inner surface of the lobes and adjacent throat but otherwise completely glabrous, lobes 1.5–1.7 mm. long, usually with a thickened papillate midrib, throat 3–4 mm. long. Stamens eventually exserted, usually surpassing the corolla-lobes; filaments 4–7 mm. long, those of the adaxial lateral pair of stamens and the single anterior median stamens 1 mm. longer than those of the two anterior lateral stamens; anthers purpurescent, 2–2.5 long, attached 1 mm. above the base. Pollen 25–28 μ, surface perhaps minutely rugulose. Style evidently surpassing the filaments. Nutlets irregularly ovoid, 3–4 mm. long, bent at a 90° angle below the middle, pericarp thick and bony, surface densely and minutely low-papillate and also coarsely roughened by low broad ridges and warts and by coarse pitting, attachment scar

large and usually bright green. Gynobase bearing chlorophyll, when maturing 4 nutlets becoming pyramidal and ca. 1.5 mm. high.

This species shares several noteworthy features with the closely related *M. longiflora*. Especially interesting is the presence of rather numerous stiff, loosely appressed, upwardly directed hairs in the throat of the corolla and on the inner face of the corolla-lobes. These relatively coarse hairs would seem to be a hindrance to any insect seeking to enter the corolla, but if they function as a barrier they would seem to have little purpose, since there is no annulus in the corolla-tube and since the anthers and style eventually become exserted from the corolla. Also unique in the genus is the development of distinctly unequal filaments. The androecium has a very clear bilateral symmetry, but the corolla seems to be otherwise regular, or at most has its two abaxial lobes only very slightly more spreading than the other three.

Moltkia Kemal-Paschii Bornm. Magyar Bot. Lapok 30: 66 (1931), is a putative natural hybrid between *M. caerulea* and *M. aurea* from the mountains of central Anatolia. Authentic specimens of the hybrid are before me. Its anthers contain extremely few grains of pollen that are perfect. From *M. aurea* it has acquired a pale corolla, but in other respects characters of *M. caerulea* predominate in the hybrid.

Moltkia longiflora (Bertol.) Wettst. Oesterr. Bot. Zeitschr. 67: 368 (1918).

Echium longiflora Bertol. [Miscl. Bot. 1:] Nov. Comment. Acad. Sci. Inst. Bonn 5: 425 (1842).
Moltkia angustiflora DC. Prodr. 10: 72 (1846).

Known only from eastern Syria and northern Iraq. A very close relative of *M. caerulea* which differs in geographic range, in habit of growth, and in fruit. It is readily distinguished from its relative by its longer, much more slender, strict fruticulose stems, and usually longer and always more slender corollas. The fruiting calyx is subsessile, not borne on a stout pedicel 1–2 mm. long, as in *M. caerulea*. The nutlets are half the size of those of *M. caerulea* and have a very much thinner pericarp bearing not low rounded but very prominent warts.

In *M. longiflora* the stems apparently arise directly from the center of a functioning winter rosette of leaves. The lower leaves on the flowering stems, though rarely persisting, are larger than the middle and upper ones. Flowering plants develop no sterile radical leaf-clusters such as those usually present in *M. caerulea*. In *M. caerulea* the stems arise from among the remnants of a basal leaf-cluster developed the previous season. Its lowest cauline leaves, usually persisting at flowering time, are commonly distinctly smaller than those higher up the stem.

Moltkia aurea Boiss. Diag. ser. 1, 4: 49 (1844) and Fl. Orient 4: 222 (1875).

Known only from western and central Anatolia. Corolla bright golden yellow, completely glabrous, 7–9 mm. long, with a short tube 3.5–4 mm.

long and an abruptly swollen campanulate throat 4–5 mm. long, lobes broader than long, 1–2 mm. long or nearly so. Filaments 3.5–6 mm. long, eventually much surpassing the corolla-lobes; anthers yellow, 1.5–2.5 mm. long, strongly recurved, attached ca. 0.5 mm. above the base, apex rounded, base of each anther-sac apiculate. Pollen 22–25 μ diameter. Nutlets with a thick pericarp, bent about 90° at the middle, 2.5–3 mm. high, maximum length 4–5 mm., clothed with an abundance of very minute elongate papillae, coarsely roughened by low broad ridges and tuberculations and frequently coarsely pitted. Gynobase pyramidal, ca. 1 mm. tall. Style exserted before the stamens but usually eventually surpassed by them.

Notable for its yellow corolla with campanulate throat. In vegetative characters and general habit it is very similar to *M. caerulea*.

Section **Echianthus** (Vis.), comb. nov.

Lithospermum § *Echianthus* Visiani, Fl. Dalmat. **2**: 247 (1847). Type species *L. petraeum*.

Moltkia § *Lithospermoideae* Boiss. Fl. Orient. **4**: 221 (1875). Type species *Lithospermum petraeum*.

Nutlets smooth, lustrous, more or less pointed. Attachment scar of nutlet and faces of the gynobase not green. Corolla gradually ampliate from the base, lacking a sharply differentiated throat. Filaments not arising from invaginations of the corolla, short to elongate, included or exserted, equal or nearly so. Anthers affixed at or very slightly below the middle, straight or only very weakly falcate. Pollen perceptibly longer than broad, globose-ellipsoidal, polar profile circular or sometimes polygonal, lateral profile frequently with obtusely angulate sides, pores equatorial, usually 6–8, frequently protrudent.

Moltkia petraea (Tratt.) Griseb. Spicileg. Fl. Rumel. et Bithyn. 2: 515 and 532 (1846).

Echium petraeum Trattinnick, Thes. Bot. 8, t. 34 (1819).

Lithospermum petraeum (Tratt.) DC. Prodr. **10**: 82 (1846); Visiani, Fl. Dalmat. **2**: 247 (1847).

Dalmatia, from the vicinity of Split south into Albania. Plant frutescent, forming a small bush 2–4 dm. tall, much branched. Leaves oblanceolate, 1–5 cm. long. Corolla blue, 7–8 mm. long, gradually ampliate or with an ill-defined tube (2.5–3 mm. long) and throat (ca. 3.5 mm.); lobes elongate, ca. 1.5 mm. long and 1 mm. broad. Filaments affixed 2.5–3 mm. above base of corolla and eventually surpassing the corolla-lobes 3–3.5 mm. Anthers blue, 1–2 mm. long, straight or very weakly curved, affixed at or very slightly below the middle, apex rounded, base emarginate. Pollen smallest in the genus, 16–20 μ long, pores 8. Style surpassing the corolla 2–4 mm. Nutlets 2.5–3 mm. long.

In Europe widely cultivated in rock-gardens. Under garden conditions it crosses with *M. suffruticosa* and produces fertile hybrids. Two of these crosses bear binomials *Lithospermum intermedium* Froebel and *L. Froebelii* Sündermann, Allgem. Bot. Zeit. **12**: 92 (1906).

Moltkia suffruticosa (L.) Brand in Koch, Synop. Deutsch. u. Schweiz. Fl. ed. 3, **3**: 1999 (1903).

Pulmonaria suffruticosa L. Sp. Pl. ed. 2, **2**: 1667 (1763).
Lithospermum suffruticosum (L.) Kerner, Sched. Fl. Aust.-Hung. **1**: 52 (1881).
Lithospermum graminifolium Viviani, Ann. de Bot. 1^2: 163, t. 14 (1804).
Lithodora graminifolia (Viv.) Griseb. Spicileg. Fl. Rumel. et Bithyn. **2**: 530 (1846); Reichenb. Icon. **18**: t. 114 (1858).
Moltkia graminifolia (Viv.) Nyman, Consp. Fl. Europ. 519 (1881).

A plant of northern Italy. From a trailing caudex of slender, loosely branched stems producing sterile clusters of very slender and elongate (5–15 cm. long) leaves and slender erect leafy flowering stems 1–2 dm. tall. Flowering stems arising from among the remnants of a sterile leaf-cluster of the previous season, its leaves 2–6 cm. long. Corolla blue, elongate, gradually ampliate, 15–17 mm. long; lobes elliptic, 3–3.5 mm. long, rounded. Filaments 2.5–3 mm. long, affixed 1.5–2 mm. below the sinus of the corolla-lobes (i.e., ca. 12 mm. above the base of the corolla). Anthers yellow, straight, ca. 3 mm. long, exserted from the corolla-tube but scarcely if at all surpassing the erect corolla-lobes, affixed ca. 1 mm. above the base, tip stoutly apiculate, base of theca acute, usually unequal. Pollen 20–22 μ long, pores (7 or) 8. Style very slender, eventually surpassing the corolla 3–4 mm.; nutlets 3 mm. long.

Moltkia Dörfleri Wettst. Anz. Akad. Wiss. Wien **55**: 284 (1918) and Oesterr. Bot. Zeitschr. **67**: 361 and 404, t. 3 (1918).

Known only from the mountains of northeastern Albania. Plant an herbaceous perennial, producing scattered simple erect leafy stems 3–5 dm. tall from a thick sympodial rhizome. Leaves lanceolate, all cauline, the lowest imperfectly developed. Corolla purple, elongate, gradually ampliate, 19–22 mm. long; lobes broad, rounded, 2–2.5 mm. long, 3.5–4 mm. broad. Filaments compressed, 1.5–2 mm. long, shorter than the anthers, affixed 13–14 mm. above the base of the corolla. Anthers yellow, elongate, straight, 2.5–3.5 mm. long, included (apex 0.5–1.5 mm. below the sinus of the corolla), affixed 1 mm. above the retuse base, apex bearing a pair of acuminate tips. Pollen largest in the genus, 28–31 μ long, pores 5–7 but usually 6, equatorial. Style filiform, eventually exserted 2–5 mm. beyond the corolla-lobes. Nutlets 4 mm. long, plump, minutely mottled with purple.

