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**THE HYOBRANCHIUM
AND THROAT MYOLOGY OF THE
ADULT AMBYSTOMIDAE
OF THE UNITED STATES
AND NORTHERN MEXICO**

by

John E. Krogh

and

Wilmer W. Tanner



BIOLOGICAL SERIES — VOLUME XVI, NUMBER 1

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TABLE OF CONTENTS

INTRODUCTION	1
MATERIALS AND METHODS	4
GENERAL FEATURES OF THE HYOBRANCHIAL SKELETON	4
GENERAL FEATURES OF THE MUSCULATURE	23
SPECIES DESCRIPTIONS	27
Pacific Giant Salamander, <i>Dicamptodon ensatus</i> (Eschscholtz)	27
Olympic Salamander, <i>Rhyacotriton olympicus</i> (Gaige)	30
Ringed Salamander, <i>Ambystoma annulatum</i> Cope	33
Reticulated Salamander, <i>Ambystoma cingulatum</i> Cope	35
Northwestern Salamander, <i>Ambystoma gracile</i> (Baird)	38
Jefferson's Salamander, <i>Ambystoma jeffersonianum</i> (Green)	40
Malbec's Salamander, <i>Ambystoma malbeci</i> Bishop	42
Long-toed Salamander, <i>Ambystoma macrodactylum</i> Baird	44
Spotted Salamander, <i>Ambystoma maculatum</i> (Shaw)	47
Mole Salamander, <i>Ambystoma talpoideum</i> (Holbrook)	49
Marbled Salamander, <i>Ambystoma opacum</i> (Gravenhorst)	51
Texas Salamander, <i>Ambystoma texanum</i> (Matthes)	53
Chihuahua Salamander, <i>Ambystoma rosaceum</i> Taylor	55
Tiger Salamander, <i>Ambystoma tigrinum</i> Green	56
Eastern Tiger Salamander, <i>Ambystoma tigrinum tigrinum</i> (Green)	56
Northwestern Tiger Salamander, <i>Ambystoma tigrinum melanostictum</i> (Baird)	57
Clouded Tiger Salamander, <i>Ambystoma tigrinum nebulosum</i> Hallowell	57
DISCUSSION	59
SUMMARY	66
ACKNOWLEDGMENTS	68
LITERATURE CITED	69

THE HYOBRANCHIUM AND THROAT MYOLOGY OF THE ADULT AMBYSTOMIDAE OF THE UNITED STATES AND NORTHERN MEXICO

by

John E. Krogh¹

and

Wilmer W. Tanner²

ABSTRACT

The 16 species and subspecies of the Ambystomidae of the United States are placed into six groups according to their throat morphology as follows: The *Dicamptodon* group, the *Rhyacotriton* group, the *A. Annulatum-A. cingulatum* group, the *A. gracile-A. jeffersonianum-A. mabeei-A. macrodactylum-A. maculatum* group, the *A. talpoideum* group, the *A. opacum-A. texanum* group, and the *A. rosaceum-A. t. tigrinum-A. t. melanostictum-A. t. nebulosum* group. *Dicamptodon* appears to be the most primitive group and *Rhyacotriton* the most specialized. Based

on the morphology of the throat region it is suggested that *A. rosaceum* be placed in the tiger salamander group as a subspecies of *A. tigrinum*.

The results of this investigation support the hypothesis that Ambystomidae is primitive to Salamandridae and to Plethodontidae. The findings which have led to this conclusion are based upon the protrusibility of the tongue, and upon the structure and presence of the epibranchial, otoglossal, second radial, and second basibranchial cartilages of the three families.

INTRODUCTION

The ambystomid salamanders are strictly North American in distribution, ranging from southern Alaska and extreme southern Labrador in the north to the southern parts of the central Mexican Plateau. Most salamander taxonomists recognize five living genera—*Dicamptodon*, *Rhyacotriton*, *Rhyacosiredon*, *Ambystoma*, and *Bathysiredon*. Two of these, *Rhyacosiredon* and *Bathysiredon*, are found only in Mexico. *Dicamptodon* and *Rhyacotriton* are found along the Pacific Coast of the United States, and the genus *Ambystoma* is essentially coextensive with the entire family range. This study deals with the ambystomids of the United States, plus one Mexican species *Ambystoma rosaceum*. There are about 30 species in the entire family, and of this number 13 are found within the boundaries of the United States.

Most workers believe that *Dicamptodon* and *Rhyacotriton* are related and differ from *Ambys-*

toma in certain features. Tihen (1958) subdivides the genus *Ambystoma* as follows: (An asterisk following the name indicates that it is found in the United States.)

Subgenus: *Ambystoma*

The mexicanum group

Ambystoma kansense
Ambystoma lermaensis
Ambystoma mexicanum

The tigrinum group

Ambystoma amblycephalum
Ambystoma bombypellum
Ambystoma fluvinatum
Ambystoma granulosum
Ambystoma hubbardi
Ambystoma lacustris
Ambystoma ordinarium
Ambystoma rosaceum
Ambystoma subsalsum
*Ambystoma tigrinum**

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The opacum group

- Ambystoma opacum*°
- Ambystoma talpoideum*°

The maculatum group

- Ambystoma gracile*°
- Ambystoma jeffersonianum*°
- Ambystoma laterale*°
- Ambystoma macrodactylum*°
- Ambystoma maculatum*°

Subgenus: *Linguaelapsus*

- Ambystoma annulatum*°
- Ambystoma cingulatum*°
- Ambystoma mabeei*°
- Ambystoma schmidti*
- Ambystoma texanum*°

Subgenus: *Bathysiredon*

- Bathysiredon dumerili*

Tihen (1958) has suggested that the family Ambystomidae had its origin in the late Mesozoic and was probably derived from Asiatic hynobiids. He further suggests that *Dicamptodon* and *Rhyacotriton* were established in the western part of the continent at this early date, and that the remainder of the family had its beginning at a later date in the northeastern part of the continent.

There is a lack of agreement among taxonomists as to the relationships of the various families of salamanders. Some investigators (Dunn, 1926; Noble, 1927) consider the Ambystomidae to be primitive in relation to the Salamandridae and seem to be convinced that the Plethodontidae can be derived from the Salamandridae, whereas others (Regal, 1966; Bishop, 1943) would derive them from the Ambystomidae. The primary objective of this study has not been to help resolve this question, since our studies are directed primarily at the generic and species levels. However, the data do suggest certain conclusions pertaining to inter-familial relationships, and these are discussed later in the paper.

Inasmuch as this paper is concerned only with the hyobranchial apparatus and the myology of the throat, it contains some inherent limitations, and the conclusions which will be drawn are subject to modification based on evidence from other sources.

One of the first workers to study the anatomy of the throat region in ambystomid salamanders was Cope (1887). The findings of several subsequent workers were later summarized by Piatt (1940). With respect to certain structures, our observations do not agree with those made by these earlier workers, as will be pointed out hereinafter.

Other nonanatomical approaches to the study of amphibian evolution have been made in the past. Some investigators (Boulenger, 1910; Sampson, 1900; Brandes, 1901; Kerr, 1919; Barbour, 1926) have used developmental patterns in the study of amphibian evolution. Noble (1927) contends that, while habits are changeable among the higher vertebrates, they are the direct result of inherited organization in the lower vertebrates, and he suggests that these habits may even be more stable than many structural features in these lower forms. Accordingly, he has used courtship behavior extensively, based on the premise that the more specialized the behavioral pattern the greater the probability that it will be found only in closely related forms.

One of the obvious manifestations of the process of evolution is the series of anatomical changes in a group of organisms which accompany and reflect the changes that occur in the environment.

The throat region is a fruitful area of anatomy on which to study salamander evolution since it is involved in both feeding and breathing mechanisms. Feeding structures associated with the aquatic habitat are notably different from those found in terrestrial forms. Terrestrial forms are unable to utilize water for the capture, manipulation, and softening of food items, but they have evolved instead a tongue to accomplish these purposes in a terrestrial environment.

Regal (1966) has used tongue structure in the classification of terrestrial salamanders. He describes the aquatic tongue as consisting of a mere thickening of the mouth floor around the branchial elements. He groups terrestrial tongues into three types based on their freedom from the floor of the mouth, and the ability to extend the tongue out of the mouth by means of the hyoid elements. The ambystomids have a terrestrial-type tongue that is free at the lateral and posterior margins but is not as protrusible as the tongue found in the Salamandridae and the Plethodontidae. As a result of this structure, the ambystomids are restricted to larger food items. Salamanders with the more advanced tongues are able to flip the tongue out of the mouth to catch small, elusive insects, and, in addition, they are able to use the more conservative methods for the capture of larger food items.

Some of the other structures which are also associated with feeding and breathing mechanisms that have been studied by various workers include teeth, skull bones, and vertebrae (Tihen, 1958); the direction of tooth replacement

(Regal, 1966); and the hyobranchial apparatus (Cope, 1887; Smith, 1920; Francis, 1934; Tanner, 1952; Wake and Özeti, 1969).

The present study is based exclusively on the dissection of adult salamanders. Larval forms have been avoided owing to the great variability that exists in their development. Brandon (1961) points to the fact that earlier workers had concentrated their descriptions on either newly hatched or fully grown larvae but that nothing was known for many of the intermediate sizes. He prepared a table based on balancers, limbs (buds and toes), and skin pigmentation to be used to identify all sizes of larvae.

Dunn (1940), in his paper on the races of *Ambystoma tigrinum*, makes the statement that larvae and recently transformed young are usually useless in racial discrimination. Furthermore, the anatomical changes that occur at metamorphosis are rather extensive, and the adult stage of development, therefore, appears to be the most reliable ontogenetic level at which an anatomical investigation could be undertaken. For a quantitative treatment of the changes in weights and in linear measurements of the body and organs that occur at metamorphosis, the reader is referred to Latimer and Roofe (1964).

Inasmuch as we have considered in this paper only those ambystomids that normally occur in the United States (with the exception noted above), the question of neoteny does not concern us. On the other hand, a complete treatment of the family would include specimens from populations in which there is complete or partial neoteny, and an investigator undertaking such a study would be forced to compare gilled animals with nongilled forms. Complete neoteny is found in populations of the *tigrinum*, *mexicanum*, and *Bathysiredon* groups of Tihen (1958), and partial neoteny is found throughout the family.

We have been able to confirm the platelike otoglossal cartilage of *Dicamptodon* as reported by Cope (1887), but our findings concerning this structure in *Ambystoma gracile* and *A. texanum* do not agree with his observations. The otoglossal cartilage in these latter two species is not platelike as in *Dicamptodon* but is annular in shape.

We have found the otoglossal cartilage to be of special importance in the process of feeding. The vomerine teeth are located on the roof of the mouth directly opposite the otoglossal in the Ambystomidae, and this cartilage appears to function as a rod with which to impinge food against these teeth. The otoglossal is either absent or drastically reduced in the Salaman-

dridae and Plethodontidae, and the vomerine teeth in these two families do not form a transverse series opposite the position of the otoglossal as in the Ambystomidae, but tend rather to be scattered throughout the mouth. The salamandrids and plethodontids use the entire tongue to press food up against their teeth, whereas the ambystomids with their rather immovable tongues rely heavily on the otoglossal cartilage for this purpose.

We have found, contrary to the statements of earlier workers (Tihen, 1958, for example), that the majority of the hyobranchium in *Dicamptodon* is not solidly ossified, but rather is mostly cartilaginous. The only structures which are solidly ossified in *Dicamptodon* are the tips of the ceratohyals and the epibranchials. The second basibranchial cartilage is partially ossified in most of the specimens studied, but in a few of them it was completely cartilaginous. An epibranchial cartilage, the presence of which is considered to be primitive (Özeti and Wake, 1969), was observed in all of the specimens we have studied. The first basibranchial cartilage and also the ceratohyal are primitively ossified, and they were at least partly ossified in most of the species observed in this study.

For the most part, the muscle terminology we have used is in agreement with that suggested by Drüner (1901), Francis (1934), Edgeworth (1935), and Piatt (1939). We have used the name *interhyoideus posterior* for the most posterior of the ventral hyoid constrictors, and we agree with Piatt (1940) that the terms *gularis* and *quadratopectoralis* should be used only in the Plethodontidae. Piatt has also stated that the subhyoideus is a special anterior derivative of the interhyoideus, and that no such muscle exists in the Ambystomidae. In all of the specimens we have observed, however, this muscle is present, extending forward from the posterior tip of the ceratohyal to join the fibers of the interossequadrata near the midline of the throat. In *Rhyacotriton*, the subhyoideus inserts even further forward along the posterior edge of the mandible.

Previous studies on the hyobranchial apparatus and throat myology of the ambystomid salamanders have been sketchy and incomplete. The families Salamandridae and Plethodontidae have been studied relatively recently (Piatt, 1935; Hilton, 1947a; Hilton, 1947b; Tanner, 1952; Özeti and Wake, 1969) and rather completely, but the same cannot be said for the Ambystomidae. It has been this need for further study which has provided the major stimulus for this investigation.

