STUDIES IN THE BORAGINACEAE, XXVII SOME GENERAL OBSERVATIONS CONCERNING THE LITHOSPERMEAE

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IN THE PREVIOUS PAPERS of this series the genera composing the tribe Lithospermeae have been redescribed and individually discussed, Jour. Arnold Arb. 34: 258–299 (1953) and 35: 1–81 (1954). The tribe having been surveyed, we are now prepared to present a new key to the twenty-three genera concerned, and also some general observations concerning the tribe as a whole. Listed alphabetically the twenty-three genera of the Lithospermeae are as follows: *Alkanna*, *Ancistrocarya*, *Arnebia*, *Buglossoides*, *Cerinthe*, *Cystistemon* (includes *Vaupelia*), *Echioides*, *Echium*, *Halacsya*, **Lasiarrhenum*, *Lithodora*, *Lithospermum*, *Lobostemon*, **Macromeria*, *Maharanga*, *Moltkia*, **Nomosa*, *Onosma*, **Onosmodium*, **Peritostema*, *Podonosma*, **Psilolaemus*, and *Stenosolenium*. Six of the twenty-three genera are endemic to America (those marked with the asterisk), and sixteen are endemic to the Old World. Only one genus, *Lithospermum*, has species present in both the Old and the New World.

To be excluded from the Lithospermeae are a number of genera which at one time or another have been referred to it. These include *Moritzia*, *Thaumatocaryon*, *Antiphytum*, *Amblynotopsis*, *Amphibologyne*, *Sericostoma*, *Echiochilon*, *Megastoma*, *Myosotis*, *Mertensia*, *Trigonotis*, *Pulmonaria*, *Bothriospermum*, *Moltkiopsis*, *Mairetis* and *Neatostema*. Of these genera, *Pulmonaria* is best referred to the Anchuseae and *Bothriospermum* to the Cynoglosseae, and the remaining fourteen to the Eritricheae.

As to habit the Lithospermeae are prevailingly herbaceous perennials. Species having only an annual duration are relatively few and occur only in *Buglossoides*, *Arnebia*, *Stenosolenium*, *Cystistemon* (including *Vaupelia*), *Echium*, and *Cerinthe*. The cymes are abundantly bracted and usually conspicuously so in all members of the tribe except *Ancistrocarya*. Floral dimorphy in several forms is present in five genera within the tribe. Heterostyly in a very elaborate form is present in *Lithospermum*, *Echioides*, and *Arnebia*, and in a simple form in *Lithodora*. Elsewhere among the Boraginoideae heterostyly is reported only among species of *Anchusa* and *Pulmonaria* of the Anchuseae, among *Mertensia*, *Cryptantha*, and *Amsinckia* in the Eritrichieae, and in one species of *Paracaryum* in the Cynoglosseae. Gynodioecism is widespread within *Echium*. Outside the Lithospermeae it is known only in a few species of *Myosotis* and *Lindelofia*. Cleistogamy is developed in some species of *Lithospermum* and elsewhere in the subfamily is known only in *Neatostema*, *Cryptantha* and *Pectocarya*.

Deviations from radial symmetry in the flower are more common and widespread in the Lithospermeae than in any other group within the family. The corolla becomes distinctly zygomorphic in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, and *Macromeria*. In addition, zygomorphy less evidently developed is also present in corollas of some species of *Cerinthe* and *Onosma*. Deviations from radial symmetry in the androecium occur in many Lithospermeae. Within the corolla the individual filaments may differ from one another in length, or in the form of their attachment, or in the height at which they are affixed to the corolla. Androecia deviating from radial symmetry occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Cerinthe*, *Echioides*, *Arnebia*, *Stenosolenium*, and *Macromeria*. Outside the Lithospermeae decidedly zygomorphic corollas occur only in *Echiochilon* and *Lycopsis*. Differentiation among the members of the androecium, within the corolla, occur outside the Lithospermeae in *Echiochilon*, *Moltkiopsis*, *Lycopsis*, *Caccinia* (includes *Heliocarya*) and *Amsinckia*.