Although readily accommodated in *Moltkia*, this species has a number of unusual features. Its habit of growth is more suggestive of some of the perennial species of *Lithospermum* than of any of its congeners. Its annual flowering stems arise from a bud on the rhizome, and its lowermost leaves (small and imperfect) are conspicuously smaller than its middle and uppermost ones. The rhizome is unique in this group of genera. It is obviously sympodial, being made up of annual increments 3–4 mm. long which are thickest (7–10 mm.) near their attachment and then gradually contracted towards the stem-bearing end. The corolla is purple rather

than blue or yellow. Unlike those in other species, the anthers are longer, not shorter than the filaments, and are decidedly included rather than exserted from the corolla-tube. All species of *Moltkia* have a more or less papillate epidermis on the corolla-lobes. In *M. Dörfleri* the epidermal papillae have the maximum development and furthermore are usually tipped by an abortive trichome. Because of the large apiculate papillae, the corolla-lobes of the species appear to be puberulent when viewed under moderately high magnification. In this genus the calyx persists for some time after the nutlets have fallen away, and in all species save the present one eventually turns brown and falls off entire. In *M. Dörfleri,* however, the calyx-lobes disarticulate at the base and fall away individually before the base of the calyx detaches from the stem. I have studied five collections of this species (*Dörfler 446, 450, 472, 502* and *848*), duplicates of the five upon which the species was originally based. The last two of these, nos. *502* and *848*, i.e., the last two cited by Wettstein, have glabrous anthers. The other three collections, however, and particularly no. *472*, are notable for bearing scattered coarse appressed hairs on the sides of the anthers.

3. **Halacsya** Dörfler, Allgem. Bot. Zeitschr. 9: 46 (1903). — a renaming of *Zwackhia* Sendt. (1858), not Körber (1855).

Zwackhia Sendt. ex Reichenb. Icon. Fl. Germ. 18: 65, t. 1316 (1858). Type species *Z. aurea* Sendt.

Plant herbaceous, perennial. Leaves strigose, veinless, alternate. Cymes scorpioid, evidently bracted, solitary and terminal on leafy stems, becoming elongate and racemose at maturity. Calyx 5-parted, evidently pedicellate; lobes firm, lanceolate, equal or nearly so. Corolla yellow, completely glabrous, lobed to the middle; limb slightly oblique, most deeply lobed on the abaxial side; lobes narrowly imbricate in the bud, eventually ascending, elongate, broadly lanceolate or lance-elliptic, acutish, the two abaxial lobes smallest and least spreading; tube about as long as the lobes, lacking an annulus, upper third strongly ampliate and forming a short, ill-defined throat; throat bearing 5 rounded or triangular squamate appendages which alternate with the stamens and are borne at or slightly below the level of the filament attachments. Stamens borne at equal height low in the throat; filaments short, compressed, equal or nearly so; anthers oblong-lanceolate, only the apical portion exserted from the throat, affixed directly above the basal sinus, base cordate, apex acute and tipped by a short thickish prolongation of the narrow connective, margin of theca densely and coarsely short-ciliolate. Pollen sphaeric or slightly prolate, 30–37 μ long; pores equatorial, 3, usually swollen; polar profile circular or somewhat three-sided (with the pores medial on each of the three faces); lateral profile circular or slightly longer than broad. Style precociously long-exserted, terminated by a very small obscurely lobed or parted stigma. Nutlets compressed ovoid, bent, incurved above the middle, densely tuberculate or tuberculate-rugose, gray, opaque, back broadly convex, venter prominently keeled, suture closed and fused; attachment scar transversely

elliptic, basal on the erect lower half of the nutlet body; embryo weakly curved, tip of the cotyledons above the attachment scar and vertical to it. Gynobase depressed pyramidal when fully developed, attachment faces distinct, with narrow elevated cartilaginous margins.

An extremely well marked monotype which is known only from serpentine areas in southern Yugoslavia and adjacent Albania. For a general account of the plant and an excellent colored plate see K. Maly, Wiss. Mitt. Bosn. u. Herzegowina 20: 674–5, t. 11 (1907).

Halacsya Sendtneri (Boiss.) Dörfler, Allgem. Bot. Zeitschr. 9: 47 (1903).

Moltkia Sendtneri Boiss. Diag. ser. 2, 3: 138 (1857). — Bosnia, *Sendtner 479.*
Mertensia Sendtneri (Boiss.) Janka, Oesterr. Bot. Zeitschr. 9: 314 (1859).
"*Moltkia aurea* Boiss." sensu Sendt. Das Ausland 21: 424 (1848).
Zwackhia aurea Sendt. ex Reichenb. Icon. Fl. Germ. 18: 65, t. 1316 (1858). — Bosnia, *Sendtner 479.*
Mertensia serbica Janka, Oesterr. Bot. Zeitschr. 9: 314 (1859). — Serbia, *Pancic.*

Although the flowers of *Halacsya* eventually develop conspicuous yellow corollas 11–13 mm. long, they become sexually mature when very small and long before the corolla becomes conspicuous. Above the conspicuous flowers in the cyme is a series of gradually smaller ones which may have open corollas, long-exserted styles, and fully developed, even dehiscent anthers when the corolla is only 3–5 mm. long and accordingly only a fraction of its eventual size. In some of these juvenile flowers the corolla may even open when only 2.5 mm. long and when it is actually shorter than the calyx (ca. 3 mm. long). Usually the anthers have attained maximum dimensions (1.9 mm. long) and the style is well exserted when the corolla and calyx become as much as 5 mm. long. The corolla of such flowers is lobed to the middle and evidently zygomorphic, having the two abaxial lobes very distinctly (0.5–1 mm.) shorter than the posterior three. Their mature anthers, borne on filaments only half their eventual length, are disproportionately large in the incompletely developed corolla. They are almost completely exserted from the very short corolla-tube. In fact, in these juvenile flowers, the tip of the anther may almost reach the tip of the shorter corolla-lobes. The style emerges from the corolla very soon after it opens, and when the latter is only 4–6 mm. long may have attained as much as 10–15 mm. in length. It is only after the style is greatly extended and the anthers have dehisced that the corolla rapidly enlarges and achieves its mature form. A somewhat similar condition occurs among some of the American relatives of *Lithospermum,* as for example in *Onosmodium*, but I know of no parallel among any of the *Lithospermum* relatives in the Old World. In this group of genera such precocious sexuality appears to have some correlation with the type of corolla aestivation, since it is associated either with species that have their corolla-lobes valvate in the bud or with those, such as *Halacsya*, which have distinctly elongate corolla-lobes only very narrowly imbricate in the bud.

Fully developed flowers have a calyx 5–6 mm. long, a pedicel 1.5–3 mm. long, and a conspicuous deeply lobed yellow corolla 11–13 mm. long. The completely glabrous corolla has a funnelform outline but is lobed to the middle. The lobes of the slightly oblique limb are oblong-lanceolate and unequal. The two anterior lobes are 4–5.5 mm. long and 1.5–1.8 mm. wide, and the three larger posterior ones 5.5–6.6 mm. long and 2.5–3 mm. wide. The sinus on the anterior side of the corolla is 0.5–1 mm. deeper than that on the posterior. The tubular lower half of the corolla, ca. 1.5 mm. thick at the base, is most strongly ampliate in the upper third and so forms an ill-defined throat 4–5 mm. thick at the base of the lobes. There is no nectary developed near the base of the tube. The most unusual feature of these corollas is the five scale-like appendages borne in the throat, 4–5 mm. above the base of the tube. These are minute, rounded, or deltoid squamae which alternate with the stamens and are borne very slightly below the level of the filament attachments. At maturity they are usually a quarter to a third as long as the filaments. The primary vein supplying the corolla-lobes passes beneath the scales and is not detoured over them. They are, therefore, lamelliform and epidermal in origin and accordingly very different from the invaginate type of appendage present in such genera as *Lithospermum*.

The stamens of this genus are very distinctive. The short filaments (0.5–0.9 mm. long) are affixed at equal heights in the corolla 4.5–5 mm. above the corolla-base and usually very slightly above the squamate appendages. They are equal or nearly so, or possibly the posterior filaments may be almost inperceptibly longer than those of the anterior three. The anthers are oblong-lanceolate, 1.5–1.9 mm. long, acute and stoutly appendiculate at the apex and distinctly cordate at the base. Their attachment is just above the basal sinus, about 0.3–0.4 mm. above the base of the theca. The most unusual feature of the anther is the ciliate fringe of short stout hairs decorating the margins of the theca. In fully developed flowers the anthers on the more deeply lobed anterior side of the corolla have their upper half or third projecting above the base of the adjacent corolla sinus. On the posterior side of the corolla usually only the tip of the anther is to be seen projecting above the base of the sinus.

The stoutly beaked nutlets are about 3 mm. long and are gray and densely tuberculate. The body is somewhat dorsi-ventrally compressed and above the middle is bent about 45° inward towards the center of the flower. The ventral keel is prominent and the suture completely closed and fused. The attachment scar is basal on the erect lower half of the nutlet and is broader than long. When maturing four nutlets the gynobase is broadly pyramidal. Its attachment surfaces are distinct and each has a narrow pale cartilaginous margin.

The plant is perennial and apparently forms a loose multicipital caudex. The radical leaves, 5–15 cm. long, occur in sterile clusters. The simple erect or ascending stems, 2–4 dm. tall, have middle and lower leaves of about equal size and spring from a site occupied by a cluster of radical leaves of the previous season.