MATERIAL AND METHODS

The materials which have been used in this study were made available for dissection by the Brigham Young University Natural History Museum, California Academy, Museum of Natural History, U.S. Natural History Museum, and from museum collections of other universities throughout the United States. Numerous specimens were also obtained from the field collections of private individuals. Specimens of the Ambystomidae which we dissected are: *Dicamptodon ensatus*, *Rhyacotriton olympicus*, *Ambystoma rosaceum*, *A. tigrinum*, *A. opacum*, *A. talpoideum*, *A. gracile*, *A. jeffersonianum*, *A. macrodactylum*, *A. maculatum*, *A. annulatum*, *A. cingulatum*, *A. mabeei*, and *A. texanum*. We have also dissected the subspecies *A. t. tigrinum*, *A. t. nebulosum*, and *A. t. melanostictum* of the tiger salamander. For comparison we also dissected one specimen of *Salamandra salamandra*.

In the case of some species there were as few as two specimens available for dissection, and in the case of the Long-toed Salamander, *Ambystoma macrodactylum*, only one was available. We have therefore made no attempt to ascertain the degree of individual variation within each species. In making some conclusions concerning phylogeny, we have attempted to use morphological structures which tend to have low variability between individuals of the same species. All of the dissections were performed with the aid of a stereoscopic microscope at magnifications varying from 10 to 30 diameters. All measurements were made with calipers to one-tenth of a millimeter.

The origin, insertion, size, and shape of thirteen muscles are described in detail for each

specimen, and the hyobranchium is, likewise, described for each. The percentages of ossification and/or chondrification for the various elements of the hyoid apparatus are mentioned and their significance in determining phylogeny is discussed.

Since most of the muscles are bilaterally symmetrical, two depths are shown on some illustrations in order to reduce the number of drawings. All of the descriptions and illustrations have reference to adult specimens. Eosin dye was used only occasionally to distinguish muscular from connective tissue on very small specimens. A few specimens were also cleared according to the Schultz-Potash technique as modified by Hansen and Tanner (1958) and then stained with alizarin red and stored in glycerin. The majority of the specimens have been preserved in 60 percent alcohol and have been accessioned in the collections of the Museum of Natural History at Brigham Young University in Provo, Utah.

We have selected 48 morphological characters, and have used them in the deduction of a phylogeny for the genus *Ambystoma* according to the method of Wishart (1969). The morphology which is included in this paper includes information on feeding and breathing structures, and does not attempt to include any of the numerous other body systems or information concerned with life history. The reader is therefore reminded as to the limitations of this work, and he is advised that the findings discussed herein be used in conjunction with information from other sources in the final decisions concerning relationships of the Ambystomidae.

GENERAL FEATURES OF THE HYOBANCHIAL SKELETON

There has been considerable controversy concerning the terminology of the hyobranchial skeleton, as evidenced by the large amount of synonymy which exists in the literature at the present time. We have followed Wiedersheim (1877), Noble (1931), Piatt (1935, 1938), Tanner (1952), Wake (1963, 1966), and Özeti and Wake (1969) as far as hyobranchial skeleton terminology is concerned. We use the terms ceratobranchial rather than hypobranchial, epibranchial rather than ceratobranchial, first basibranchial rather than copula or basihyal, second basibranchial rather than os triangulare, and radial cartilages rather than cornua.

In larval forms, the hyoid arch is present as well as portions of four branchial arches. Fol-

lowing metamorphosis, however, there is a reduction of both the hyoid and branchial arch components, leaving only portions of the hyoid arch and the first two branchial arches in the adult. The majority of these structures is usually cartilaginous with centers of ossification most commonly occurring in the center of the first basibranchial, the tips of the epibranchials, the posterior tips of the ceratohyals, and the medial portion of the second basibranchial.

The first basibranchial cartilage is the main supporting element inasmuch as it provides a base of attachment for most of the other components. It is located in a midventral position, and the central portion is usually ossified, as mentioned above. Özeti and Wake (1969) indi-

eated that the shape of the first basibranchial was characteristic of each genus in the Salamandridae, and it appears that the same trend can be found in the genera of ambystomids presented in this paper. In *Dicamptodon* this structure is truncate, in *Rhyacotriton* it is shaped like an elongated pear, and in *Ambystoma* it is either pear-shaped or shield-shaped (Fig. 1-16).

In adults, the hyoid arch consists of two elements on each side — the first radial cartilage and the ceratohyal. In the larval stage, these two structures articulate with each other, but in the adult condition they are often separated or attached by way of a ligament. The first radial cartilage attaches to the anterior edge of the ceratohyal. There are no muscles which attach to these first radial cartilages. The anterior end of the ceratohyal is flat and spatulate in shape while the posterior end becomes rounded in cross section and curves dorsally to attach to the quadrate by way of the hyoquadrate ligament. The anterior end serves as an attachment point for the subarcualis rectus I, and the posterior end is the point of origin for the subhyoideus. In the majority of specimens observed, the posterior tip of the ceratohyal was ossified. Özeti and Wake (1969) report that from one-half to two-thirds of the ceratohyal is ossified in salamandrids, and Tanner (1952) reported a complete lack of bone in these structures in the plethodontids which he studied.

The two second radial cartilages arise from the sides of the first basibranchial and also curve anterolaterally while tapering gradually to a point. They are usually longer than the first radials and are typically curved dorsally to articulate with the otoglossal cartilage. In contrast to the first radials, the second radials do have muscles attached to them. This second pair was shown by Drüner (1901) to arise at metamorphosis. He showed in *Salamandra* that the second pair of radials forms while the first pair is still present. Later, while investigating *Triturus*, Bogoljubsky (1924) also found a second pair of radials forming while the first pair was still in place. The first pair was later lost, and only the second pair was found to be present in the fully transformed adult. Özeti and Wake (1969) found several genera of salamandrids (*Chioglossa*, *Salamandrina*, *Taricha*, *Triturus*, *Notophthalmus*, *Cynops*, and *Paramesotriton*) to have only one pair of radials in the adults, and, moreover, there were muscles attached to this pair. In those salamanders which have two pairs of radials, it seems likely that the second pair is homologous with the single pair of other genera.

Özeti and Wake (1969) report an "interradial cartilage" extending between the two second ra-

dials, and a structure by the same name had been reported earlier by others (Drüner, 1901; Kallius, 1901; Stadtmüller, 1936). Oppel (1900) found a ligamentous plate, the "sehnenplatte," in the substance of the tongue in *Salamandra maculosa* which serves for the attachment of the hyoglossus muscle and also for the insertion of the abdominohyoideus (rectus cervicis profundus). One of the morphological characters that has been used to distinguish primitive salamanders is the otoglossal cartilage (Dunn, 1926). Cope (1887) figured the otoglossal cartilage in his drawings of the hyobranchial skeleton of ambystomids and shows this structure forming an arc between the tips of the second radials. We likewise have found this structure in the specimens which were dissected. It is a semicircular ring of cartilage, the ends of which are attached to the tips of the second radials with the arch directed dorsad into the substance of the tongue. In some species, it may be jointed at the midline. It serves as an attachment for the rectus cervicis profundus and genioglossus muscles. It is hinged at its junction with the 2nd radial and apparently rotates forward with the radial cartilages as the tongue is extended in feeding. Tanner (1952) indicated that the "lingual cartilage" was missing in all of the Plethodontidae which he studied, and Dunn (1926) states that it is missing in all Plethodontidae, although Piatt (1935) reported finding it in several plethodontids. We believe that the interradial cartilage referred to above is in reality the otoglossal cartilage and that the "sehnenplatte" or "lingual cartilage" is a vestige of this structure as it exists in salamanders in which the tongue has attained a greater degree of freedom from the floor of the mouth than that which is seen in the Ambystomidae. Its position dorsal to the first basibranchial, its attachment to the second radial cartilages, and the fact that the rectus cervicis profundus also inserts on this structure in some of the Salamandridae seem to confirm such a belief.

The first branchial arch is formed by a narrow, curved bar of cartilage consisting of the first ceratobranchial and the epibranchial. The proximal end of the first ceratobranchial attaches to the posterolateral edge of the first basibranchial and extends posterolaterally and also somewhat dorsally, such that the posterior portion lies parallel with the ceratohyal. It is a flat oval in cross section and is wholly cartilaginous in the ambystomids observed, with the exception of one specimen in which a small ossification center was found (Table 1). Others (Hilton, 1947b; Özeti and Wake, 1969), in working with the salamandrids, have found this element to be well

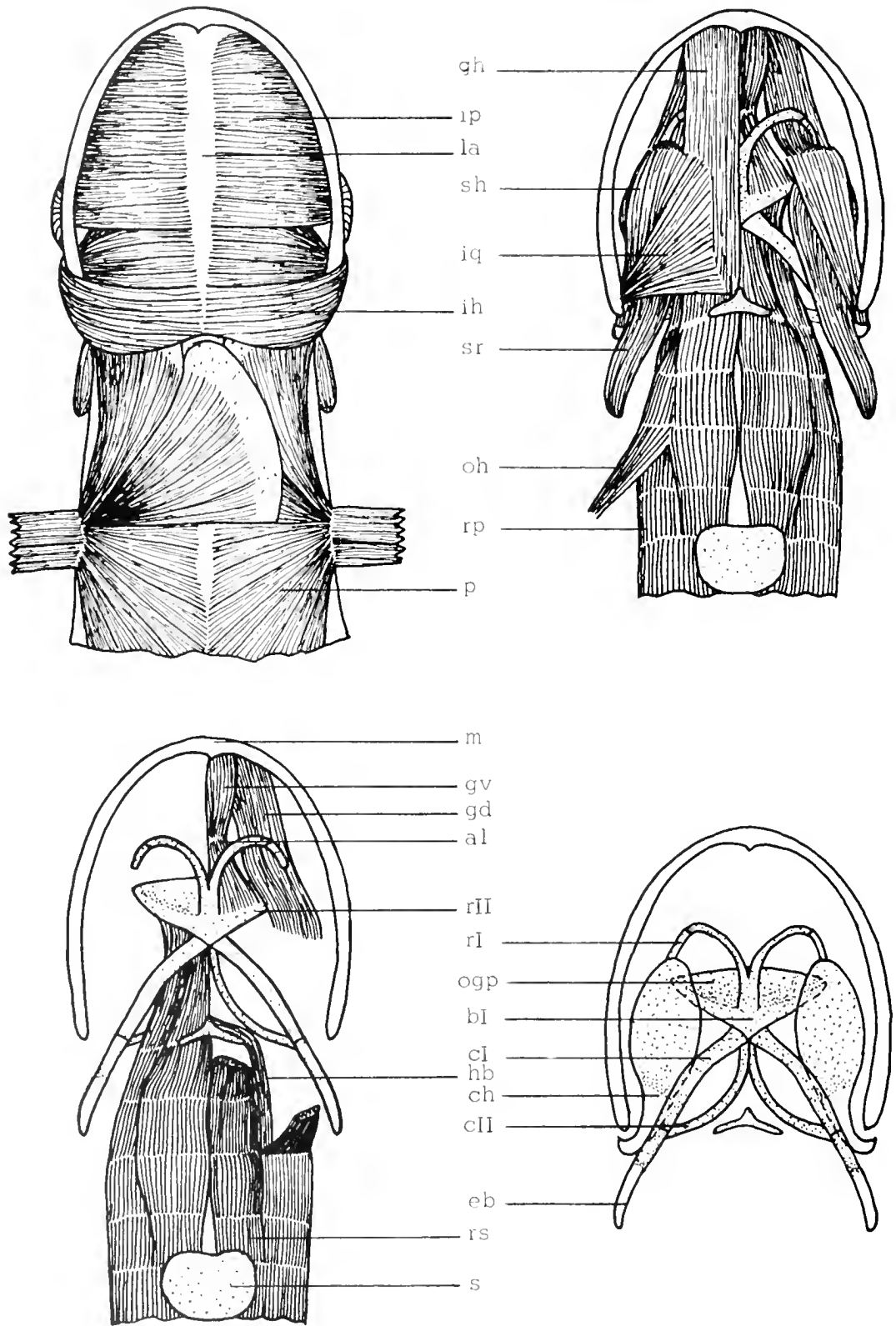


Fig. 1. *Dicamptodon ensatus*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

al, aponeurosis lingualis; bi, first basibranchial; bII, second basibranchial; ci, first ceratobranchial; cII, second ceratobranchial; ch, ceratohyal; eb, epibranchial; gd, dorsal genioglossus; gh, geniohyoideus; gv, ventral genioglossus; hb, hebstoeypsiloides; hy, hyoglossus; ih, interhyoideus posterior; ip, intermandibularis posterior; iq, interosquadrata; la, linea alba; m, mandible; og, otoglossal, ogp, otoglossal plate; oh, omohyoideus; p, pectoralis; pc, pericardium; rI, first radial; rII, second radial, rp, rectus cervicis profundus; rs, rectus cervicis superficialis; s, sternum. sh, subhyoideus; sr, subarealis rectus I, tendon.