The frequency of yellow or orange as a corolla-color among the Lithospermeae is also noteworthy. Orange, yellow, or decidedly yellowish corollas occur in *Moltkia*, *Halacsya*, *Alkanna*, *Onosma*, *Podonosma*, *Cerinthe*, *Lithospermum*, *Echioides*, *Arnebia*, *Psilolaemus*, *Perittostema*, *Onosmodium*, and *Macromeria*. Within the tribe blue or bluish or pink corollas occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Onosma*, *Cystistemon*, *Podonosma*, *Cerinthe*, *Arnebia*, *Stenosolenium*, *Buglossoides*, and *Ancistrocarya*. White corollas are normal in species of *Lithospermum*, *Buglossoides*, *Lasiarrhenum*, *Nomosa*, and *Onosmodium*. Blue, pinkish, or white corollas predominate in the other tribes of the Boraginoideae. Orange, yellow or yellowish corollas, however, are developed in other tribes by only a relatively few species of *Nonnea*, *Symphytum*, *Anchusa*, *Neatostema*, *Cryptantha*, *Hackelia*, *Amsinckia*, *Rindera*, *Lindelofia*, and *Cynoglossum*.

The corolla has an unappendaged throat in seventeen of the twenty-three genera of the Lithospermeae. Within the tribe there are only six genera in which intrusive faucal appendages are developed, viz. *Lithospermum*, *Buglossoides*, *Macromeria*, *Perittostema*, *Halacsya* and *Alkanna*. In the three other tribes of the Boraginoideae, however, the corolla is almost always provided with faucal appendages. Indeed, within the Anchuseae, Eritrichieae and Cynoglosseae there are only eight genera, out of more than sixty, in which the corolla is devoid of faucal appendages in all or nearly all of the species, i.e., *Moltkiopsis*, *Mairetis*, *Neatostema*, *Echiochilon*, *Sericostoma*, *Amphibologyne*, *Amsinckia* and *Trichodesma*. In the other genera in these three tribes the faucal appendages are well developed or are weak or absent only in a few species in which the corolla is much reduced in size, e.g., *Cryptantha*, *Plagiobothrys*, and *Pectocarya*.

The corollas of the Lithospermeae, unlike those in other tribes of the family, may bear stipitate glands on their inner surfaces, particularly so those in and directly below the corolla-throat. Stiped glands, sometimes in considerable abundance, are a feature inside the corollas of some or all

species of *Lithospermum*, *Macromeria*, *Lasiarrhenum*, *Perittostema*, *Arnebia*, *Buglossoides*, *Lithodora*, and *Alkanna*.

The corolla-throat in *Ancistrocarya* and in one species of *Lithodora* is densely strigose, a condition paralleled outside the tribes only in *Sericostoma* and *Echiochilon*. The corolla-tube (as distinguished from the corolla-throat) is hairy in species of *Lithospermum*, *Macromeria*, *Echioides*, and *Arnebia*. Outside of the Lithospermeae I know of a comparable condition only in the flowers of species of *Neatostema*, *Mertensia*, *Amsinckia*, and *Rochelia*.

The stamens in the Lithospermeae show a number of unusual features. In *Cerinthe*, *Podonosma*, *Cystistemon*, *Onosma*, and *Maharanga*, the anthers are connivent and become joined, in *Cerinthe* by the entangling of the caudate bases of the thecae, and in the other genera by lateral cohesion of the anthers. Outside of the Lithospermeae this condition is most closely approximated in *Borago* and *Trichodesma*. In these two genera the anthers are connivent, but in *Borago* they remain distinct, while in *Trichodesma* they become joined by the entangling of their contorted tips.

The anthers are terminated by an elongate sterile appendage in *Cerinthe*, *Podonosma*, *Onosma*, *Cystistemon*, *Maharanga*, and *Nomosa*. Outside of the present tribe only in *Trichodesma* of the Cynoglosseae does a comparable very elongate appendage terminate the anther. Small appendages terminate the anther in *Halacsya*, *Onosmodium*, *Lasiarrhenum*, and *Buglossoides*. Outside the tribe I know of such moderately appendaged anthers only in *Myosotis* and *Rochelia*.