The genus is a very distinct one but probably has its closest relationship in *Moltkia* § *Eumoltkia*, as indicated by similarities in nutlets, style, stigma, pollen, and habit of growth. The very distinctive anthers of *Halacsya*, as well as its deeply lobed zygomorphic corolla with squamate appendages, readily distinguish it not only from *Moltkia* but from all other genera of this affinity. Although sometimes classed with *Echium* because of its zygomorphic corolla, its relationship with that genus is only of the most general sort.

4. **Alkanna** Tausch, Flora 7: 234 (1824), nom conserv. prop. Type species *A. tinctoria* (L.) Tausch [non *Alkanna* Adans. Fam. 2: 444 (1763) = *Lawsonia* L. (1753)].

Baphorhiza Link, Handb. 1: 578 (1829). Type species *A. tinctoria* (L.) Tausch.

Campylocaryum DC. ex Meisner, Pl. Vasc. Gen. 1: 280, and 2: 189 (1840). Type species *A. lutea* (DC.) Moris.

Camptocarpus C. Koch, Linnaea 17: 304 (1843). Type species *A. orientalis* (L.) Boiss.

Onochiles [Tournef.] Bubani, Fl. Pyrenaea 1: 491 (1897) — a renaming of *Alkanna* Tausch (1824), not Adans. (1763).

Plant herbaceous, mostly perennial, frequently glanduliferous. Leaves numerous, alternate, veinless. Cymes scorpioid, leafy-bracted, usually solitary or geminate at the ends of leafy stems, elongate and racemose in age. Calyx 5-lobed, short-pedicellate, in fruit moderately accrescent, broadened at the base and usually deflexed; lobes equal, narrow to broadly lanceolate, usually attenuate, in age connivent. Corolla yellow, whitish or blue, salverform or infundibuliform, regular or zygomorphic, outside glabrous or in a few species inconspicuously hairy; tube usually cylindric and with its upper portion not differentiated into a well-defined throat, glabrous or exceptionally with minute hairs below the tumid annular or 10-lobulate suprabasal annulus; limb with loosely ascending broad rounded lobes; throat on inner surface usually bearing abundant stipitate glands. Appendages of the corolla borne near the middle of the tube or at the base of the throat, included, alternating with the stamens, usually transversely oblong or trapeziform, glabrous, sometimes minutely papillate at the summit, borne at the same height in the corolla and all equal, or 3 adaxial ones borne slightly higher than the other 2 and sometimes differing in degree of development. Stamens 5, equal, included, in a few species borne at equal heights in the corolla-tube and all attached below the appendages, but in most species borne in two groups, one at a higher level than the other, the 3 abaxial stamens being affixed at or slightly above the level of the appendages and the 2 adaxial ones affixed distinctly below the appendages. Filaments a half to two thirds as long as the anthers; anthers affixed at or near the middle. Pollen conic with rounded base or rarely ovate-oblong, 16–21 μ long, broadest and bearing the 3 pores above the rounded base, summit acute with only the tip rounded or rarely broad and rounded, polar profile circular, pores very obscure. Style entire or

obscurely bilobed at the very apex, included in the corolla-tube, rarely surpassing the anthers; stigmas very small, 2, usually broader than long, apical and juxtaposed or subterminal on opposite sides of the style tip, simple or somewhat bilobed. Nutlets 4 or more commonly 1–3 aborting, verrucose or scrobiculate-rugose, short-stipitate, strongly bent, usually with the long axis more or less horizontal and the attachment apparently suprabasally lateral (attachment actually on morphological base of nutlet body), back rounded, ventral keel prominent, formed of a fused suture. Gynobase swollen, lobed to form distinct pulvini supporting the concave ovate attachment surfaces.

A very well marked and interesting genus greatly in need of monographic study. The twenty-five to thirty species occur in the Mediterranean area and eastward to Transcaucasia and northern Iran, in greatest concentration and diversity in Anatolia and Greece.

The corolla of *Alkanna* usually bears invaginate appendages, not exposed in the mouth of the corolla as in most Boraginaceae but deeply included in the corolla-tube or -throat where they are revealed only when the corolla is dissected. The included appendages of *Alkanna* possibly may have a parallel in the interstaminal appendages of *Halacsya*, but otherwise the condition is unknown in related genera. The appendages have a characteristic development in each of the three sections of the genus. Another common feature of the corolla is the abundant development of stipitate glands on the corolla walls above the stamens. These glands are present and evident in all species except *A. lutea*. In no other genus of this relationship are they so abundant and conspicuous.

The nutlets of *Alkanna* are excessively bent and evidently short-stipitate. Except for the stipitate attachment they are fundamentally similar to those of *Halacsya* and *Moltkia*. In all three genera the nutlet body is distorted as a result of a sharp medial bend, 45–90° in *Halacsya* and *Moltkia* but about 130° in *Alkanna*. The embryo inside the nutlet is bent also, that of *Alkanna* usually having a very distinct transverse flexure near the middle of the cotyledons. It is to be especially noted that these nutlets are distorted only above the middle and that below they are similar to other nutlets of the Lithospermeae. Inside their basal section, the lower half of the cotyledons is vertical to the attachment scar, and the tips of the cotyledons are directly above it, as in all truly basifixed nutlets. Although the nutlet has a bend near the middle, its basal section remains straight or practically so and bears its attachment at the lower end. In *Alkanna* the nutlet can become arched or even more sharply bent, so that its morphological tip is brought down to nearly the same level as the attachment end, and, in some species, even proximate to it. Because the nutlet is bent double, its long axis is not vertical but transverse. Because the nutlets are transverse elongate, the attachment has the appearance of being suprabasally lateral, and numerous authors have so described it. Although this may be empirically correct, it is not so morphologically, for despite appearances, the nutlets, though distorted, still retain an erect base and a truly basal attachment.

In this genus the gynobase also is distinctive. When maturing a full complement of nutlets it is not angulate and more or less pyramidal as in related genera. It is pale in color, cartilaginous in texture, and swollen, and bears each of the four broad attachment surfaces elevated on distinct cushion-like lobes. The attachment surfaces are oblique, ovate, and distinctly concave. The nutlets, when attached, have the broadened tip of their basal stipe seated in these concave surfaces.

Two types of pollen occur in *Alkanna*. In one species, *A. lutea*, the grains have a form similar to that found in *Lithospermum*, but in all other species of the genus they are somewhat conic and show great similarity with the pollen of *Echium*. The conic grains are nearly as broad as long. They have a convex base and well-developed straight sides converging on a blunted rounded apex. The three pores, perhaps in ill-defined furrows, are arranged equidistant about the grain above its base, where it is broadest. The pollen of *A. lutea*, however, is somewhat ovate-oblong. It also is broadest above the convex base, and also has its pores located where its diameter is greatest. Above the level of the pores it is at first abruptly constricted, to form short but well-defined upwardly sloping shoulders, and then, above the middle of the grain, becomes very gradually narrowed. Towards its rounded summit the grain is narrowed to about half of its maximum basal diameter. I have found the pores on this ovate-oblong pollen of *A. lutea* difficult to discern. There seem to be three pores usually developed, but sometimes as many as four.

The two kinds of pollen in *Alkanna* are readily homologized as additional manifestations of a type of pollen asymmetry previously observed and discussed in *Lithospermum*, Jour. Arnold Arb. 33: 310–11, f. 1 (1952). The pollen of *A. lutea* obviously has the distinctive features previously noted in the asymmetric grains of *Lithospermum*. The pores have the same position on the grain, being borne where the grain is broadest, just above its curved convex base and directly below the first sharp constriction that forms the distinctive shoulders in all such asymmetric grains. In the conic grains found in all other species of *Alkanna*, the pores have a similar position. They are borne above the convex base where the grain is broadest and directly below the sharp constriction. These conic grains differ from the ovate-oblong ones of *A. lutea* only in the form of their upper half. In *A. lutea* the constriction is at first abrupt (forming the shoulders) and then becomes very gradual in the upper half of the grain. In the other species of the genus the first abrupt constriction continues uninterrupted into the upper half of the grain and on to its apex. The conic form of these grains is the result of an exaggerated continued upward prolongation of the usually limited constriction that forms the shoulder in other asymmetric grains.

Although showing some resemblance to that of *Lithospermum* in asymmetric form, the pollen of *Alkanna* differs in having fewer pores, usually only three. Interestingly, the triporate condition is that found in the globose or subglobose symmetric pollen of *Halacsya* and *Moltkia* §

Eumoltkia, the two groups which appear to be most closely related to *Alkanna.*

The generic name *Alkanna* Tausch (1824) has an early homonym in *Alkanna* Adans. Fam. **2**: 444 (1763), a synonym of *Lawsonia* L. (1753), cf. Schwarz in Fedde, Repert. **47**: 288 (1939) and Font-Quer & Rothmaler in Fedde, Repert. **50**: 286 (1941). However, as a name proposed for conservation, *Alkanna* Tausch is listed among the Nomina Generica Conservanda in the recently published Code of Botanical Nomenclature, Utrecht, pg. 130 (1952). If the name *Alkanna* is rejected, the next available for the genus is *Baphorhiza* Link (1829). Only three binomials have been proposed under the latter genus, *B. tinctoria* Link (1829), *B. lutea* Font-Quer & Rothmaler (1940), and *B. orientalis* (L.) Font-Quer & Rothmaler (1940). *Alkanna,* as a well-established name associated with over sixty binomials, deserves conservation, and pending final judgment, should be retained.

Section **Eualkanna.**

Alkanna § *Baphorhiza* DC. Prodr. **9**: 97 (1846).