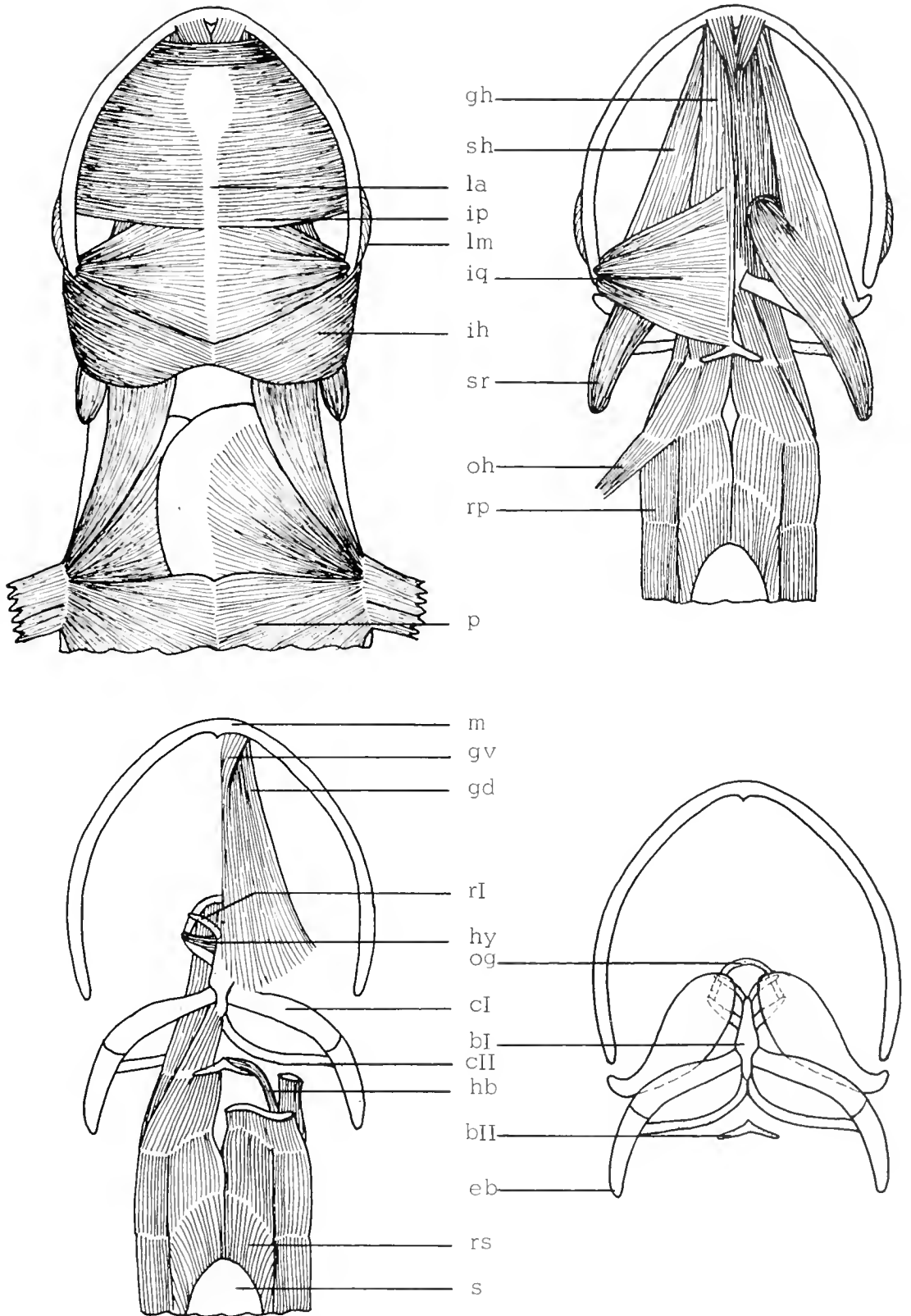


Fig. 2. *Rhyacotriton olympicus*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

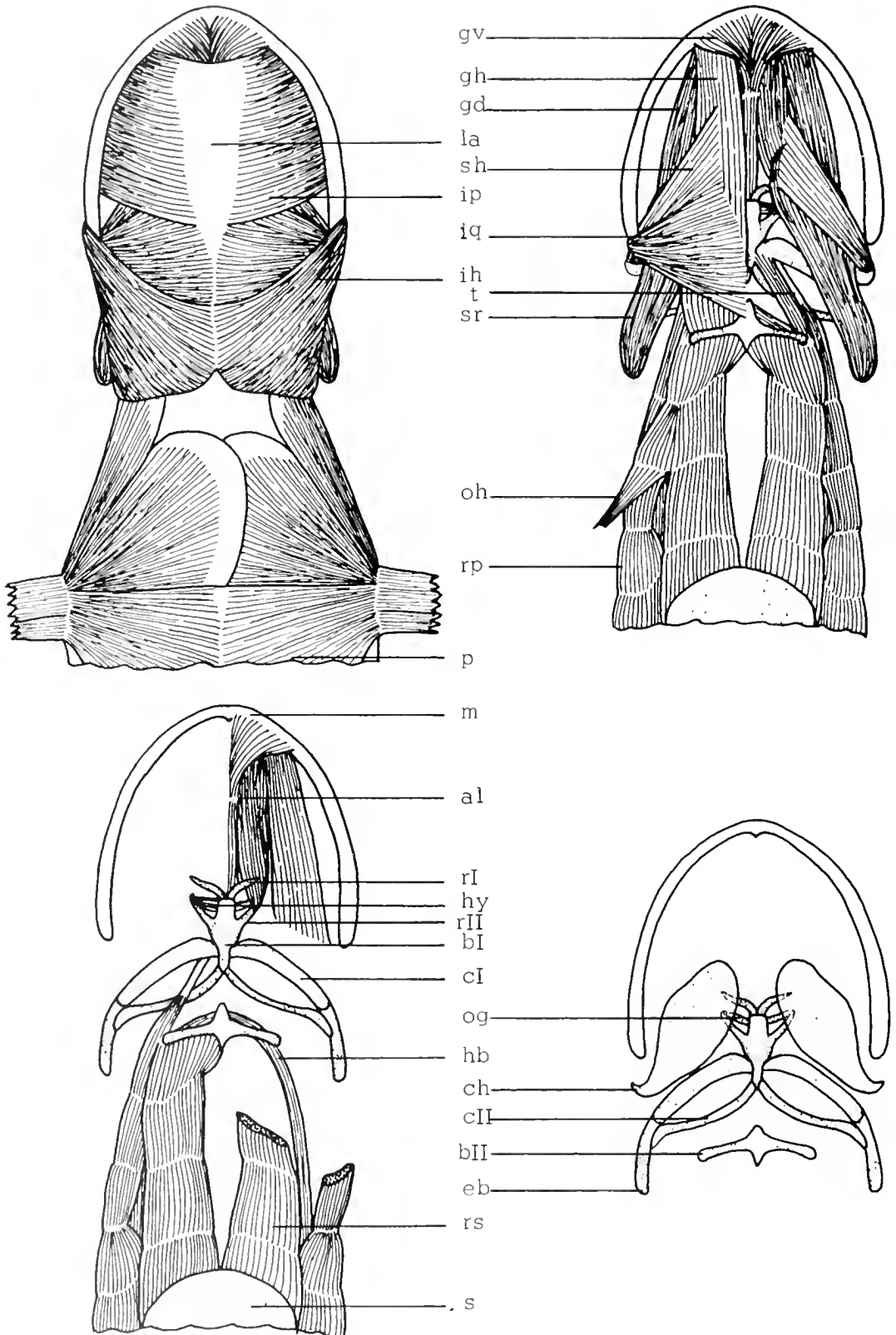


Fig. 3. *Ambystoma annulatum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

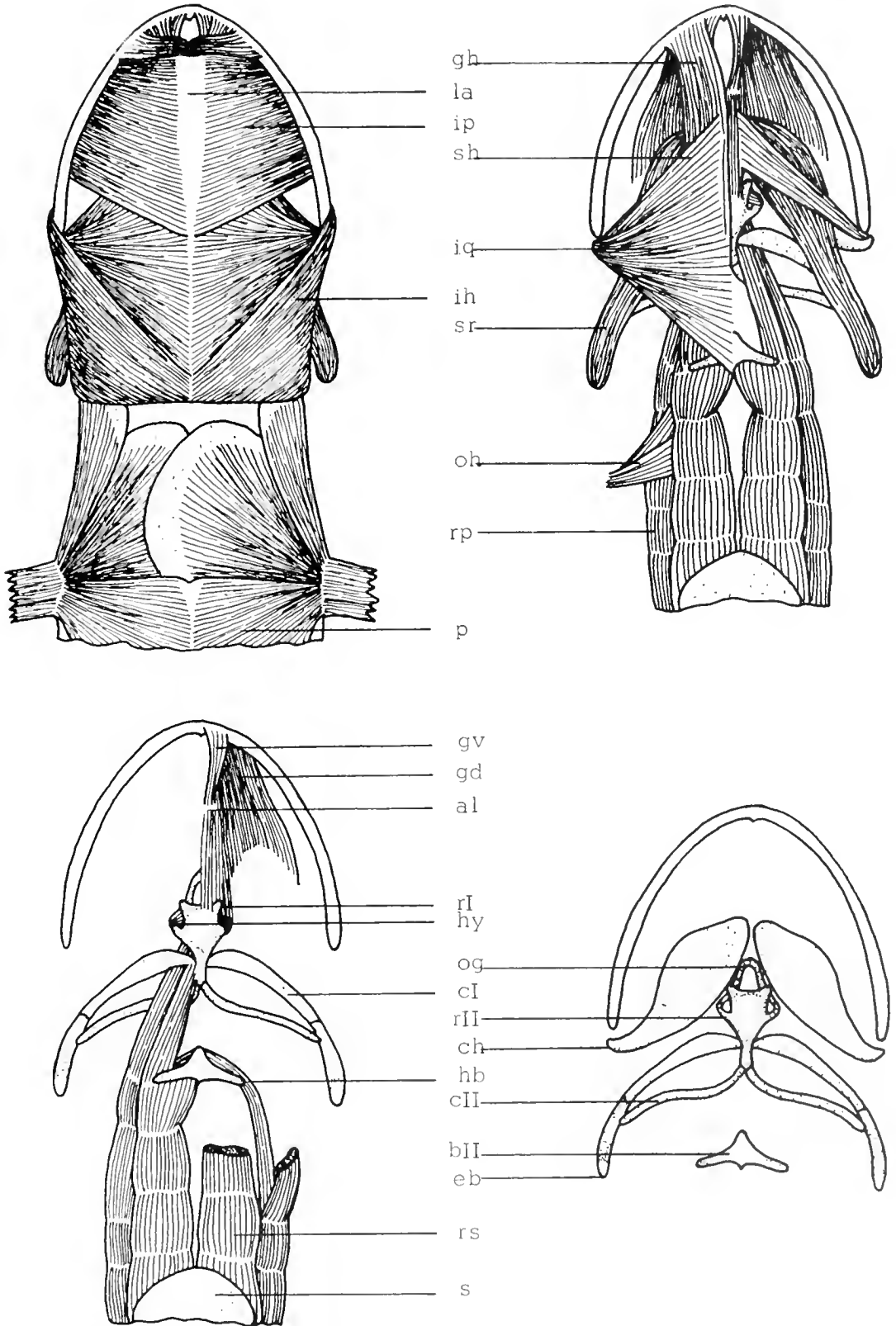


Fig. 4. *Ambystoma cingulatum*. Upper left: Superficial throat musculature, Upper right: Intermediate muscles the throat, Lower left: Deep muscles of the throat, Lower right: Hyobranchial skeleton.