In *Lasiarrhenum*, *Nomosa*, and one species of *Macromeria* the connective on the dorsum of the anther is hairy, and in *Halacsya* the margins of the thecae are densely short-ciliolate. These conditions appear to be unique in the family.

The filaments within the individual corolla are not whorled but affixed at different elevations above the corolla-base in species of *Lithodora*, *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Stenosolenium*, *Arnebia*, and *Echioides*. This unusual behavior is duplicated outside of the Lithospermeae only in *Echiochilon*, *Lycopsis*, and *Amsinckia*. The five filaments within the corolla are of different lengths in species of *Arnebia*, *Moltkia*, *Alkanna*, *Echium*, and *Lobostemon*. Outside of this tribe I know of this latter condition only in *Moltkiopsis*, *Echiochilon*, and *Caccinia*.

Although the pollen of the Boraginaceae, outside of the Lithospermeae, has not been systematically studied, there have been enough random examinations to indicate that the pollen of the Lithospermeae is notable for a high frequency of asymmetric types. Such pollen has the upper and lower halves of the grain differing in size and configuration. In lateral outline the grain may be ovate, conic-ovate, oblong-ovate, or be constricted above the pores and approach the outline of an hour-glass or a shoe-print. It is encircled by a row of pores, not about the equator, but below it, where the grain has its maximum diameter. Pollen of this sort is developed in *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Onosmodium*, *Nomosa*, *Lasiarrhenum*, *Ancistrocarya*, *Lithospermum*, *Podonosma*, *Cysti-*

stemon, and *Onosma*. At present this type of pollen is known only in genera of the Lithospermeae.

The style in the Lithospermeae may be short to elongate and be either included in the corolla or exserted from it. In *Arnebia* it may be simple, bilobed, forked, or bis-bifid. It is simply forked in *Echium* and *Stenosolenium* and frequently bilobed in *Lithodora* and *Alkanna*. The forked or bilobed style is not duplicated in other tribes of the Boraginoideae. Each lobe of the forked style is usually terminated by a stigma. When the style is simple it commonly bears two stigmas juxtaposed and terminal on its summit. In some genera, however, the two stigmas are separated and frequently over-topped by a bilobed sterile apex of the stylar column. In such cases the stigmas assume a subterminal position on the style and may become evidently lateral on it.

The subterminal stigmas are best developed in species of *Buglossoides* and *Lithospermum*. Unless the peculiar stigma of *Myosotis* proves to be similar, subterminal stigmas are well developed in other tribes of the Boraginoideae only in the genus *Sericostoma*. In most genera of the Lithospermeae the style is terminated by a pair of juxtaposed stigmas. Within the tribe the two stigmas usually remain distinct. In other tribes of the subfamily they are prevailingly united.

The nutlets of the Lithospermeae are prevailingly straight, erect, and basifixed, and in form are either ellipsoidal (and usually plump) or they are ovoid with the venter tending to be angulate and the apex coarsely beaked. Nutlets that are strongly compressed dorsi-ventrally, though frequent in the Eritrichieae and Cynoglosseae, are rare in the Lithospermeae and indeed are practically restricted to a few species of *Arnebia*. The ventral keel in various degrees may be obscure, broad and rounded, or narrow and prominent. There may be no evidence of a ventral suture or the suture may be marked only by a line that may be indistinct or sometimes interrupted. The suture is always tightly closed with its margins usually fused or firmly joined and never overlapping.

Several genera of the tribe have nutlets sufficiently unusual to be deserving of special comment. The 2-celled, 2-seeded nutlets of *Cerinthe* are well known. They apparently represent the congenital union of a pair of single-seeded nutlets. The condition is unique in the Boraginoideae. Also unique is the form of the nutlets of *Ancistrocarya*. From just above the broad base these gradually narrow into a very prolonged, slender, curved, sword-like beak which is hamate at the apex. The beak, which is nearly as long as the fertile portion of the nutlet, is a sterile prolongation of the pericarp-apex.