Stamens borne at unequal heights in the corolla, two affixed below the appendages and surpassed by them and three affixed at or slightly above the level of the appendages and surpassing them; appendages transversely oblong or trapeziform, invaginate; pollen conic, with a broad convex base and a rounded tip, 16–17.5 μ long, 14–16 μ broad, broadest and bearing the 3 equally spaced pores 5–7 μ above the base, polar profile circular, lateral profile with a broad rounded base and straight, strongly convergent sides; corolla zygomorphic, densely glanduliferous inside above the appendages; plant perennial.

This section embraces all but two of the twenty-five or thirty species of the genus. Its best known and most widely distributed species are *Alkanna orientalis* (L.) Boiss. and *A. tinctoria* (L.) Tausch.

In this section the corollas are distinctly zygomorphic. The two abaxial lobes of the corolla (outermost in the bud) are more spreading than the other three, the three abaxial stamens are borne higher on the tube than the other two, and the corolla tube below the stamens has constrictions that are usually conspicuously stronger on the abaxial side. The corolla, blue, whitish, or yellow, has a well-developed tube and an abruptly expanding limb but no well-differentiated throat. It is usually completely glabrous. Only in a few species is it sparingly hairy outside, particularly on the lobes, or inside about the nectary low in the tube. In all species the corolla bears an abundance of stipitate glands on the inner surface of the tube above the stamens. In most species the tube of the corolla is longer than the breadth of the limb. At or above the middle it bears small invaginate appendages alternating with the stamens. Interestingly, those on the abaxial side of the tube tend to have a very slight but still perceptibly higher position (and rarely also a greater or a less development) than those on the opposing side of the tube. Associated with the appendages are two groups of

stamens, an abaxial set of three affixed at or slightly above the level of the appendages, and an adaxial set of two affixed distinctly below them. The anthers of the upper group much surpass the appendages, while those of the lower group at most reach up only to the base of the appendages. The filaments are short, shorter than the anthers, and those of the upper stamens possibly very slightly longer than those of the lower stamens.[2]

Section **Allolepis**, sect. nov.

Stamina infra appendiculas corollae aequaliter affixa; antheris appendiculas superantibus; appendiculis quadratis grandis solum infra medium invaginatis; granulis pollinis conicis eis sectionis Eualkannae similibus; faucibus corollae evidenter differentiatis tubo longioribus intus glandulis stipitatis obsitis; planta perennis.

A monotypic section containing only *A. scardica* Griseb., a plant of the mountains of northern Albania and adjacent Montenegro. Of this very distinct species two generous collections have been available for dissection (*Dörfler 123* and *713*). The blue corollas are regular and are sparsely villulose outside above the middle and very minutely hairy inside below the tube-nectary, but are otherwise glabrous. They have a short tube and a large well-differentiated campanulate throat about twice as long. The inner surface of the throat is abundantly stipitate glandular. The corolla appendages, borne at the base of the large throat, are the largest in the genus. They are quadrate in form and have only their lower third or half formed by invagination. The veins supplying the corolla-lobes enter the appendage and make a detour, not over the summit of the appendage, but only over its lower half. The upper half or two thirds of the appendage is a lamelliform prolongation of its invaginate basal portion. It is epidermal in origin. The stamens of *A. scardica* are the largest in the genus. The filaments (about half the length of the anthers) are affixed distinctly below the appendages, all at the same height above the base of the corolla. The anthers (ca. 1.5 mm. long) are borne with their middle at about the same level as the base of the corolla appendages and, unlike those of all congeners, project not only below the appendages but above them also.

Section **Campylocaryum** A.DC. Prodr. 9: 102 (1846).

Stamens affixed at equal heights in the corolla and borne entirely below the obscure, weakly developed, low-convex appendages; pollen ovate-oblong, 20–21 μ long, 14–16 μ broad, broadest and bearing its 3 pores ca. 8 μ above the hemispheric base, thereafter at first abruptly and then (above

[2] The organization of the androecium in *Alkanna* was given incorrectly in my recent discussion of *Moltkiopsis*, cf. Jour. Arnold Arb. **34**: 3 (1953). As in *Alkanna* two of the five stamens of *Moltkiopsis* have filaments shorter and attached slightly lower on the corolla than the other three. Unlike *Alkanna*, however, the two shorter and lower stamens in *Moltkiopsis* are not juxtaposed nor are they adaxial. They are separated by a long stamen (the abaxial medial one) and appear to represent the two abaxial lateral members of the androecium.

the middle of the grain) more gradually narrowed to the rounded summit, polar profile circular, lateral profile with short, steeply sloping shoulders above the broad rounded base and above the middle with nearly straight sides weakly converging towards the rounded summit. Corolla regular, tube becoming ampliate above the middle and forming a moderately well differentiated throat, bearing no stipitate glands on its inner surface; plant annual.

A monotypic section containing only the single species *A. lutea* (DC.) Moris of southern France, eastern Spain and Sardinia. It is the only annual species in the genus. Its small yellow corollas are regular. Except for minute hairs associated with the annulus, they are completely glabrous. Unlike those of other species in the genus, the corollas of *A. lutea* bear no stipitate glands in the throat. The very small stamens are borne below the middle of the corolla. The appendages at the base of the ill-defined throat are very weakly developed and obscure. At most, they are usually only vague convexities and are revealed only when the corolla is viewed under high magnification. The nutlets are very small.

5. **Echium** [Tournef.] L. Sp. Pl. 139 (1753) and Gen. Pl. 68 (1754). Type species *E. vulgare* L.

Isoplesion Raf. Fl. Tellur. **4:** 86 (1836–38). — based on *E. italicum* L., *E. giganteum* L., *E. pyrenaicum* L., and *E. rubrum* Jacq.

Larephes Raf. Fl. Tellur. **4:** 86 (1836–38). Type species *E. parviflorum* Moench.

Argyrexias Raf. Fl. Tellur. **4:** 86 (1836–38). Type species *E. candicans* L.

Megacaryon Boiss. Pl. Orient. Nov. Dec. **1:** 7 (1875) and Fl. Orient. **4:** 203 (1875); Lacaita, Jour. Linn. Soc. Bot. **44:** 393 (1919). Type species *E. orientale* L.

Echium § *Eleutherolepis* Coincy, Cong. Intern. Bot. Paris, Actes 349, fig. (1900). Type species *E. albicans* Boiss.

Echium § *Gamolepis* Coincy, Cong. Intern. Bot. Paris, Actes 349, fig. (1900). Type species *E. angustifolium* Lam.

Echium § *Pachylepis* Coincy, Bull. Herb. Boiss. ser. 2, **3:** 261 (1903). Type species *E. candicans* L.

Plants annual, biennial or perennial, small to very large, herbs, shrubs or small trees, hispid or strigose; leaves usually without evident veins. Inflorescence consisting of elongating scorpioid cymes borne terminally on the stems and leafy branches, or of abundant usually small scorpioid cymes aggregated into a usually dense very elongate thyrse; cymes simple or sometimes forked, densely flowered, abundantly and evidently bracted. Calyx 5-fid or rarely with a short tube, usually pedicellate; lobes usually slender and attenuate, rarely becoming broadly lanceolate or somewhat elliptic, accrescent and connivent in fruit, the two adaxial lobes usually smallest. Flowers monomorphic or gynodioecious, perfect or with the stamens and pollen imperfectly developed. Corolla blue, purple or pink, rarely white or red, resupinate, more or less distinctly zygomorphic, some-

times tubular but usually narrowly to broadly infundibuliform, usually most prolonged on the two-lobed abaxial side; limb usually oblique; lobes ascending, sometimes equal or rarely the three adaxial ones largest, but prevailingly with the two abaxial ones most developed; tube usually short, commonly bent or abaxially swollen just above the base; outside of corolla usually hairy, usually marked with short vertical inflexures under the stamen-attachments; inside of corolla without faucal appendages or stipitate glands, glabrous except for hairs associated with the annulus; annulus borne extremely close to the base of the corolla-tube, very small, sparingly strigose or more or less villose or glabrous, commonly represented by 5–10 lobes but rarely reduced to merely a lineate ring or to 5–10 swellings. Stamens 5, the adaxial pair borne highest on the corolla, the medial abaxial one lowest and the two abaxial lateral ones at an intermediate level, or the two abaxial laterals and the medial one all affixed at or about the same level and below the adaxial pair, or rarely all the stamens borne at or about the same level; the single medial abaxial stamen practically always distinguishable to some degree by the distinctive form of its filament and manner of attachment; filaments slender and elongate, sometimes all included but usually with two or more exserted, commonly declinate, glabrous or very rarely pilose, all equal or of two or three different lengths, usually with a thickened, somewhat decurrent base, the odd medial stamen frequently joined to the corolla by a membrane for a distance above its proper base. Anthers small, short-oblong to oblong, displayed in an inverted position with the emarginate base uppermost, attached to the filament in a pit near the middle of the broad, somewhat cartilaginous connective. Pollen ovoid or conic-ovoid (16–26 $\times$ 13–25 μ), broadest above the broadly rounded base and then gradually narrowed to the rounded apex; polar profile circular, usually with the pores slightly protrudent or their position marked by three nicks in the circumference; pores 3 (perhaps associated with short furrows), arranged equidistant about the broadest part of the grain. Style exserted, always bearing some slender appressed hairs, usually flattened and under transmitted light usually showing 2 distinct vascular strands at least above the middle, forked below the summit or exceptionally unbranched; lobes attenuate, frequently unequal; stigmas 2, distinct, terminal, capitate, very small. Nutlets ovoid or lance-ovoid, usually brownish and tuberculate, rarely lobulate-tuberculate or smooth or nearly so, dull or exceptionally lustrous, erect or somewhat divergent, straight or slightly incurved or sometimes strongly bent ventrally at the middle; venter with a well-developed elongate keel bearing a nearly obliterated suture, base rounded or more commonly narrowed and even constricted just above the attachment; attachment scar flat or slightly concave, usually small, medial or more commonly tending to be restricted to the ventral half of the nutlet base, usually more or less flabelliform, marked ventrally by a conspicuous pit (i.e., the open end of the funicular canal) and dorsally by an arc of two or more broken vascular strands. Gynobase flat or sometimes broadly pyramidal, usually maturing four nutlets.