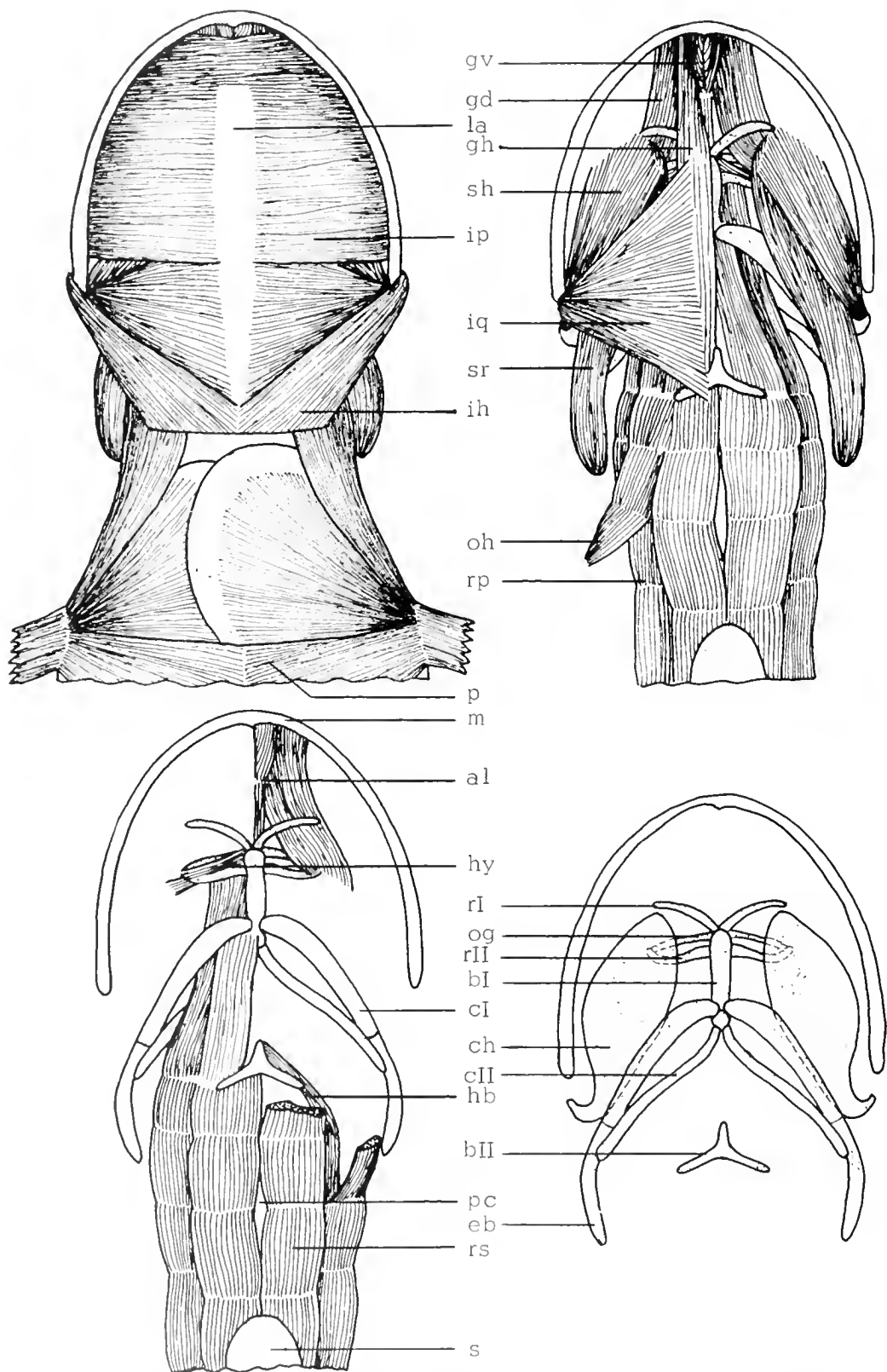


Fig. 5. *Ambystoma gracile*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

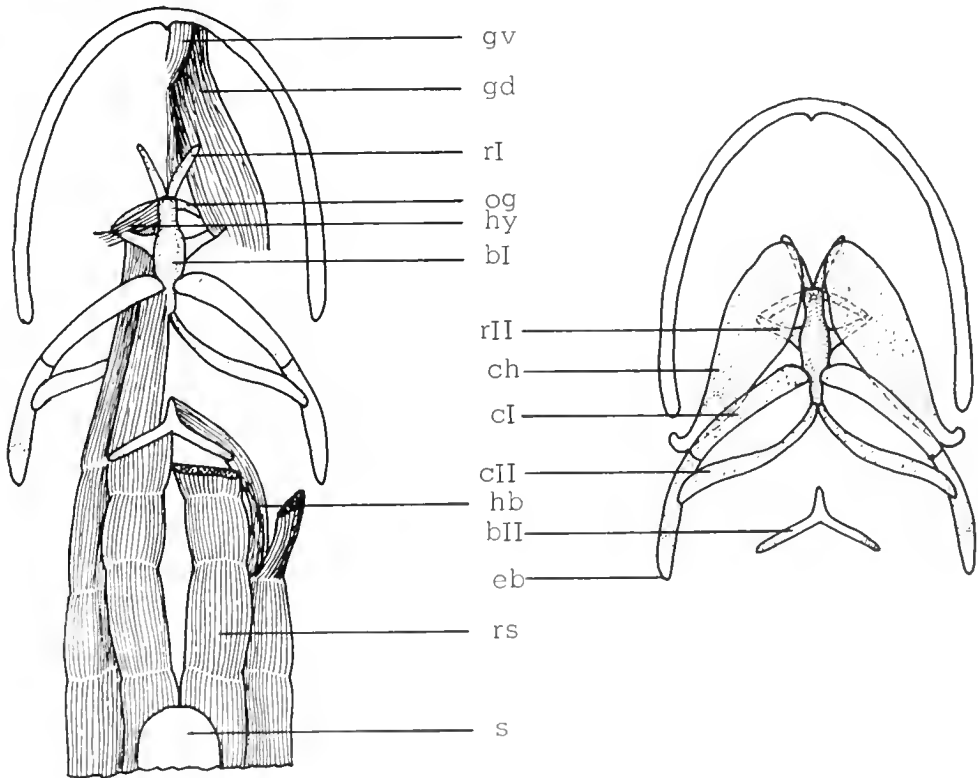
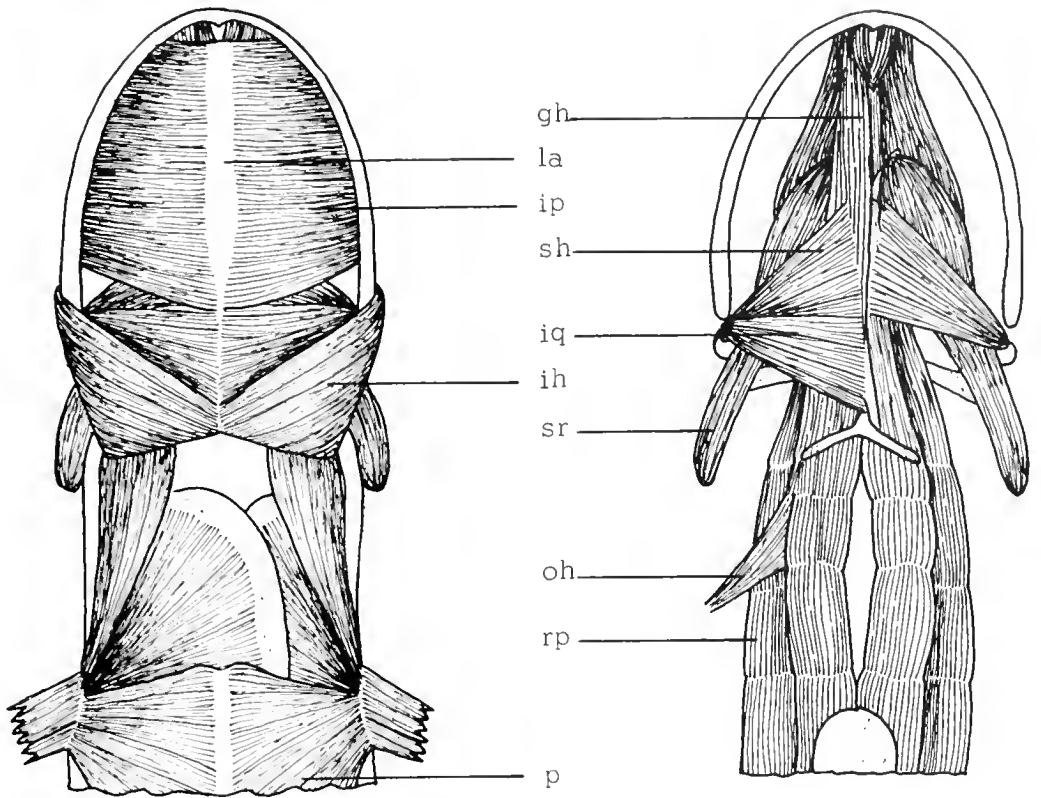


Fig. 6. *Ambystoma jeffersonianum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

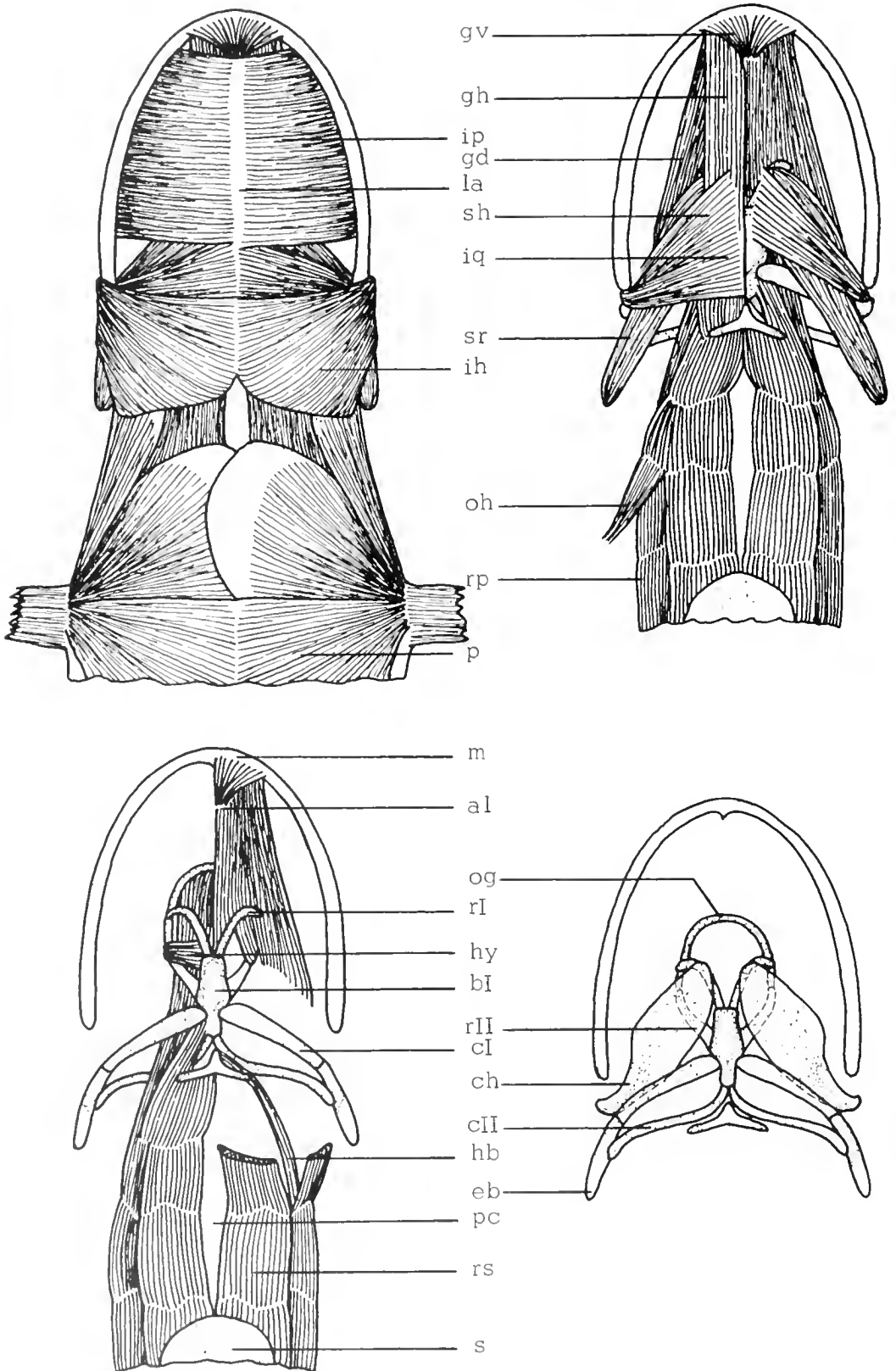


Fig. 7. *Ambystoma mabeyi*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

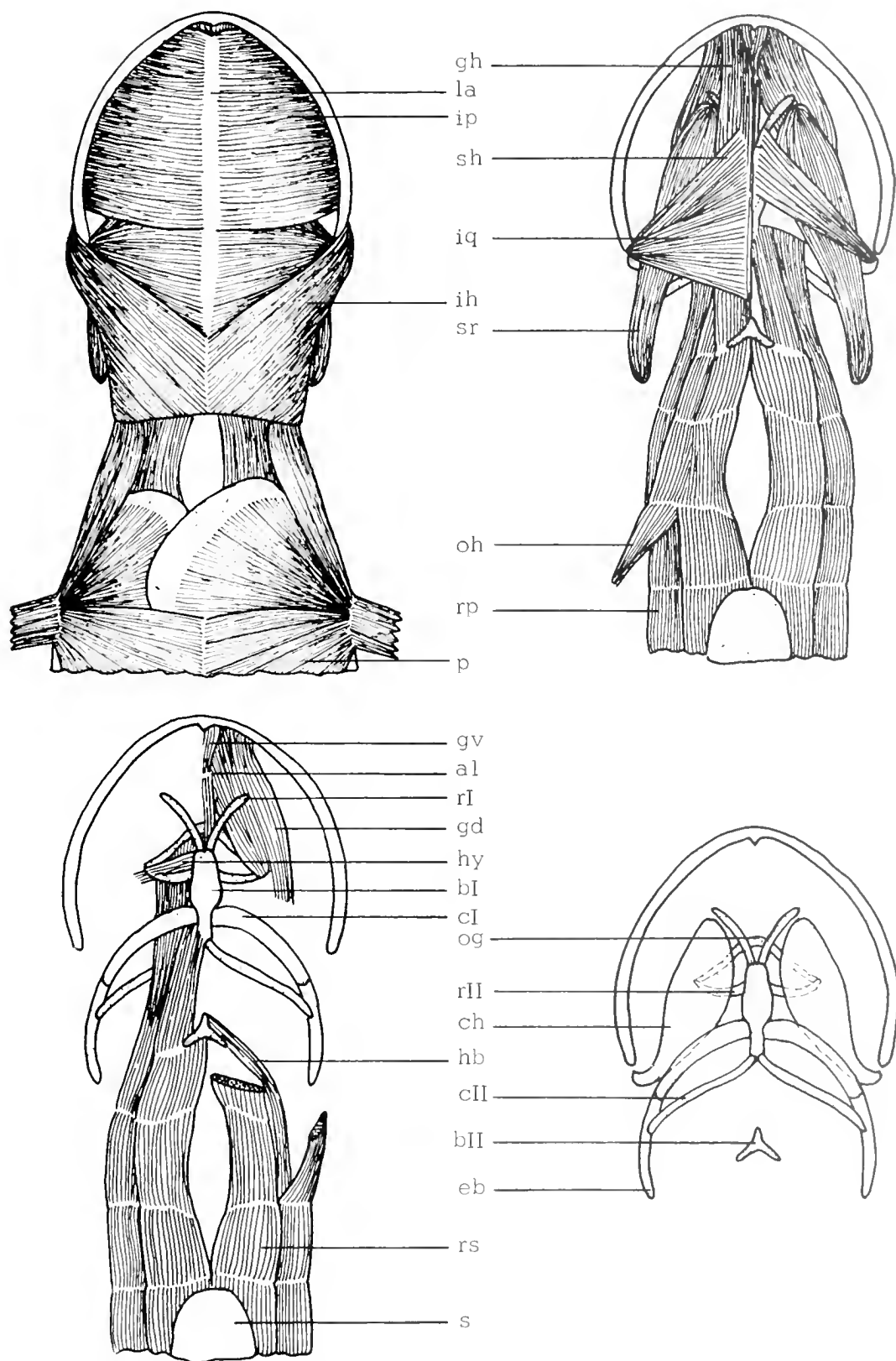


Fig. 8. *Ambystoma macrodactylum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