The bent nutlets of *Moltkia*, *Halacsya*, *Alkanna*, *Podonosma*, and some insular species of *Echium* represent another very unusual form of nutlet. Outside the tribe it is weakly represented only in *Neatostema* and some species of *Plagiobothrys*. In the Lithospermeae mentioned, the nutlets are basally affixed to the gynobase but only the lower half of the nutlet is erect. Above their middle they are bent 30–130° towards the ventral side. The seed within the nutlet is also bent. The cotyledons are vertical to

the attachment-end of the nutlet and the tip of the cotyledons is directly above the nutlet-attachment, the proper relation in a basifixed nutlet. In *Alkanna* and *Podonosma* the nutlet-body is so strongly curved that the attachment actually has the appearance of being lateral.

The nutlets of the Boraginoideae characteristically have a more or less convex dorsum and a usually angulate or medially carinate venter. An extreme departure from this conventional form is found in the nutlets of *Arnebia tetrastigma*. In that species, the sole member of *Arnebia* § *Euarnebia*, the nutlet has a plane or even slightly concave dorsum and a venter that is broadly convex with the ventral keel only very obscurely developed. The nutlets are also aberrant in having a cordate base and a T-shaped scar.

The nutlet of *Stenosolenium* bears its attachment-scar not sessile on the base of the nutlet-body but rather ventral to the proper base of the nutlet at the lower end of a downwardly directed hollow stipe originating high up on the ventral side of the nutlet. In all other genera of the Lithospermeae the attachment is on the base of the nutlet-body. It is small, short and substipitate in *Alkanna* and *Podonosma* but is relatively large, sessile, and commonly flabellate or ovate in other genera. The attachment is usually restricted to the base of the nutlet. In *Arnebia guttata* and *A. tetrastigma*, however, it has a noticeable prolongation upwards for a short distance above the base on the nutlet-venter. As a consequence it becomes somewhat T-shaped, especially in *A. tetrastigma*.

The attachment-scar is usually not only basal on the nutlet but also horizontal. When oblique it usually slopes upward only towards the ventral side of the nutlet-body and commonly only slightly so. A basal attachment-scar sloping upward, not towards the venter of the nutlet but rather towards the dorsum, is present only in *Buglossoides* § *Eubuglossoides* and perhaps in *Ancistrocarya*. The attachment of the nutlets in *Lithodora* is anomalous. The true base of the nutlet is permanently affixed to the gynobase, the nutlet being freed along a new plane of abscission developed a short distance above the morphological base of the nutlet.

The nutlets of the Lithospermeae may be smooth, verrucose, tumulose, or rugose, and the epidermis lustrous or opaque and smooth and shiny or minutely muriculate, verruculose, or papillate. The smooth, lustrous, pallid, porcelain-like nutlets characteristic of most species of *Lithospermum* occur elsewhere in the tribe only in *Macromeria*, *Onosmodium*, *Lasiarrhenum*, *Psilolaemus*, *Ancistrocarya*, and *Buglossoides* § *Margarospermum*. Roughened or at least opaque nutlets prevail in other genera of this group. In other tribes of the Boraginoideae the nutlets may be armed with numerous glochidiate subulate appendages, or the back of the nutlet may bear a coroniform or annulate appendage, or it may be encircled by an entire, toothed or lobed, spreading or upturned margin. Among the genera of the Lithospermeae, however, only a few species, in *Onosma*, *Echium*, and *Ancistrocarya*, have appendaged nutlets. Those of *Onosma tricerospermum* Lag., of Spain, bear three conspicuous spreading rigid subulate spines on the dorsum. The nutlets of all other species of *Onosma*

are unappendaged. In some of the Canary Island species of *Echium* (cf. Webb. & Berth., Phytogr. Canar. t. 146, 1844), the pericarp develops a few very exaggerated protuberances that give the nutlet the appearance of being coarsely lobed. The slenderly rostrate nutlets of *Ancistrocarya* have already been described. The nutlets of the Lithospermeae (like those of the Anchuseae) never bear glochidiate appendages nor epidorsal annulate or coroniform crests, nor is the back ever encircled by a differentiated margin.