A genus in great need of a monographer. It has never had a complete methodical study, and no comprehensive system exists for the classification of its species. Past work on the genus has been almost exclusively floristic. Some of this has been very discriminating, but in general it has been provincial in scope and much of it over-solicitous concerning minor variations. Named species have been needlessly multiplied and broader identities and relationships misunderstood or ignored. The nomenclature of the species is chaotic. Many of the familiar binomials no longer have precise application and have come to need special definition each time they are used. The genus in its present state is one of the most confused and confusing of the Boraginoideae and will probably continue so until it has been surveyed and organized by a monographer.

Echium has a very close relation in the South African genus *Lobostemon*. So close is the relationship, in fact, that with reason the two could be merged. Other affinities of *Echium* are much less evident. The genus, however, in a number of significant details shows similarity with *Moltkia, Halacsya,* and *Alkanna,* and in some degree probably has particular relations with that group of three genera. Though this affinity seems a very generalized one, it is at least closer than any existing between *Echium* and the other groups of the Lithospermeae.

Some fifty or more species of *Echium* are restricted to the Atlantic islands and especially to the Canary Archipelago, and to the Mediterranean area and adjacent regions. The ancestors of the modern genus probably became isolated in these two regions at an early date, since evolution in *Echium,* proceeding independently in the two centers, has had time to produce specialized modifications in habit of growth and distinctive elaborations of floral structure in each. It seems also probable that *Lobostemon* has arisen from other ancestors of modern *Echium* which became isolated in South Africa. That southern genus is obviously very closely related to modern *Echium* and is distinguished only by a high degree of specialization and modification of the annulus in the corolla-tube. Its particular specializations are essentially no more remarkable than the extreme and highly evolved growth-form evolved by the *Echia* of the Atlantic islands and may very well have been elaborated in about the same length of time. The indications are that *Echium* has been a plastic group which formerly had a very wide distribution and that subsequently, with its geographic range reduced to three isolated regions, has become specialized in a distinctive manner in each of them.

The species of the Mediterranean area are annual, biennial, or perennial herbs with a general facies of a sort conventional among the herbaceous borages. They may be loosely branched, with relatively few elongating scorpioid cymes terminating stems and leafy branches, or have an erect main axis bearing very numerous small cymes aggregated into a dense very elongate thyrse. A few become somewhat suffruticose at the base, but most are distinctly herbaceous, and the majority are annuals or biennials. With the exception of a few very coarse biennials, such as *E. orientale* and

E. pomponium, the species are all less than a meter tall and most of them only about half that height.

On the Atlantic islands, however, the endemic species have become large plants, and some of them have developed the woody habit to a degree unparalleled elsewhere among the Boraginoideae. Some are coarse, long-lived, monocarpic plants, at first forming huge basal rosettes and later massive columnar inflorescences a meter or more tall. Others bear their leaves on the younger parts of a continuously elongating axis which after a period of years is terminated in a large, even gigantic thyrse. Some such plants attain as much as five meters in height. Still others are shrubs or small trees, decidedly ligneous and prevailingly with a loose branching of the candelabra type, normally becoming one to two meters in height. Most of the species of this latter type bear their leaves clustered at the ends of the loose branches and hence have the distinctive traits of the so-called "rosette-trees."

In evaluating the remarkable development of *Echium* on the Madeira, Canary, and Cape Verde islands, it is to be recalled that their distinctive habit is also paralleled on these islands by representatives of genera in other families which also have only lowly herbaceous, or at most only small fruticulose congeners elsewhere, e.g., *Sempervivum*, *Limonium*, *Sonchus*, etc. Although the particular factors which govern it may be in dispute, the fact remains that similar behavior is known to be associated with plants isolated on particular oceanic islands in various parts of the world. Good examples of this behavior are to be seen in the Revillagigedo and Juan Fernandez Islands, both off the west coast of America. Indeed, on the Juan Fernandez Islands there is another member of the Boraginoideae that parallels the behavior of the Atlantic islands *Echia*. This endemic genus, *Selkirkia*, is a small rosette-tree. It is one of the very few arborescent Boraginoideae and the only rosette-tree outside of *Echium*. Interestingly, it gives every evidence of being only an extreme insular modification of the herbaceous continental genus *Hackelia*.

Among the Lithospermeae the frutescent habit seems to be developed more frequently than in other tribes of the Boraginoideae. Certainly at least a tendency in this regard may have been well developed among the ancestors of modern *Echium*. Although evolution among the Mediterranean species seems to have been directed towards the development of the short-lived herbaceous habit, the shrubby habit persists in *Lobostemon* and may also have been present to some degree among the species of *Echium* originally isolated on the Atlantic islands. There is, however, no good reason for believing that the original *Echia* of the islands were more than suffruticose, or, at most, any more fruticose than modern *Lobostemon*. I cannot believe that the giant *Echia* of the islands have retained a primitive arborescent habit now lost by the more lowly congeners on the mainland, as has been suggested in some similar cases by those who insist that in the modification of stem-structure evolution can only proceed from the woody to the herbaceous (i.e., from trees and shrubs to herbs) and never *vice versa*. To accept this dictum would force us to consider those particular islands

in which plants display behavior comparable to that of *Echium* as merely refugia in which conservative old plants have been preserved and little changed. Very pertinent here is the high degree of incidence of the candelabra-type branching and the rosette-tree habit among woody insular representatives of groups which are elsewhere herbaceous. Though the habit of these plants is arborescent and distinctly woody, the type is an uncommon one. It is difficult to believe that this relatively uncommon growth form could be primitive in all the many genera of many different families which have only insular representatives displaying it. The frequency of its development on certain oceanic islands, particularly in members of groups elsewhere herbaceous, gives good reason for believing that it is somehow associated with the particular insular environment. It appears to be merely an epharmonic response shared by a wide variety of originally herbaceous or at most fruticose plants that have been allowed to develop in isolation under an equitable oceanic climate with all the benefits of a prolonged growing season. Although it must be accepted as an almost universal rule that evolution has proceeded from the arborescent towards the herbaceous, and stem structure from the ligneous to the herbaceous, there are reasons for believing these prevailing directions can in some instances be reversed under special insular conditions, and that under these conditions it is possible for a group of lowly plants to elaborate *de novo* woody stems and the arborescent habit. I am of the opinion that the insular *Echia* are a group of this sort, and that their arborescent habit and woody stems are elaborations rather than primitive. The gigantism and woody habit of these insular species are to be recognized as representing a high degree of specialization and as epharmonic in character.

The corollas of *Echium* are zygomorphic, and evidently so in all species except for a few in the Canary Islands. They are almost always distinctly bilabiate and most prolonged on the side which is bilobed and bears the individualized medial stamen. The side with the bilobed lip and the medial stamen is without doubt the side of the corolla facing away from the axis of the cyme. It is abaxial! Unhappily numerous authors have incorrectly identified it as to position. This confusion appears to have resulted from a misunderstanding of the peculiar behavior of the flower at anthesis. Unlike the flowers of most borages, those of *Echium* mature and display their corollas only on the dense curved uppermost section of the scorpioid cyme. At anthesis the pedicels bearing them are strict. Borne on the rounded uppermost part of the cyme and always directed towards the youngest part of the inflorescence, the pedicels tend to become more or less horizontal. The flowers they bear, accordingly, do not face away from the straightened, usually vertical older parts of the cyme as in most borages, but rather backwards over its coiled summit. They have become more or less horizontal in an unorthodox manner and in doing so have become resupinate. This condition — backwardly facing resupinate flowers — appears to be present in all species of the genus. To a casual observer and to the insect visitor the corolla of *Echium* has a three-lobed lower lip and a usually prolonged two-lobed upper one. In a functional and empiric sense these

can be referred to respectively as the anterior and posterior lips. If, however, they are to be identified morphologically, then the forward three-lobed lip is unquestionably the adaxial and the usually prolonged two-lobed rear lip is with equal certainty the abaxial one. Confusion of terminology in the past appears to have resulted from a lack of general awareness that the corollas of *Echium* are backwardly directed and accordingly resupinate.

In *Echium*, because the corollas are zygomorphic and have developed distinguishable upper and lower lips, the manner in which they are displayed on the cyme and the fact that they become resupinate are readily established. This mode of display, however, is not unique. In Southern California, recently, it was observed in *Cryptantha* and *Amsinckia* and, most interestingly, also in *Phacelia,* a member of the Hydrophyllaceae which also develops scorpioid cymes. In *Amsinckia intermedia* F. & M. the habit is well developed, and the resupinate nature of the corolla is also readily determined, since the corolla-limb is oblique (with the abaxial pair of lobes less spreading than the other three), and since the stamens are borne at three superimposed levels in the corolla-tube and the abaxial medial stamen is always identifiable by the high point of attachment and the usually large size. As in *Echium* the corollas of *Amsinckia* face backwards at anthesis and bear their identifiable odd stamen and the two-lobed abaxial lip uppermost. Additional examples of this habit of bearing backwardly directed resupinate flowers at the summit of the scorpioid cyme will doubtless be found in other species and genera of the Boraginaceae. Although it is difficult to believe that the habit has escaped previous attention, I am forced to report that I can find no mention of it in the literature.