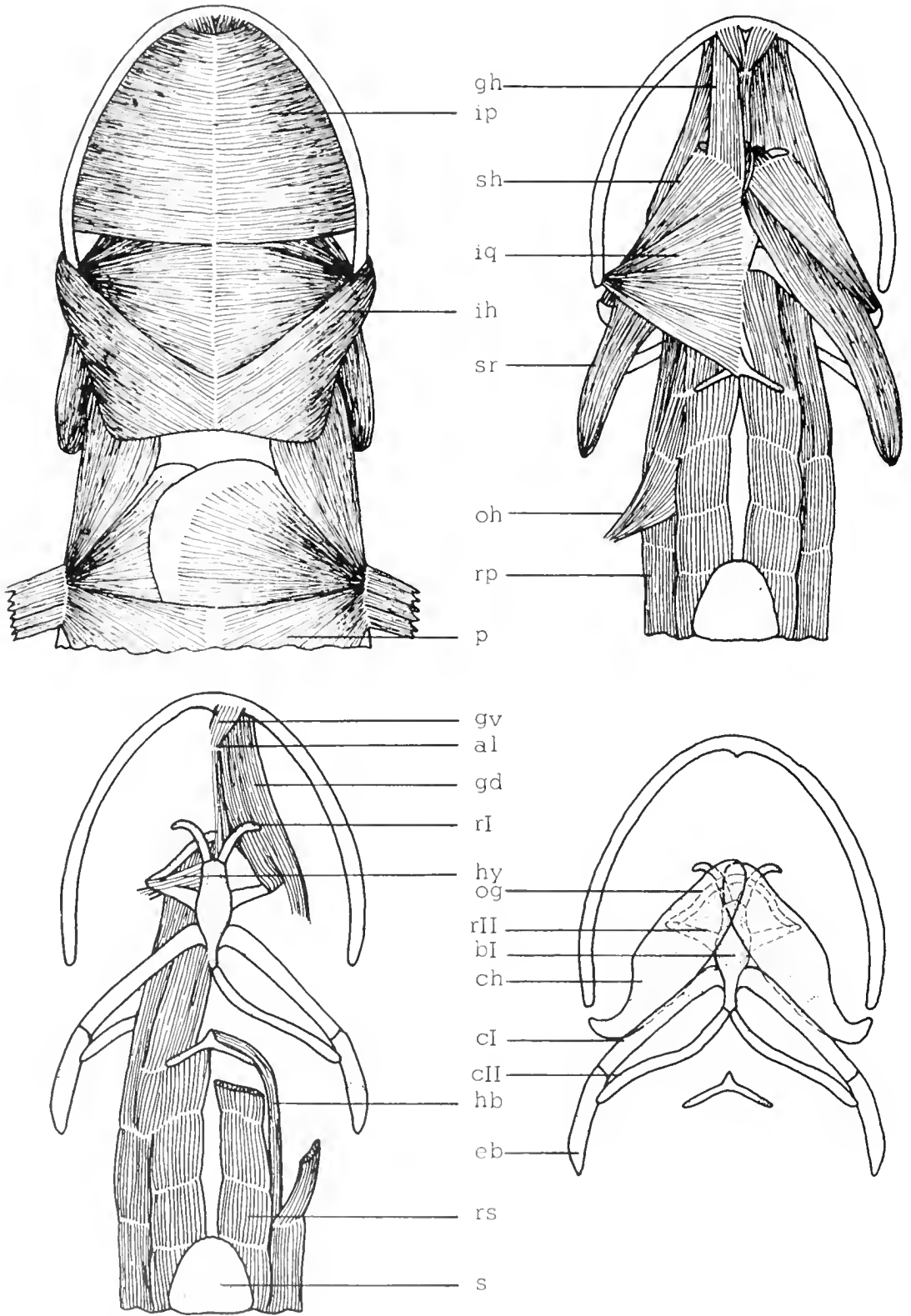


Fig. 9. *Ambystoma maculatum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

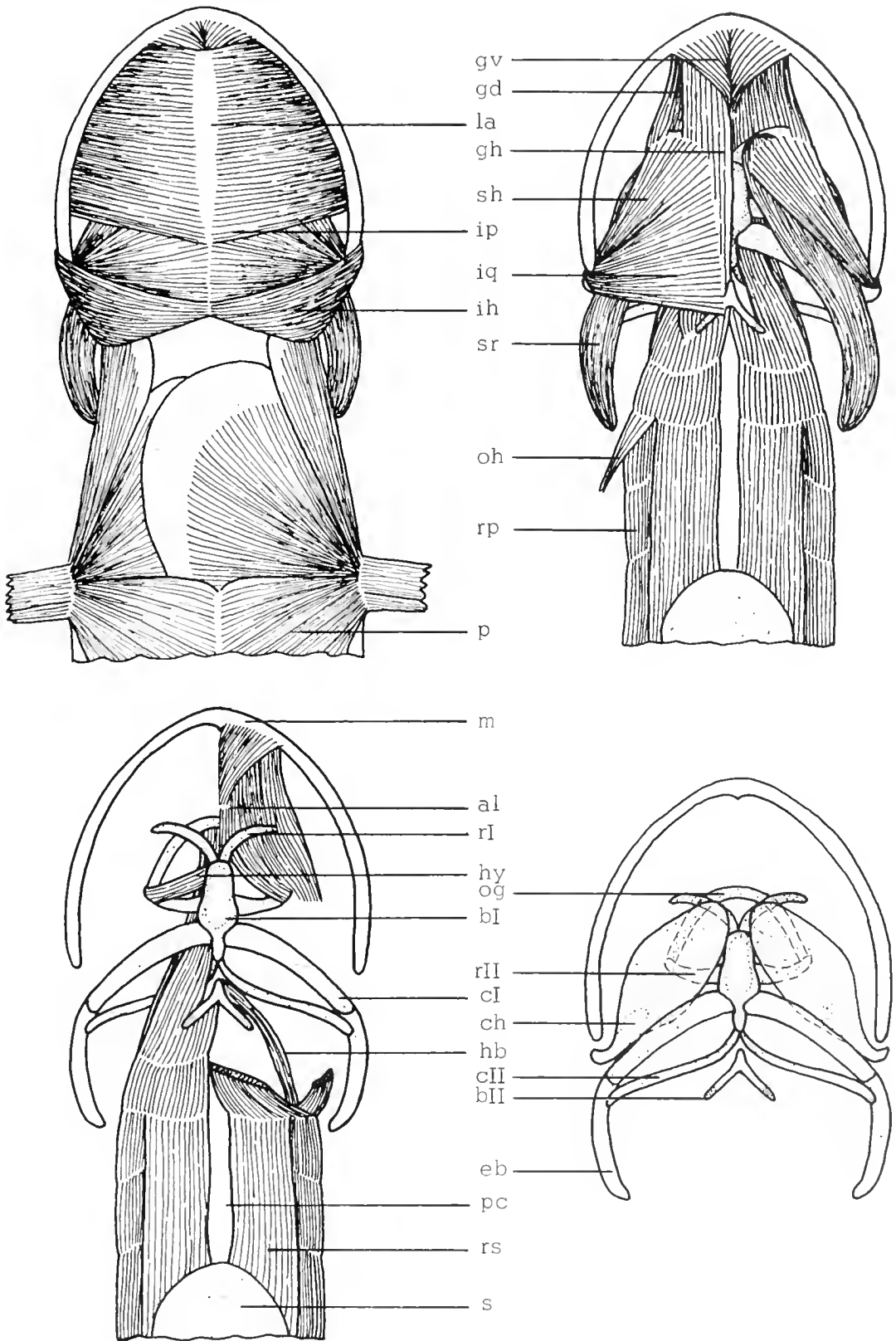


Fig. 10. *Ambystoma talpoideum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