My observations as to the orientation of the zygomorphic corollas in the Boraginoideae do not accord with the much quoted classical statements of the matter by Döll, Fl. Baden 2: 775–6, 778 (1859) and Eichler, Blüthendiagramme 1: 197 (1875). The calyx lobes of the boraginaceous flower are numbered by Eichler in the following order, 1, 3, 5, 2, and 4. Lobe no. 2 is identified as the one at the rear of the flower and as having a position opposite the rachis of the scorpioid cyme. This order appears to be correct, for in those flowers having very unequal calyx-lobes (e.g., *Cerinthe*) the largest outermost lobe, i.e., no. 1 according to Eichler, is always one of the two lobes on the abaxial or front side of the flower. With the calyx-lobes recognized as serviceable points of reference, it can be stated that according to Eichler the axis of the irregular corolla of *Echium* passes between the corolla-lobes alternating with calyx-lobe no. 4 and through the middle of the corolla-lobe alternating with calyx-lobes nos. 3 and 5. This gives the flowers of *Echium* a very strongly oblique plane of symmetry and places the 2-lobed lip of the corolla on the adaxial side of the flower.

In my study of herbarium material, I have found in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, *Lycopsis*, and *Amsinckia*, that the axis in the bilaterally symmetrical corolla is oriented in such a manner that the 2-lobed lip of the corolla is abaxial and the 3-lobed lip adaxial. In these genera the plane of symmetry is only weakly oblique. It passes through the middle of the rear corolla-lobe (that alternating with calyx-lobes nos. 4 and 2) and between the corolla-lobes alternating with calyx-lobe no. 3. This is the same orientation that prevails in the zygomorphic corollas of the Solanaceae. It represents a deviation of only 36° from a truly medial orientation, not 72° as called for by Eichler.

Only in *Macromeria*, *Echiochilon*, and *Heliocarya* have I found in the Boraginaceae zygomorphic corollas with medial orientation, that is to say, so oriented that the rear (adaxial) lip was 2-lobed and the abaxial lip 3-lobed. In the flowers of these genera the axis apparently passes between the two rear corolla-lobes (those alternating with calyx-lobe no. 2) and also through the middle of the forward corolla-lobe, that alternating with calyx-lobes nos. 1 and 3. Medial orientation similar to this prevails in the corollas of the Verbenaceae and Labiatae. It represents an angular deviation of 36° from the axis of symmetry in *Echium*.

Enough evidence has accumulated from the study of herbarium specimens to cast considerable doubt on the accuracy of accounts in the books concerning the orientation of the bilaterally symmetric flowers of the Bora-

ginoideae. What is now needed is observations of flowers in the fresh state. The orientation should be determined not merely in the flowers having evidently zygomorphic corollas, but also in those in which the corolla may be only very obscurely bilateral or which depart from radial symmetry only in the androecium. Studies of symmetry are especially needed in *Lithodora*, *Moltkia*, *Stenosolenium*, *Arnebia*, *Echioides*, *Cerinthe*, *Onosma*, *Podonosma*, and *Moltkiopsis*. The orientation in the corolla of these genera needs to be determined not only in relation to the axis of the cyme, but also in relation to calyx-lobe no. 1, and particularly so when the latter is distinguishable by its size.