Among the continental species of *Echium* the corolla is always prolonged on the abaxial side and usually very distinctly so. It is most commonly obliquely funnelform but in some species can approach a distinctly tubular form. It may attain as much as 30 mm. in length, as in the attractive large funnelform corollas of *E. plantagineum,* or be very small (only 8–12 mm. long), as in the subtubular flowers of *E. arenarium* and *E. parviflorum.* The zygomorphy of these corollas is always evident, not only in their outward form, but also in the arrangement and differentiation among their stamens. In their departure from radial symmetry the corollas of the Mediterranean *Echia* are the most extreme in the Boraginaceae. Except in *E. italicum* and its allies, the stamens are always borne at three evidently different levels on the corolla walls. In all species the medial (abaxial) member is clearly individualized by its form, manner of attachment, and lowest position.

The insular species are not only distinct as to growth-form, but also in the character and degree of specialization of their corollas. A few of the island plants have tubular corollas, e.g., *E. stenosiphon* and *E. onosmaefolium,* but in most of the insular species the corolla is relatively short and broad and somewhat obconic in form. The corolla usually has a limb that is nearly regular or only slightly (though still perceptibly) longest on the

abaxial side. Suprisingly, however, in five species related to *E. giganteum* (cf. Sprague & Hutch. Kew Bull. 1914: 116–122, f. 1–5, 1914), and at least also in *E. Decaisnei,* the corolla is most prolonged not on the abaxial but very definitely on the three-lobed axial side. Among the insular species, hence, the corolla may be prolonged abaxially or adaxially or be regular or nearly so. In all these corollas, however, there is some evidence of bilateral symmetry in the arrangement and differentiation among the stamens. In about half of the insular species the axial pair of stamens is affixed obviously higher on the corolla than the remaining three. In addition, the odd medial stamen is usually recognizable because of its distinctive form and manner of attachment. In the other half of the insular species the stamens may be all affixed at or about the same level on the corolla, but in most of these at least the medial abaxial stamen has distinctive characteristics and is so identifiable. Only in a few of the species, such as *E. nervosum* and *E. simplex*, are the stamens all so similar in general appearance and height of attachment that the medial one is distinguishable only with difficulty. In these species, however, the corolla is very slightly but still perceptibly prolonged on the abaxial side. Though zygomorphy is here reduced to a minimum in the androecium, there is at least a modest expression of it in the corolla form.

In general level of evolution and organization, the flowers of the insular species are in many ways more similar to those of *Lobostemon* than to those of the Mediterranean species of *Echium*. As has been indicated, its seems probable that *Lobostemon* is directly derived from *Echium* or its immediate ancestors, and like both the Mediterranean and the Atlantic island *Echia* has achieved distinctive features through a long period of isolation. Since we appear to be dealing with different products from the dissolution of a former widely ranging group, the general similarities in the flowers of *Lobostemon* and the insular *Echia* can have significance. A few species of *Lobostemon* are herbaceous perennials, and some are merely frutescent, but most of them are shrubs, usually a meter or less high. Accordingly, in both *Lobostemon* and the insular species of *Echium* relatively simple features of floral structure are combined with a prevailingly woody habit. In this combination of features we probably have the cause and the effect. Evolution of habit in the Mediterranean has been directed quite differently from that on the islands and in South Africa. The assumption of the herbaceous habit by the species of the Mediterranean area entailed not merely a shortening of the life-span of the individuals; what is more important, it also brought more frequent generations within the various races of these plants. With the generations occurring more frequently in the herbs than in the shrubs, in the same period of time tendencies for evolutionary change would proceed more rapidly and reach more extreme expression in the herbs than in the shrubs. The woody insular *Echia* and *Lobostemon,* having a slower rate of evolution than the Mediterranean herbs, should retain more of the characters of their common ancestors and so present the most over-all similarities.

The annulus in *Echium* is usually represented by ten minute glabrous

or hairy lobes. It encircles the corolla tube usually 0.15–0.2 mm. above the base and is usually less than 0.25 mm. wide. The annulus is accordingly very small and is located unusually low in the corolla-tube. It is always lobed, commonly with the lobes thickish, rounded, nearly as broad as long, and closely juxtaposed, but in some species it is reduced to hardly more than five to ten hairy swellings or to scarcely more than a lineate ring with obscure lobes. It may be glabrous, sparingly strigose, or villulose in various degrees.

The annulus in its various modifications is evidently a useful feature in characterizing species. Its value in defining larger groups within the genus, however, seems doubtful. Coincy, Act. Cong. Intern. Bot. Paris 346–52 (1900) and Bull. Herb. Boiss. ser. 2, 3: 261 (1903), proposed three sections of the genus which he distinguished solely by differences in the annulus. Between the extreme types which he emphasized, however, there are all intermediate stages. Furthermore, the groups defined by stressing the nature of the annulus are not at all convincingly natural. Indeed, they are much less so than groups which can be defined by use of growth-habit or corolla-form or stamen-arrangement.

The members of the androecium in *Echium* vary considerably from species to species in size and form and in position and manner of attachment. The abaxial medial filament is always individualized. It may differ in length from the other four filaments or be borne lower on the corolla, or the character of its base and the manner of its attachment to the corolla may be distinctive. In most continental species it differs in all these respects. Among the insular species, however, the odd filament tends to be very slightly if at all lower than those immediately adjacent and differs very little if at all in length. It is usually most easily recognized by the distinctive form and attachment of its base.

The filaments of the Mediterranean species are arranged in three groups. The adaxial pair is affixed highest on the corolla, the abaxial two laterals at an intermediate level, and the odd medial (abaxial) one lowest. In *E. italicum* and its allies these differences may be slight, but in the other continental species they are very marked. Besides differing in height of attachment, the three groups may also differ in length and degree of exsertion from the corolla. The adaxial pair tends to be most protrudent and in a few species may be alone exserted. In *E. parviflorum* and *E. arenarium* no stamens are exserted. Although prevailingly the stamens of *Echium* are glabrous, occasional forms of *E. plantagineum* and related species may have the upper pair of filaments glabrous and the other three sparingly hairy. Among the insular species the androecium is more simply organized than in the species of the Mediterranean. At most, the stamens are affixed at only two evidently differing levels on the corolla and among some species may be affixed all at practically the same level. The filaments tend to be of about the same length and are practically always equally well exserted.

In most species of this genus the filaments (and the style) have become so elongate before the corolla opens that in order to accommodate their

length to their cramped quarters they necessarily become excessively decurved, frequently to such an extent that their tip comes to lie close to their base. After the corolla opens some of this curving tends to persist even after the stamens are fully exserted and so produces the declinate filaments, a characteristic feature of the flowers of *Echium*.

It is to be noted that *Echium*, like most other genera of the Lithospermeae, has anthers that dehisce while the flower is in bud and always before the corolla opens. In the present genus, because of the decurved filaments, the anthers, when they dehisce, may have a position deep in the throat of the still unopened corolla and adjacent to the tip of the decurved style. This frequently occurs in flower buds in which the immature corolla has not yet surpassed the calyx or as yet attained half of its eventual length. If self-pollinization is possible, there is an excellent opportunity for it before the flower opens.

Neither heterostylous nor specialized cleistogamic flowers are known in *Echium*. Within the genus, however, there are species which have forms that differ in size, organization, and function of their flowers. The condition is best known in *E. vulgare*. In addition to the usual form of that species, which produces functionally bisexual flowers, there is another less common form that has distinctly smaller, functionally female flowers. In the latter the style is exserted but the short stamens are included and never mature pollen. Similar functionally female forms have been encountered among the Mediterranean species which I have dissected. The indications are that gynodioecism, of the sort long recognized in *E. vulgare*, occurs in many of the herbaceous species.

A more complicated floral heteromorphism has been recently reported by Camus, Bull. Soc. Bot. Fr. **84**: 451–57, figs. (1937), among plants of *E. candicans* L. cultivated in gardens of southern France. Some of these plants had relatively large corollas with salient stamens and style, others had smaller corollas with the stamens included but the elongate style exserted, while still others with equally small corollas had the stamens and the excessively short style both included. Each of the three types of flowers was associated with an inflorescence distinctive in form. Viable pollen was produced abundantly in the first type of flower, not at all in the second, and only scantily in the third. It would appear that we are concerned here with gynodioecism in which not one but two types of female flowers are involved. Among the herbarium material of the insular species which has been dissected I have found evidences of gynodioecism only in *E. strictum*. One of my specimens (Laguna, Teneriffe, March 1855, *Perraudière, s.n.*) has short included stamens producing no pollen and appears to be the small-flowered functionally female form of that species.

The anthers of *Echium* are usually small, relatively broad, and commonly ca. 0.6 mm. long. Only in a few of the continental species are they oblong and as much as 1.2 mm. in length. The connective is very distinctive. It is somewhat cartilaginous in texture and relatively broad and at the middle bears a well-developed pit in the depths of which the filament is attached. This pit in which the filament is joined to the anther is a

unique feature shared with *Echium* only by *Lobostemon*. The apex of the anthers is rounded or obtuse, but their base is distinctly emarginate. In the female flowers of gynodioecious species, in which the stamens are only imperfectly developed, the sterile anthers are always erect. In the perfect flowers, however, the anthers are displayed in an inverted position, with their basal end (that with the sinus) held uppermost. The line of dehiscence on the anther-theca is usually lateral to its medial line, and the expanded thecae are accordingly usually asymmetric. On certain herbarium specimens representing various different species of *Echium* (and also *Lobostemon*), the opened anthers may have the margin of the theca more or less ciliate with very slender elongate incurving hairs. Similar slender hairs may also arise from along the midline of the open empty theca. The condition is not uncommon, though it is usually best developed in specimens of *E. plantagineum* and its allies. The precise nature of these hair-like structures is uncertain. Under high magnification they are revealed to be unicellular, unbranched, and frequently collapsed. Interestingly, at irregular intervals along their length they become locally swollen. If these "hairs" be pollen-tubes they are unusually rigid for that organ, and if projecting ends of mycelium their rigid character is likewise unusual. In either case their restriction to the margin and middle of the theca is difficult to understand.