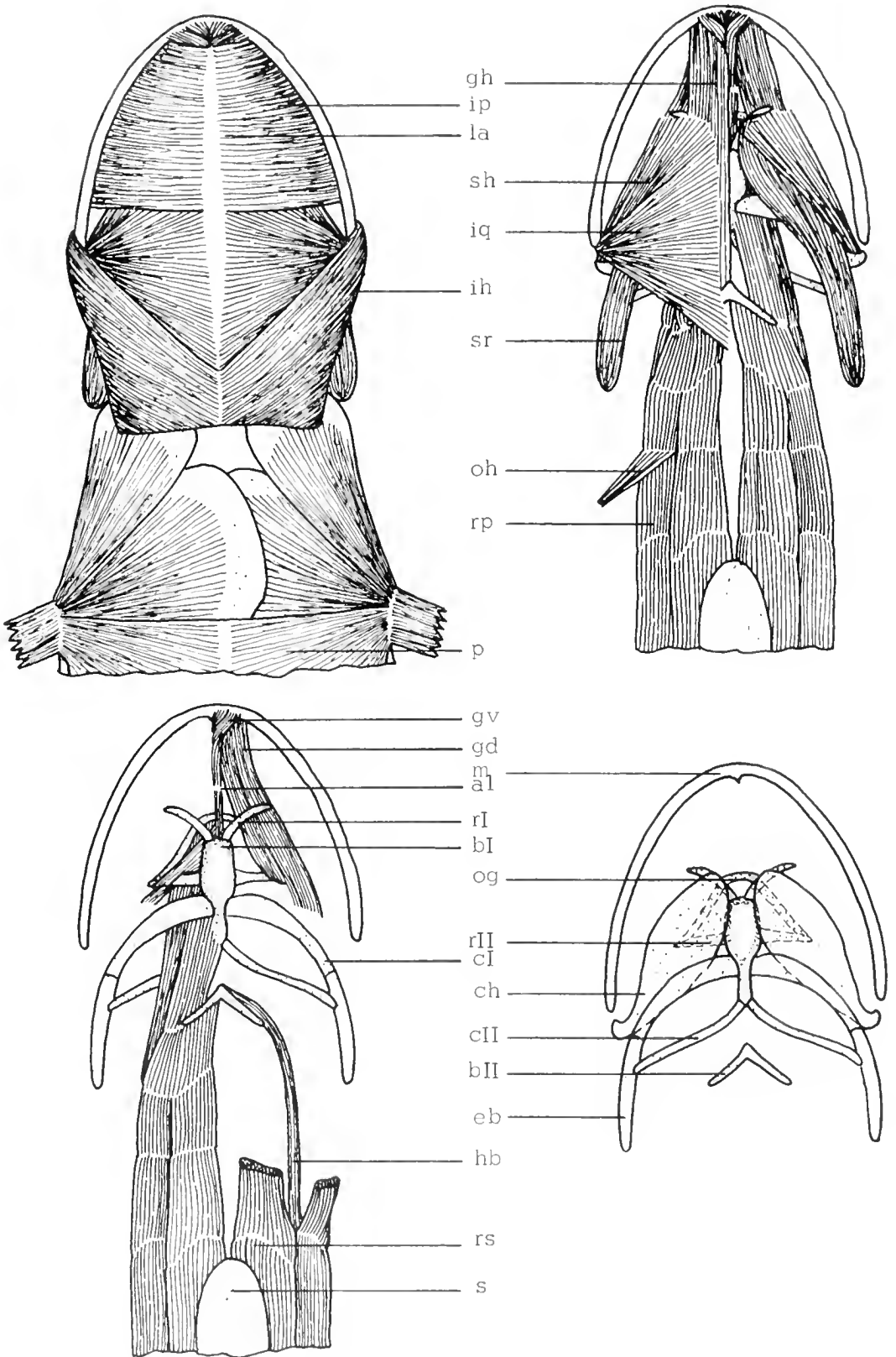


Fig. 11. *Ambystoma opacum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

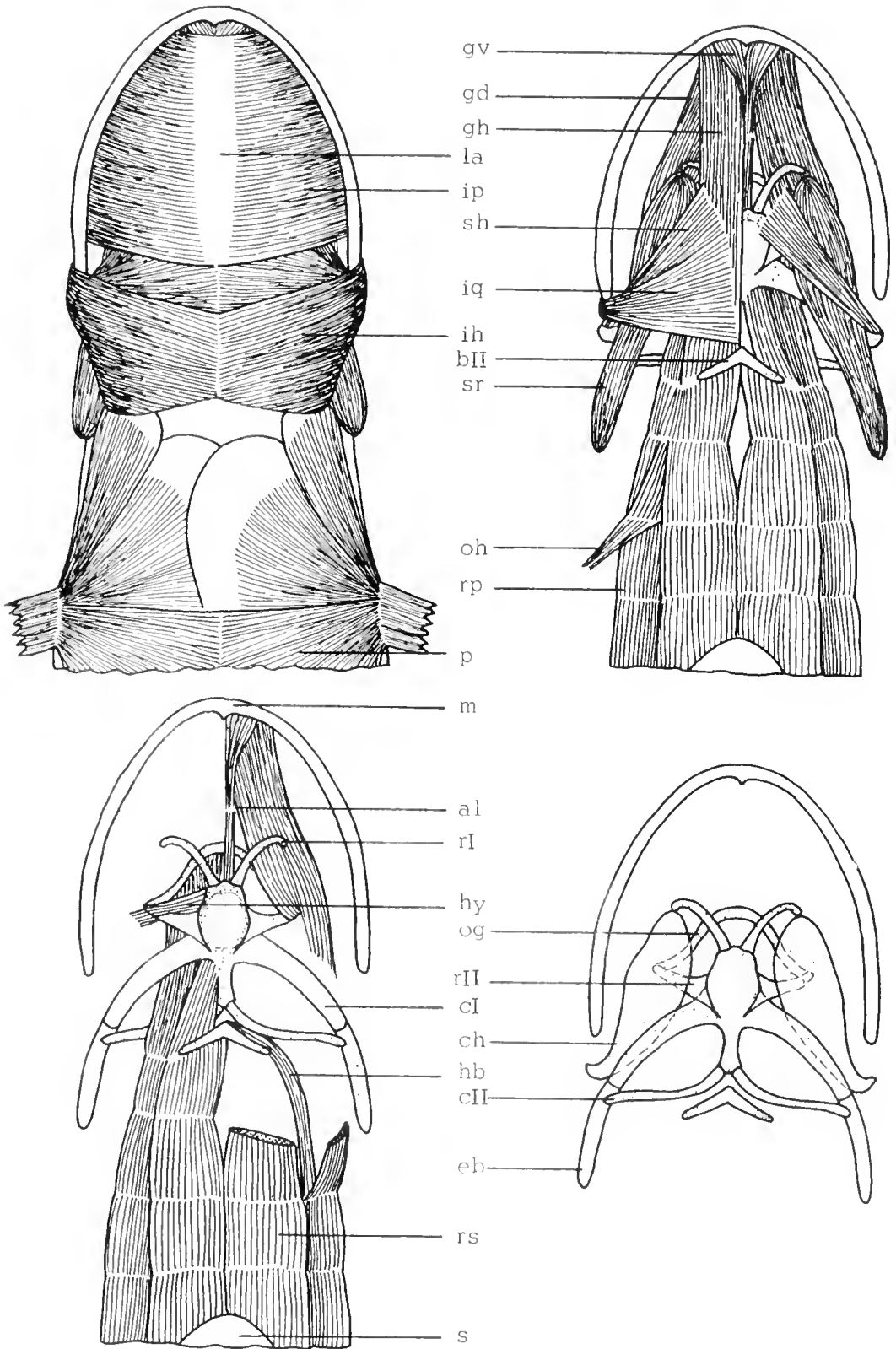


Fig. 12. *Ambystoma texanum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

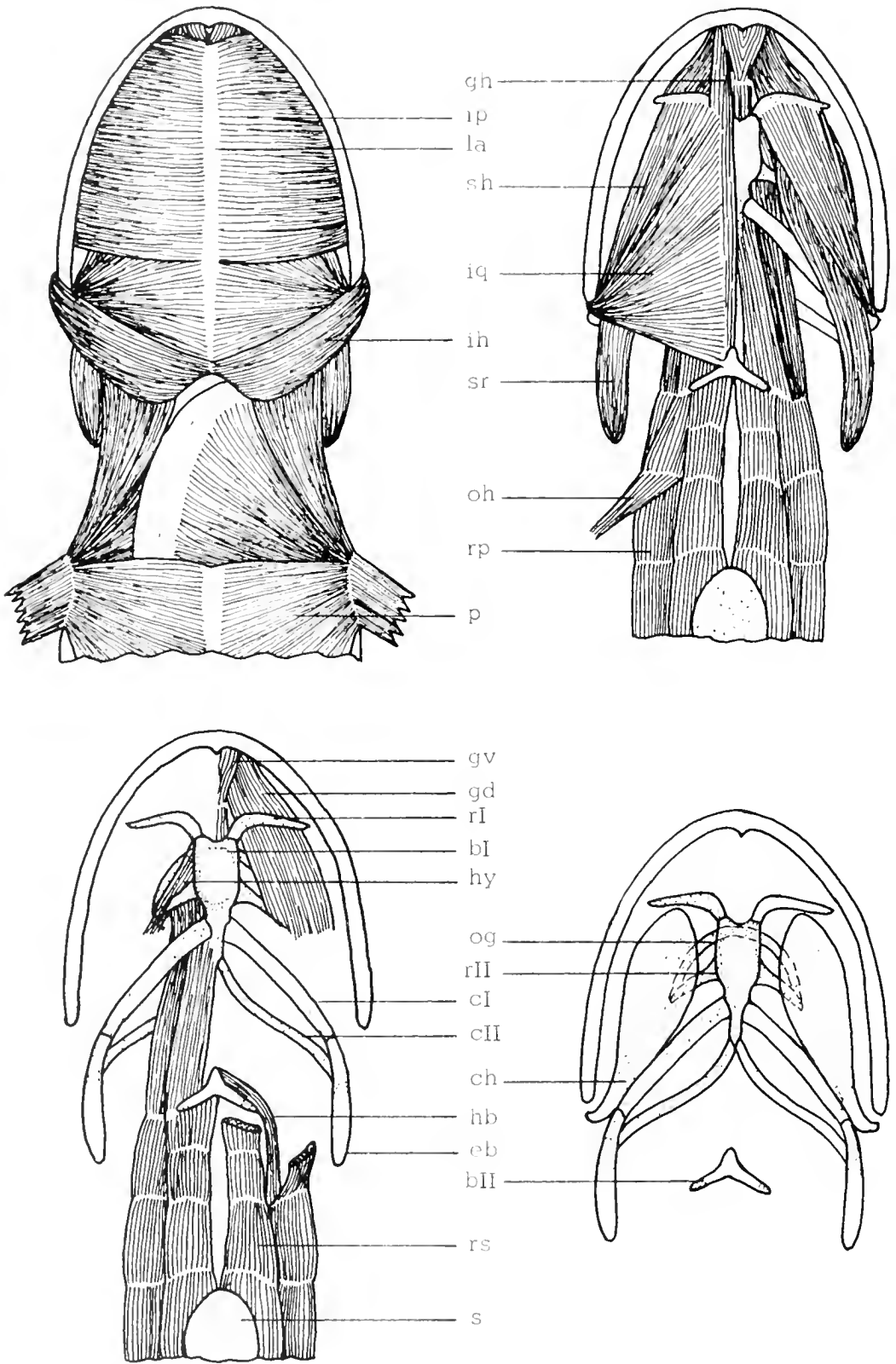


Fig. 13. *Ambystoma rosaceum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

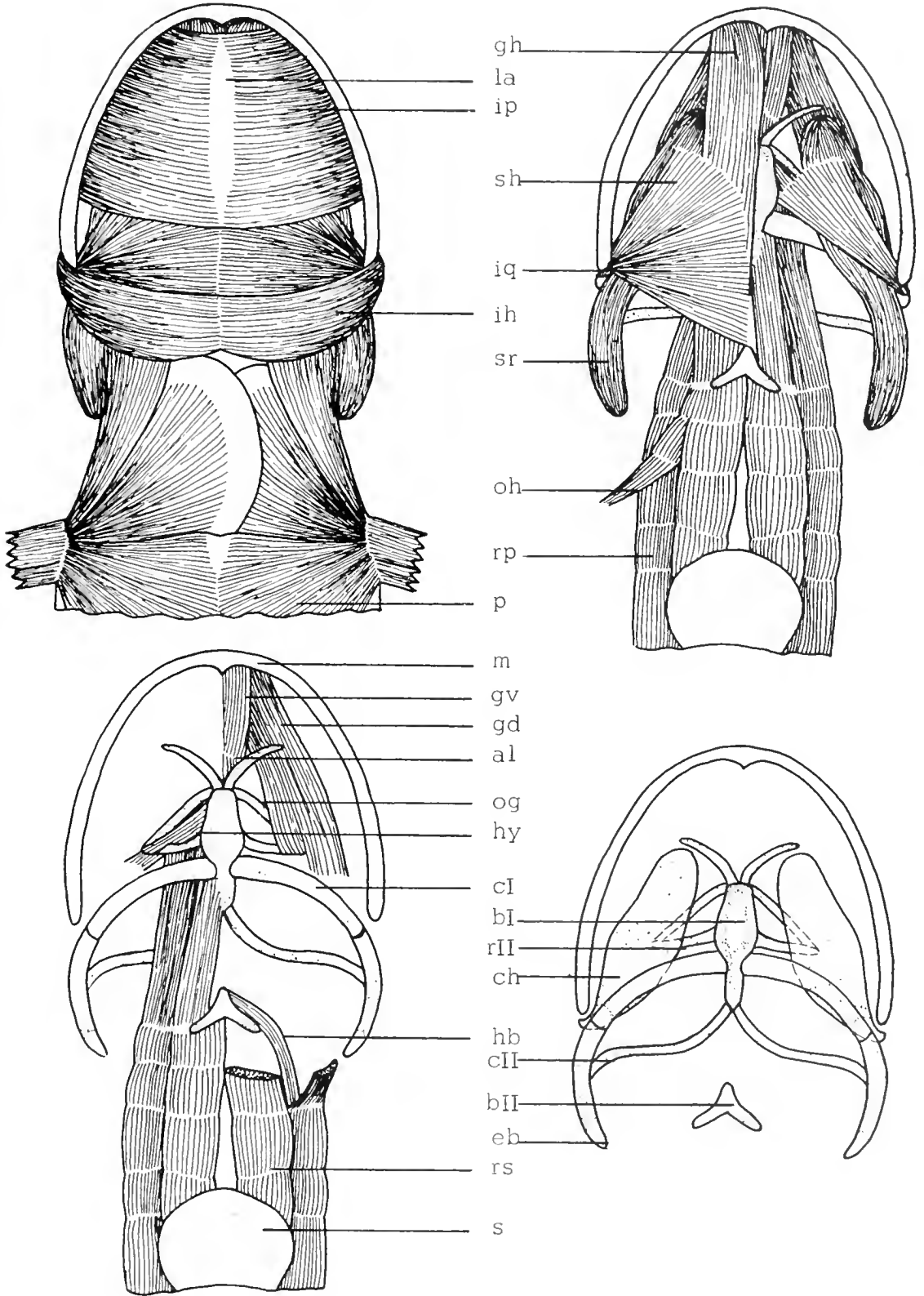


Fig. 14. *Ambystoma tigrinum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