KEY TO THE GENERA OF THE LITHOSPERMEAE

Pollen bearing only 3 pores, grains in polar profile usually distinctly 3-sided.
- Pollen-grains evidently colpate; thecae not ciliate; flowers not precociously sexual.
  - Nutlets strongly incurved, near the middle bent 90–130°, the attachment small and substipitate, appearing to be lateral but actually basal on the short erect lower section of the nutlet; herbage usually glanduliferous.
    - Corolla-lobes narrowly triangular, acute, soon reflexed; corolla-throat glabrous and devoid of faucal appendages and stipitate glands; anthers partially exserted. . . . . **Podonosma.**
    - Corolla-lobes rounded, spreading; corolla-throat usually bearing stipitate glands; stamens and faucal appendages borne low in the corolla-throat and hence deeply included. . . . . **Alkanna.**
  - Nutlets straight (or rarely bent in *Echium*); herbage not glanduliferous.
    - Anther lacking a prolonged sterile tip, remaining distinct; corolla usually evidently zygomorphic.
      - Annulus borne 1 mm. or less above the base of corolla-tube, composed of a minute collar or a ring of 5–10 minute sparingly hairy lobules; style almost always 2-lobed. . . . . **Echium.**
      - Annulus developed 1.5–6 mm. above the corolla-base, represented by 5 evident densely villous swellings or 5 squamose appendages borne below the attachment of each stamen; style simple . . . . . **Lobostemon.**
    - Anther narrowed into a prolonged terminal appendage, commonly adnate at the base or along the sides to form a synandrium; corolla regular or practically so.
      - Corolla-lobes well developed, as long as or much longer than the corolla-tube, spreading or decurved; anthers coherent only along the margins of the terminal appendage, appendage evidently longer than the theca; filaments very short and usually bearing a thickened hairy basal appendage; tropical Arabia and Africa . . . . . **Cystistemon** and **Vaupelia.**
      - Corolla-lobes short, commonly about as long as broad, conspicuously much shorter than the tubular portion of the corolla; anthers usually coherent at the base and frequently also along the margin of the thecae and even along the margin of the terminal appendage, appendage usually shorter than the theca; filaments usually elongate, not appendaged at the base.
        - Calyx-lobes narrow, elongate, more or less parallel, separated by a

very narrow usually closed sinus; corolla without ribs projecting outward between the calyx-lobes; pollen ovoid to sphaeric or strongly oblate ..... **Onosma.**

Calyx-lobes more or less triangular, separated by an open triangular sinus; corolla with puffed-out ribs that project outward between the calyx-lobes; pollen cylindric or vertically ellipsoid. Himalaya and southwestern China ..... **Maharanga.**

Pollen-grains not at all colpate; anthers with thecae margined by a ciliate fringe of short stout crowded hairs; flowers precociously sexual, style and stamens exserted while the corolla is still incompletely developed; nutlets bent ..... **Halacsya.**

Pollen bearing 6 to many pores; grains circular or somewhat polygonal in polar profile.

Nutlets united in pairs, each nutlet 2-locular and 2-seeded; pollen evidently colpate; leaves cordate-amplexicaul at base ..... **Cerinthe.**

Nutlets not united, each one 1-celled and 1-seeded; pollen obscurely if at all colpate; leaves not cordate-amplexicaul.

Pollen-grains bearing 2 rows of pores, one at each end of the elongate grain.

Nutlet-attachment at the base of a downwardly directed stipe originating on the ventral side of the ascending nutlet-body ... **Stenosolenium.**

Nutlet-attachment on the base of the nutlet-body ..... **Arnebia.**

Pollen bearing only a single encircling row of pores.

Nutlets circumscissile above the base, their major seminiferous portion falling away leaving the short basal section persisting as a usually cupulate appendage permanently affixed to the gynobase .. **Lithodora.**

Nutlets detaching at the very base.

Throat of corolla glabrous and also devoid of stiped glands and faucal appendages.

Nutlets evidently bent at or near the middle; corolla blue or purple, or (in one species) yellow; filament evidently exserted from corolla-throat except in one species ..... **Moltkia.**

Nutlets straight.

Corolla salverform, the broad spreading yellow limb usually decorated with 5 evanescent black or purplish spots; stamens borne at unequal heights in the corolla-tube; Armenia, Caucasus and Azerbaijan ..... **Echioides.**

Corolla tubular, white or yellow, bearing no dark evanescent spots, lobes erect or ascending; stamens all arising at the same height in the corolla-throat; American.

Filaments about half the total length of the corolla, arising well below the middle of the corolla, base of filaments shaggy with slender multicellular gland-tipped hairs .... **Nomosa.**

Filaments about one tenth the length of the corolla or less, arising above the middle of the corolla, glabrous throughout.

Corolla-lobes narrow, acute or acuminate, very narrowly imbricate in the bud, sinus between lobes plicate, inflexed and thickened at base; pollen ovoid; leaves coarsely veined ..... **Onosmodium.**

Corolla-lobes ovate, broadly imbricate in the bud, sinus between lobes not plicate nor inflexed nor thickened at base; pollen ellipsoidal; leaves veinless or nearly so ..... **Psilolaemus.**