Pollen of *Echium* shows little variation from species to species, differing only slightly in size and only moderately in the relation of length to breadth. The grains are ovoid or conic-ovoid and bear their three pores equidistant about their broadest part just above the broadly rounded base. In general they much resemble the grains of *Alkanna*, but above the pores are more gradually constricted and their apex accordingly broader and less pointed. The extremes, in the more than forty samples examined, are 16–26 $\times$ 13–25 μ. The grains of the Mediterranean herbs (commonly 22–25 $\times$ 13–25 μ) are larger than those of the island species, commonly 18–22 $\times$ 20 μ.

The nutlets of *Echium* are basifixed and have a prominent, very elongate ventral keel formed of a fused suture. In *E. orientale* and in *E. Rauwolfii* they are nearly smooth and in the latter even lustrous, but in almost all other species they are dull and more or less tuberculate. In some of the Canary Islands species, such as *E. simplex*, the pericarpial protuberances become so large and so very coarse that the nutlet has the appearance of being lobed. The nutlet body, though straight or at most only obscurely incurved in most species, becomes very distinctly bent in some of the island species, e.g., *E. exasperatum, E. Webbii, E. giganteum* and allies. In these latter the nutlet is sharply bent at the middle at an angle of ninety degrees in a manner suggestive of the nutlet of *Moltkia* and *Halacsya*, which it tends to resemble. The attachment scar on the nutlets of *Echium* is basal, usually horizontal or nearly so, and commonly flabelliform. Among the insular species it is frequently green in color, as is frequently the case in *Moltkia*. The nutlet body tends to be narrowed at the base and is frequently somewhat constricted just above the attachment. The scar,

accordingly, is usually much smaller than the maximum diameter of the body. The disrupted funicular canal usually forms a conspicuous pit in the ventral angle of the scar. The ends of several vascular strands form an arc towards its dorsal edge.

The gynobase is usually flat. Occasionally, however, it may become distinctly pyramidal, and the nutlets borne upon it are parallel only when incurved. Straight nutlets on such an elevated gynobase are somewhat diverging. The style is always sparingly but distinctly hairy and usually contains two distinct vascular traces, at least above the middle. It is simple and terminated by two small, distinct, closely juxtaposed stigmas in *E. rubrum*, but in all other species is distinctly forked below the tip. The two lobes tend to be subulate and commonly are unequal in length. They are each terminated by a very small stigma.

As here defined, *Echium* includes *E. orientale* L., a species which recent botanists have separated from *Echium* and treated as forming the monotypic genus *Megacaryon* Boiss. The distinctive characters of the plant are supposed to be its rank habit of growth and its very large, nearly smooth nutlets. In biennial habit and the organization of its corolla and androecium, the species agrees with other continental species. In coarseness of habit it is no more remarkable than *E. pomponium*, another continental species. In any case, in a genus such as *Echium*, which contains such great diversity in types of habit — from lowly annuals to woody plants up to five meters tall — it is utterly inconsistent to emphasize habit in any attempt to justify the generic segregation of *E. orientale*. Smooth nutlets, though uncommon in *Echium*, do occur in *E. Rauwolfii*. With this fact recognized it becomes evident that *E. orientale* is particularly notable only from the relatively large size of its nutlets, certainly no basis for the recognition of a segregate genus.

6. **Lobostemon** Lehm. Linnaea **5**: 378, t. 5 (1830); Levyns, Jour. Linn. Soc. Bot. **49**: 393–445 (1930). Type species *L. echioides* Lehm.

Lobostema Spreng. Gen. **1**: 126 (1830), a variant spelling of *Lobostemon* Lehm.

Echiopsis Reichenb. Handb. 192 (1837). Type species *Echium fruticosum* Pers.

Isorium Raf. Fl. Tellur. **2**: 61 (1836). Type species *Echium formosum* Pers. (= *L. grandiflorus* Levyns).

Traxara Raf. Fl. Tellur. **4**: 85 (1836–38). Type species *Echium capitatum* L.

Oplexion Raf. Fl. Tellur. **4**: 86 (1836–38). Type species *Echium ferox* Pers. (= *L. argenteus* Buek).

Penthysa Raf. Fl. Tellur. **4**: 86 (1836–38). Based upon *Echium fruticosum* L., *E. glaucophyllum* Jacq., and *E. laevigatum* L.

Echiostachys Levyns, Jour. Linn. Soc. Bot. **49**: 445 (1934). Based on *Echium incanum* Thunb., *E. spicatum* Burm. f., and *L. Ecklonianus* Buek.

Echium § *Trichobasis* DC. Prodr. **10**: 13 (1846). Type species *Echium caudatum* Thunb. (= *E. spicatum* Burm. f., Prodr. Cap. 4, 1768 = **Lobostemon spicatus** comb. nov.).

Lobostemon § *Trichobasis* (DC.) Gürke in E. & P. Nat. Pflanzenfam. IV, Abt. **3A:** 128 (1893).

Echium § *Synlobus* DC. Prodr. **10:** 15 (1846). Type species *Echium formosum* Pers.

Lobostemon § *Synlobus* (DC.) Gürke in E. & P. Pflanzenfam. IV, Abt. **3A:** 128 (1893).

Plant perennial, sometimes suffrutescent or herbaceous but usually distinctly fruticose, mostly small shrubs; hispid or strigose or nearly glabrous; leaves thickish, numerous, veinless or nearly so, all cauline. Cymes densely to loosely scorpioid, forked or simple, conspicuously bracted, frequently becoming very loose at maturity, few- to many-flowered, usually borne terminally or subterminally on leafy branches but sometimes reduced to few-flowered axillary glomerules and aggregated to form a loosely spicate or a very dense cylindric thyrse. Calyx usually 5-parted, only rarely tubular below the middle, sessile or distinctly pedicellate, small or nearly half as long as the corolla; lobes equal or very unequal (or sometimes all dissimilar), frequently with the anterior lateral ones best developed, sometimes with the anterior three more or less united, moderately or very weakly accrescent at maturity. Flowers monomorphic. Corolla blue, pink, white or red, small to large, nearly regular or more commonly somewhat zygomorphic, tending to be prolonged on the abaxial side, outside somewhat strigose or glabrous, inside without stipitate glands or true faucal appendages, glabrous except for hairs on and about the infra-staminal appendages or on the tube below them; corolla-lobes ascending or spreading, rounded, subequal or with the abaxial two perceptibly the largest; limb frequently oblique; tube cylindric or slightly bent and swollen abaxially; throat usually gradually expanding, commonly funnelform and as long or longer than the tube but in some species becoming very abruptly ampliate and shallow and not much if at all longer than the tube; annulus highly specialized and represented by the infra-staminal appendages. Stamens 5, all arising at or near the same altitude on the corolla, or the axial pair highest on the corolla, the medial abaxial one lowest and the two abaxial lateral ones at an intermediate level; filaments slender, usually with a prolonged decurrent base, arising at or below the middle of the corolla, equal or unequal, the abaxial one usually shorter than the two adaxial, all exserted or some or all included, weakly or not at all declinate; the abaxial medial stamen frequently distinguishable by its low attachment or its short length. Infra-staminal appendages (apparently modifications of the annulus) borne at or below the attachment of the stamens and at equal altitudes on the corolla walls and usually conspicuously above the corolla-base, usually tumid and frequently with squamose margins, conspicuously villose at least on the edge, sometimes spreading and shelf-like but usually with the rim ascending and forming a villose cup or a pocket-like recess, sometimes merely a tumid area bearing a cluster of hairs or a transverse densely villose arcuate ridge, at other times represented merely by a short thickened section of the decurrent base of the filament which is densely villose about its thicker upper end. Anthers small, short-oblong, attached to the filament in a pit

near the middle of the thickened connective, usually displayed inverted with the base uppermost. Pollen ovoid or conic-ovoid (16–28 × 13–22 μ), broadest above the broadly rounded base and then gradually narrowed to the narrow rounded apex, polar profile circular, usually with the pores slightly protrudent or their position marked by three nicks in the circumference; pores 3, arranged equidistant about the broadest part of the grain. Style slender, with or without appressed slender hairs, not lobed, terminated by 2 very small juxtaposed stigmas, included or exserted, straight or somewhat declinate. Nutlets erect, one to four maturing, sparingly to abundantly tuberculate or even muricate or nearly smooth, venter angulate, prominently keeled, the suture obliterated; dorsum usually with a medial keel at least above the middle but sometimes keeled to the base and with lateral keels also; attachment scar usually large, basal, horizontal or somewhat oblique. Gynobase depressed pyramidal, the attachment faces usually large and well defined.

A group of South African plants containing 25–30 species. It has obvious affinities with *Echium* and was probably derived from the same immediate ancestors. The nature of its relations with *Echium* has been discussed under that genus. *Lobostemon* is distinguished from *Echium* only by having the annulus in the corolla modified into conspicuous, specialized infra-staminal appendages which, unlike the lobes of the annulus in *Echium* and other Boraginoideae, are borne not merely near the base of the corolla but also conspicuously above it. In *L. echioides* the extreme modification and elevation of the annulus has produced flowers with features conspicuously different from those in *Echium,* but in *L. montanus* the flowers are very similar in appearance and general organization to those found in *Echium,* and indeed differ from them only in the large rather than small size of the annulus-lobes. The differences between *Lobostemon* and *Echium* are those between a very small, inconspicuously hairy, simple annulus always borne very close to the base of the corolla and a large villose annulus, frequently with conspicuous squamate outgrowths, which may be near the corolla-base but is usually evidently above it. The only absolute difference, it is to be noted, is that of size. According to D. M. Britton, Brittonia 7: 248 (1951), ". . . all the Lobostemons examined have a basic chromosome number of seven. All the Echiums except *Echium hispidissimum* R. Lit. ($2n$ = 14 and 28), have a basic chromosome number of eight." Although it has become traditional to give generic recognition to the South African plants, it is to be recognized that with much justification they could be treated as constituting merely one of the well-marked sections of *Echium*.