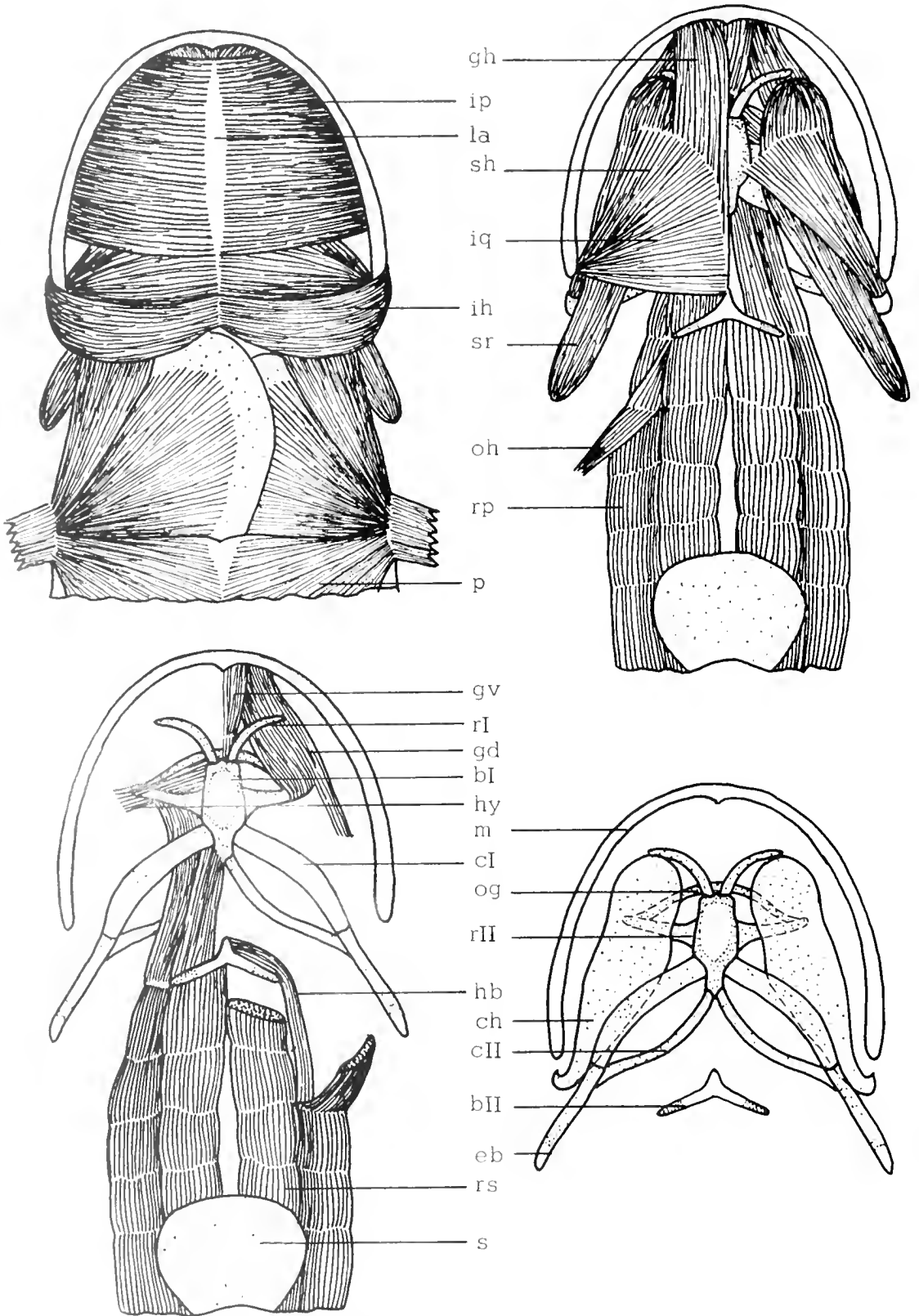


Fig. 15. *Ambystoma tigrinum melanostictum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

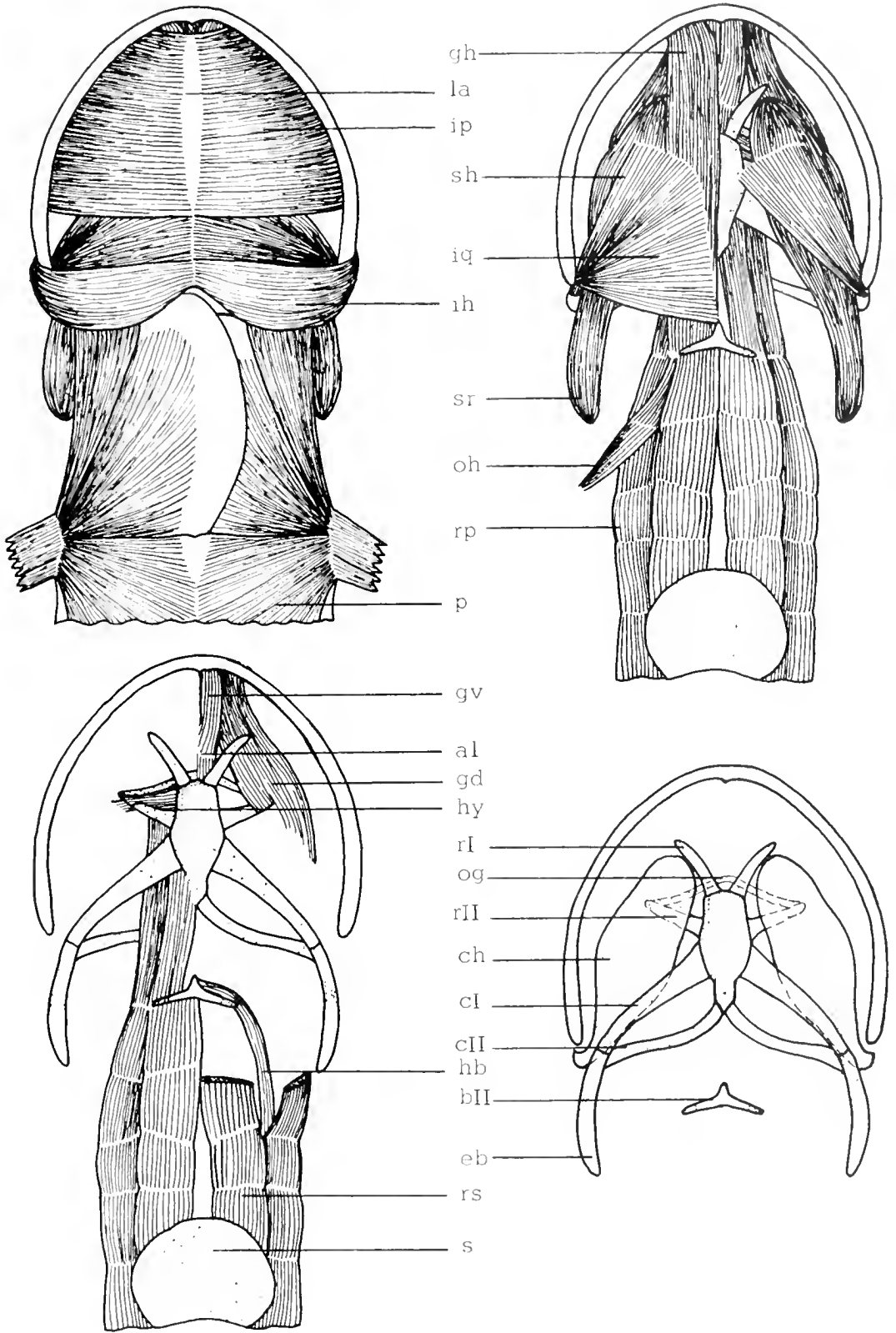


Fig. 16. *Ambystoma tigrinum nebulosum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

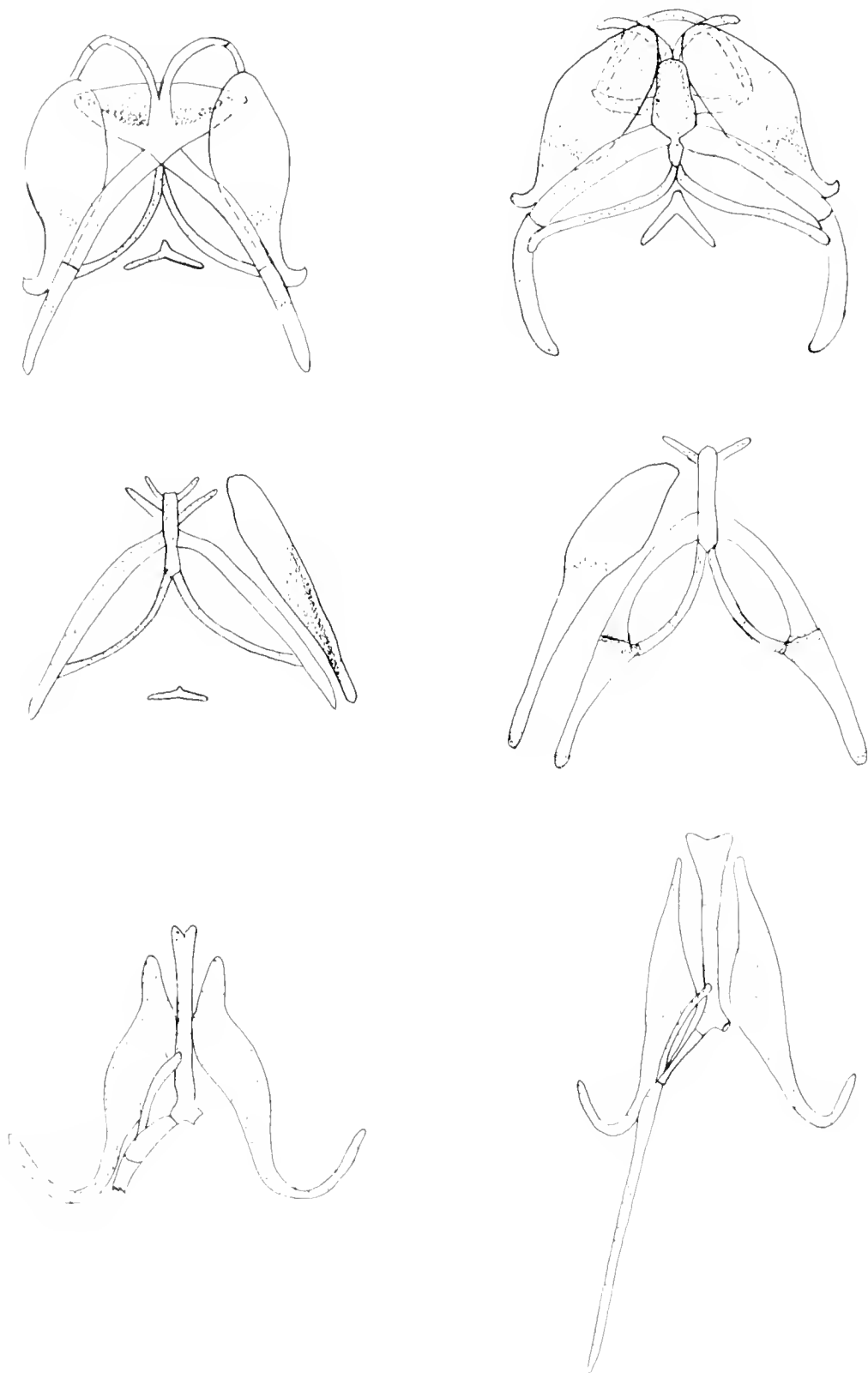


Fig. 17 Representative hyobranchial skeletons of Ambystomidae, Salamandridae, and Plethodontidae. Upper left: *Dicamptodon ensatus*. Upper right: *Ambystoma talpoideum*. Middle left: *Salamandra salamandra*. Middle right: *Taricha torosa*. Lower left: *Bolitoglossa rufescens*. Lower right: *Thorius narisovalis*. Middle left and middle right from Ozeti and Wake (1969). Lower left and lower right from Tanner (1952).

ossified. The distal end of the first ceratobranchial attaches to the proximal end of the epibranchial, the articulation of which is usually perceptible only as a thin line separating these two elements. There is no second epibranchial. The posterior tip of the epibranchial is ossified in nine of the fourteen species which we have dissected and serves as an attachment for the subarcualis rectus I muscle. Özeti and Wake (1969) report that the epibranchial is usually almost entirely

ossified in the Salamandridae but that some genera have lost this element or have experienced a fusion of the latter with the ceratobranchial. These investigators also report that the epibranchial is longer than the ceratobranchial, but we have found that the ambystomid epibranchial is consistently shorter than the first ceratobranchial with which it is articulated (Table 13).

Table 1. Average percent ossification of hyobranchial elements.

Species	bl	bII	cl	cII	rl	rII	ch	cb
<i>Dicamptodon ensatus</i>	0.0	0	0.0	0	0	0	15.0	56.5
<i>Rhyacotriton olympicus</i>	0.0	0	0.0	0	0	0	0.0	0.0
<i>Ambystoma annulatum</i>	77.0	43	0.0	0	0	0	0.0	12.0
<i>Ambystoma cingulatum</i>	73.0	62	2.2	0	0	0	5.0	15.0
<i>Ambystoma gracile</i>	0.0	78	0.0	0	0	0	0.0	0.0
<i>Ambystoma jeffersonianum</i>	37.4	80	0.0	0	0	0	6.4	39.7
<i>Ambystoma mabeci</i>	37.0	63	0.0	0	0	0	6.8	58.0
<i>Ambystoma macrodactylum</i>	34.0	50	0.0	0	0	0	5.0	0.0
<i>Ambystoma maculatum</i>	25.0	73	0.0	0	0	0	10.6	32.0
<i>Ambystoma talpoideum</i>	32.6	76	0.0	0	0	0	3.6	0.0
<i>Ambystoma opacum</i>	41.0	0	0.0	0	0	0	2.7	11.0
<i>Ambystoma texanum</i>	38.0	65	0.0	0	0	0	3.3	0.0
<i>Ambystoma rosaccum</i>	28.0	69	0.0	0	0	0	4.8	36.0
<i>Ambystoma tigrinum</i>	40.0	72	0.0	0	0	0	5.0	17.0
<i>Ambystoma tigrinum melanostictum</i>	37.5	71	0.0	0	0	0	0.0	21.0
<i>Ambystoma tigrinum nebulosum</i>	59.0	59	0.0	0	0	0	8.0	60.0

The second branchial arch consists of a pair of slender, curved bars of cartilage which articulate proximally with the posterior end of the first basibranchial and curve posterolaterally to articulate distally with the first branchial arch at a point about two-thirds along the latter's length. It is entirely cartilaginous in all specimens which we have observed. The space between these two arches is covered by the intercartilaginous membrane (Drüner, 1901) except for the mesial portion through which the rectus cervicis profundus passes.