The most recent study of *Lobostemon* is by Levyns, Jour. Linn. Soc. Bot. 49: 393–452, f. 1–16, t. 29 (1934). Unhappily the author compartmentized her study, and despite the obvious relations of the genus with *Echium*, appears to have made no attempt to familiarize herself with the variety of structures in that genus. Her discussion of the infra-staminal appendages as organs *sui generis* and her selection of *L. echioides* as the most primitive species in her discussion of phylogeny are equally un-

acceptable for anyone having familiarity with the range and types of floral structure in *Echium*. Also unacceptable is her segregation of the allies of *L. spicatus* and her erection of the genus *Echiostachys* for them. This proposed segregate genus differs from the species remaining in *Lobostemon* only in the herbaceous habit and very dense cylindrical thyrse. The differences in habit and inflorescence dignified are no more striking nor important than those existing between groups of species in *Echium*, and are no more worthy of generic recognition.

In general organization the corollas of *Lobostemon* are very similar to those of *Echium* and in some species are almost identical. The only important differences are those concerned with the elaboration of the annulus and the accompanying elongation of the basal section of the corolla-tube. As in *Echium* the corollas of *Lobostemon* are more or less evidently zygomorphic and tend to be most elongate on the two-lobed abaxial side. Accompanying this is another strong tendency, that for the abaxial medial stamen to be differentiated, commonly by being shortest, and frequently also by being affixed lowest on the corolla walls. In *L. echioides* and its relatives, though the corolla may be practically regular, a close examination usually reveals the abaxial pair of lobes slightly but still perceptibly larger than the other three, and furthermore, the abaxial medial stamen appreciably shorter than its companions. Although in the *L. echioides*-group the filaments usually arise directly above the appendages and accordingly from the same height above the corolla-base, sometimes (especially the axial pair) they tend to become decurrent for a short distance above the appendages before becoming free. However, when this tendency is present, it is always most weakly expressed in the medial stamen. In other groups of the genus the filaments are usually all evidently decurrent for some distance above the appendages. The differentiation among the stamens is similar to that in the Mediterranean species of *Echium*. In *L. montanus* the filaments are all decurrent 5–6 mm. and become free at nearly the same level above the corolla-base, and all are about the same length. Although the corolla is most prolonged on the abaxial side, the abaxial filament is only very obscurely shorter and lower than its companions. In other relatives, e.g., *L. fruticosus*, *L. argenteus*, and *L. glaucophyllus*, the adaxial pair of filaments are evidently longest and the abaxial stamen is shortest. The other stamens may be intermediate in size and position. It is a general rule in *Lobostemon* for the abaxial stamen to be shortest and for the remaining four stamens to be either nearly equal in length or the higher pair to be longest. In *L. montanus* all stamens may be exserted, but in its relatives frequently only the highest (the adaxial) pair of filaments equal or surpass the tips of the corolla-lobes. The short stamens are practically always included. This unequal exsertion of the stamens has numerous parallels among the Mediterranean *Echia*. Interestingly, the flowers of *Lobostemon*, unlike those of *Echium*, frequently have the paired stamens with members although practically equal, still not precisely equal in length. Indeed, in some flowers, although there are three well-marked groups of stamens, because of the slight but still evident differences in length within the pairs

there are no two stamens within the corolla which are precisely the same length.

The infra-staminal appendages of *Lobostemon* are the most distinctive feature of the genus. These structures, as apparently first suggested by Bunge, Heliocarya pg. 11 (1871), appear to be specialized elaborations of the annulus, a structure which in *Echium* consists of an annular arrangement of five to ten very small lobes borne scarcely above the base of the corolla. The appendages in *Lobostemon* are usually borne on the ridges representing the downwardly decurrent base of the filaments. In *L. montanus* they are located 0.5–1 mm. above the base of the corolla and are in the position at which the annulus is developed in most Boraginoideae. They consist merely of a short specialized section of the ridge below the filament-attachment which is swollen, darkened, and apparently secretory in nature, and conspicuously villose about the thicker and usually somewhat excavated upper end. These infra-staminal appendages of *L. montanus* give every evidence of being no more than a specialized development of a five-lobed annulus. In other species of *Lobostemon,* however, the relation of the infra-staminal appendage to the annulus in other genera is much less obvious. Their position is no longer near the base of the corolla, the conventional position of the annulus, but rather well above it and at times even as much as half-way up the corolla. That section of the corolla which is below the annulus, which in other genera is weakly developed (usually less than 1 mm. long) is in *Lobostemon* elongated and in some species of the genus actually forms the tube of the corolla. It is as a result of intercalary growth in this basal section of the corolla that the annulus has achieved its relatively high position on the corolla. Besides being borne well above the corolla-base, the annulus of *Lobostemon* has become relatively large and has also developed distinctive forms. In some species it consists merely of five villose areas (*L. spicatus*) or five swellings, each decorated by an arcuate lineate ridge bearing abundant hairs (*L. argenteus*). Usually it develops squamate marginal outgrowths and is evidently villous at least on the edge. The squamate margins may be entire or (in *L. hispidus*) more or less distinctly three-lobed. The appendage may be spreading to form a bracket-like shelf (*L. fruticosus*) or be upturned to form a cup or a pocket-like cavity (*L. glaucophyllus*). The most remarkable development of these appendages is in *L. echioides* and allies. In these the appendages are borne at the summit of a well-developed cylindric tube which may be nearly half the total length of the corolla. Since above the tube the corolla expands abruptly and widely into a broad open shallow throat, the appendages filling the opening to the tube are fully exposed to view. They have the general appearance and function of faucal appendages. Unlike true faucal appendages, however, they do not alternate with the stamens. They subtend the protruding stamens which arise directly above them. This condition is unique, for in all other Boraginaceae in which it is developed, the annulus is at most only an obscure structure hidden deep in the corolla, where it functions

either as a nectary or as a collar about the nectary at the base of the ovary.

The anthers and the pollen have all the distinctive features of those of *Echium* and are indistinguishable from them. As in *Echium,* the anthers dehisce before the flower bud reaches full size or the corolla is ready to open. At this early stage the filaments are decurved within the bud and the dehiscing anthers clustered at the middle of the bud cavity. The style may be erect and the stigma pressed against the folded corolla-lobes or be recurved with its stigmas among the dehiscent anthers. In most species of *Lobostemon* it would appear that the plants can escape self-pollination only if they are self-sterile. Although the longer filaments of *Lobostemon,* as in *Echium,* are strongly decurved within the flower bud, they show less inclination to remain declinate after they become exserted from the open corolla. In most species the filaments at maturity are straight or only slightly curving. As in *Echium,* however, they are bent abruptly subapically and thereby effect the inversion of the anther.

The cymes of *Lobostemon* tend to be less dense or less abundantly flowered than in *Echium*. Most of these South African plants have a cyme which is looser than the densely flowered, distinctly biseriate, very elongating scorpioid cymes characteristic of *Echium*. The closest approach to the latter type is in *L. montanus* and its relatives, the group most like *Echium* in its floral structures. In the species-group of which *L. glaucophyllus* is typical, the flower buds are not very crowded on the younger parts of the cyme and furthermore are almost uniseriate. At maturity these cymes become very loosely flowered and racemose. In *L. echioides* and allies the inflorescence is more suggestive of *Anchusa* than of *Echium*. Two groups of species have the cymes reduced to very numerous few-flowered glomerules and the latter aggregated into an elongate thyrse. The dense cylindrical thyrse of *L. spicatus* and its allies is very similar in organization to that of *Echium rubrum*. The most distinctive thyrse is that of *L. argenteus,* in which usually two-flowered glomerules, subtended by large bracts, are scattered along the upper parts of the branch to form an elongate, interrupted pseudo-spike.

In *Lobostemon* the pedicels, as in *Echium,* are strict, but unlike in *Echium* the open flowers are usually borne not on the curved summit of the scorpioid cyme but below the summit near the point where the axis of the cyme first becomes straight or nearly so. The open flowers, borne on strict pedicels at the tip of the straightened portion of the cyme axis, are accordingly nearly vertical. This behavior of the flower is especially clear in those species such as *L. glaucophyllus* and allies, in which the cymes are especially loose. It is a transitional state between the customary manner of floral display in the Boraginaceae, in which the flowers, borne on spreading pedicels on the straightened part of the cyme, have the corollas facing directly away from the axis, and the manner in *Echium,* in which the flowers, borne on strict pedicels on the curved summit of the cyme, have the corollas facing in the opposite direction and accordingly inverted. *Echium* has backwardly directed resupinate corollas. *Lobostemon* has the

corolla usually erect and facing upwards. Only in one *Lobostemon, L. argenteus,* a species with an interrupted pseudo-spike of one- to three-flowered axillary glomerules, are the flowers distinctly resupinate.

The style in the allies of *L. echioides* may be completely glabrous, but in most species of *Lobostemon,* as in *Echium,* it bears some appressed slender hairs, at least below the middle. As in *Echium rubrum* and allies, but unlike most species of *Echium,* the style of *Lobostemon* is unlobed and terminated by a pair of very minute stigmas. It may be included or only slightly longer than the corolla.

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