The second basibranchial is a small element located in the tendonous inscription which separates the geniohyoides from the rectus cervicis superficialis. It usually assumes the shape of a three-pointed star in which one arm is directed anteriorly with the other two arms pointing posterolaterally. In most of the specimens studied in this paper, the second basibranchial is cartilaginous on the tips of the lateral arms, the remainder being ossified. In a few specimens, the entire element is cartilage. In the larval state, this structure is connected with the first basibranchial by a slender median rod which disappears at metamorphosis, leaving the two basibranchials separated from each other. In most genera of the Salamandridae, the second basibranchial is lost (Özeti and Wake, 1969), and in the Plethodontidae it is reported by some authorities as completely missing (Dunn, 1926; Tanner, 1952; Wake, 1966), although Piatt (1935) recorded its presence in several plethodontid genera.

GENERAL FEATURES OF THE MUSCULATURE

The following paragraphs constitute some general statements as to position and size of the throat muscles. More detailed descriptions will be found in the following section which deals with each species.

Intermandibularis Posterior

This muscle is found just under the skin of the throat and covers about two-thirds of the area between the two rami of the mandible. There

are two intermandibularis muscles in the larva, a small anterior portion, and a larger posterior portion. It is the posterior portion that persists in the adult, and the anterior portion, the intermandibularis anterior, is lost at the time of transformation, or if it persists it is so completely fused with the posterior muscle that no separation can be made in adults. The origin of the intermandibularis posterior is along the dorso-medial surface of the mandible. In most specimens there is a small open area at the angle of

the chin where there are no fibers and the ventral portion of the genioglossus can be seen upon removal of the skin. The insertion is at the midline fascia of the throat—the linea alba. The width of this fascia is variable among the several species studied. In *Rhyacotriton* and *A. gracile* the fibers of the anterior portion extend without interruption across the midventral line. Also, in *A. cingulatum* the anterior portion of the intermandibularis posterior is noticeably separate from the large posterior portion of the muscle. The anterior portion of the interosquadrata is covered ventrally by the posterior fibers of this muscle.

This is one of the least variable muscles of the throat area. Contraction results in the raising of the floor of the mouth, which is a component of the breathing mechanism. This action also helps to force food items up against the vomerine teeth in feeding.

Interhyoideus Posterior

It has been suggested (Piatt, 1940) that this muscle in the Plethodontidae gives rise to two adult muscles, the gularis and the quadratopectoralis. In the ambystomids we have seen no tendency toward subdivision of the interhyoideus posterior, and it would therefore appear that this muscle is undifferentiated as noted by Piatt (1940). The origin is in fascia which attaches to the tip of the mandible, the quadrate, the squamosal, and the otic capsule and is continuous with the fascia cephalodorsalis. The fibers extend ventromesial to insert into the skin of the gular fold and the fascia along the midventral line.

This muscle would appear to function in swallowing food and in breathing, inasmuch as it is in a position to constrict the pharynx. It might also act in head flexion, since the posterior fibers are attached to the skin of the gular fold.

Table 2. Numere Characters¹

Species	Museum Number	Attribute Numbers																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Dicamptodon</i>	32467	0.50	0.75	1.29	0.52	0.21	0.55	0.27	0.47	2.09	0.52	0.93	1.10	0.53	0.55	0.35	0.72	0.36	0.00	0.00	0.00	16.0	60.0
<i>Dicamptodon</i>	32465	0.49	0.71	1.09	0.55	0.21	0.45	0.25	0.40	1.90	0.55	1.21	0.91	0.50	0.53	0.29	0.71	0.39	0.00	0.00	0.00	14.0	53.0
<i>Rhyacotriton</i>	12480	0.40	0.64	1.03	0.80	0.27	0.50	0.29	0.27	1.07	0.54	1.15	1.17	0.63	0.35	0.18	0.91	0.37	0.00	0.00	0.00	0.00	0.00
<i>Rhyacotriton</i>	12479	0.35	0.62	0.97	0.89	0.33	0.38	0.21	0.33	1.20	0.56	1.26	0.85	0.47	0.29	0.31	1.16	0.31	0.00	0.00	0.00	0.00	0.00
<i>A. annulatum</i>	32521	0.38	0.67	1.02	0.83	0.23	0.46	0.27	0.43	0.62	0.60	1.48	1.15	0.69	0.39	0.29	0.73	0.39	73.0	48.0	0.00	0.00	20.0
<i>A. annulatum</i>	32522	0.37	0.67	1.06	0.83	0.24	0.45	0.26	0.58	0.71	0.58	1.39	1.08	0.63	0.40	0.40	0.72	0.38	78.0	54.0	0.00	0.00	0.00
<i>A. annulatum</i>	32523	0.36	0.66	1.10	0.91	0.21	0.48	0.25	0.55	0.55	0.53	1.14	1.33	0.71	0.41	0.13	0.67	0.37	84.0	42.0	0.00	0.00	0.00
<i>A. annulatum</i>	32524	0.39	0.67	1.09	0.97	0.21	0.41	0.26	0.71	0.81	0.63	1.70	1.25	0.79	0.41	0.24	0.71	0.39	75.0	32.0	0.00	0.00	10.0
<i>A. annulatum</i>	32525	0.39	0.63	1.03	1.05	0.24	0.49	0.27	0.59	0.77	0.54	1.18	1.22	0.66	0.37	0.37	0.71	0.35	78.0	12.0	0.00	0.00	16.0
<i>A. cingulatum</i>	33307	0.42	0.71	1.11	0.75	0.25	0.50	0.29	0.72	0.22	0.57	1.33	1.17	0.67	0.40	0.56	0.77	0.38	80.0	60.0	0.00	0.00	18.0
<i>A. cingulatum</i>	33309	0.44	0.75	1.13	0.71	0.23	0.43	0.26	0.93	0.33	0.61	1.59	1.20	0.74	0.45	0.18	0.82	0.34	72.0	52.0	0.00	0.00	28.0
<i>A. cingulatum</i>	33310	0.39	0.71	0.89	0.77	0.21	0.43	0.26	0.80	0.33	0.61	1.59	1.09	0.67	0.48	0.41	0.71	0.33	90.0	63.0	0.00	0.00	0.00
<i>A. cingulatum</i>	33312	0.47	0.69	1.14	0.86	0.21	0.45	0.31	0.73	0.27	0.67	2.06	1.12	0.76	0.50	0.41	0.77	0.35	78.0	71.0	0.00	0.00	0.00
<i>A. cingulatum</i>	33308	0.40	0.67	1.03	0.82	0.21	0.46	0.28	0.69	0.38	0.60	1.52	1.17	0.71	0.48	0.38	0.66	0.37	67.0	67.0	11.0	0.00	27.0
<i>A. gracile</i>	32503	0.39	0.67	0.94	0.46	0.23	0.49	0.27	0.34	0.92	0.57	1.24	1.11	0.61	0.57	0.35	0.67	0.35	0.00	0.20	0.00	0.00	0.00
<i>A. gracile</i>	32504	0.38	0.69	0.99	0.55	0.24	0.55	0.27	0.46	0.86	0.50	1.00	1.14	0.57	0.49	0.45	0.78	0.42	0.00	74.0	0.00	0.00	0.00
<i>A. pfeffermannianum</i>	32487	0.46	0.64	1.12	0.42	0.26	0.62	0.32	0.51	0.63	0.52	1.09	1.18	0.61	0.49	0.30	0.64	0.32	36.0	91.0	0.00	0.00	27.5
<i>A. pfeffermannianum</i>	32489	0.44	0.68	1.00	0.43	0.25	0.61	0.31	0.46	0.66	0.50	1.00	1.12	0.56	0.52	0.55	0.69	0.26	34.5	85.0	0.00	0.00	32.0
<i>A. pfeffermannianum</i>	32488	0.47	0.64	0.93	0.44	0.24	0.55	0.31	0.49	0.46	0.56	1.26	1.12	0.63	0.53	0.43	0.63	0.33	39.4	80.0	0.00	0.00	0.00
<i>A. pfeffermannianum</i>	32508	0.49	0.70	1.12	0.42	0.25	0.57	0.31	0.41	0.68	0.55	1.20	1.12	0.61	0.53	0.45	0.69	0.28	39.0	82.0	0.00	0.00	48.0
<i>A. pfeffermannianum</i>	32509	0.45	0.62	0.89	0.49	0.24	0.59	0.31	0.55	0.82	0.52	1.08	1.19	0.61	0.52	0.67	0.71	0.28	38.5	76.0	0.00	0.00	36.0
<i>A. nubes</i>	33313	0.40	0.68	1.18	0.71	0.31	0.56	0.32	0.56	1.00	0.56	1.28	1.22	0.68	0.37	0.30	0.92	0.34	39.0	70.0	0.00	0.00	45.0
<i>A. nubes</i>	33314	0.41	0.67	1.26	0.75	0.28	0.57	0.31	0.48	0.86	0.54	1.19	1.03	0.56	0.44	0.36	0.75	0.36	38.0	65.0	0.00	0.00	73.0
<i>A. nubes</i>	33318	0.37	0.65	1.12	0.88	0.30	0.46	0.24	0.67	1.33	0.53	1.11	1.10	0.58	0.33	0.40	1.02	0.31	39.0	65.0	0.00	0.00	64.0
<i>A. nubes</i>	33317	0.39	0.64	1.13	0.68	0.26	0.50	0.25	0.63	0.95	0.51	1.03	1.08	0.55	0.42	0.16	0.85	0.38	37.0	63.0	0.00	0.00	55.0
<i>A. nubes</i>	33315	0.40	0.65	1.19	0.63	0.25	0.49	0.25	0.56	1.17	0.52	1.09	1.11	0.58	0.47	0.11	0.81	0.35	45.0	56.0	0.00	0.00	56.0
<i>A. macrinolatyllum</i>	13735	0.36	0.67	1.01	0.56	0.24	0.67	0.36	0.36	0.91	0.51	1.18	1.15	0.62	0.53	0.54	0.62	0.32	34.0	50.0	0.00	0.00	0.00
<i>A. maculatum</i>	32311	0.40	0.71	1.00	0.61	0.26	0.51	0.29	0.49	0.85	0.57	1.33	1.08	0.62	0.52	0.19	0.69	0.32	31.0	74.0	0.00	0.00	35.0
<i>A. maculatum</i>	32512	0.43	0.64	1.07	0.53	0.30	0.60	0.33	0.56	0.68	0.56	1.27	1.26	0.71	0.43	0.26	0.67	0.23	25.0	72.0	0.00	11.0	28.0
<i>A. maculatum</i>	32515	0.41	0.66	1.09	0.55	0.28	0.57	0.29	0.45	0.58	0.51	1.05	1.18	0.60	0.47	0.30	0.75	0.32	26.0	67.0	0.00	0.00	0.00
<i>A. maculatum</i>	32516	0.40	0.62	1.07	0.68	0.28	0.57	0.30	0.49	0.63	0.53	1.11	1.13	0.59	0.42	0.29	0.77	0.34	18.0	78.0	0.00	0.00	0.00
<i>A. maculatum</i>	32517	0.38	0.64	1.07	0.60	0.29	0.61	0.31	0.51	0.50	0.51	1.05	1.16	0.64	0.45	0.36	0.71	0.32	26.0	74.0	0.00	0.00	0.00
<i>A. talpoidatum</i>	112135	0.46	0.61	0.92	0.58	0.28	0.57	0.30	0.52	0.85	0.52	1.09	1.14	0.59	0.56	0.25	0.70	0.36	36.5	80.0	0.00	11.0	0.00
<i>A. talpoidatum</i>	112136	0.45	0.62	0.89	0.60	0.26	0.57	0.28	0.48	0.64	0.50	1.00	0.98	0.49	0.51	0.54	0.76	0.31	25.0	77.0	0.00	0.00	0.00
<i>A. talpoidatum</i>	112137	0.42	0.65	0.78	0.75	0.38	0.71	0.34	0.41	0.78	0.48	0.93	1.18	0.57	0.39	0.58	1.00	0.37	36.5	72.0	0.00	0.00	0.00
<i>A. opacum</i>	23310	0.33	0.72	0.92	0.56	0.34	0.72	0.37	0.50	0.60	0.52	1.08	1.07	0.56	0.48	0.20	0.75	0.36	53.5	0.00	0.00	0.00	0.00
<i>A. opacum</i>	32511	0.38	0.62	1.10	0.69	0.11	0.88	0.43	0.51	0.68	0.48	0.93	1.24	0.60	0.39	0.27	0.88	0.28	37.0	0.00	0.00	0.00	0.00
<i>A. opacum</i>	32510	0.43	0.68	1.16	0.58	0.30	0.57	0.32	0.62	0.81	0.56	1.28	1.04	0.70	0.42	0.33	0.70	0.37	51.0	0.00	0.00	0.00	0.00
<i>A. opacum</i>	32313	0.48	0.67	0.96	0.66	0.31	0.59	0.34	0.54	0.73	0.57	1.33	1.18	0.68	0.46	0.31	0.86	0.28	65.0	0.00	0.00	0.00	0.00
<i>A. texanum</i>	13098	0.43	0.65	1.04	0.66	0.26	0.57	0.30	0.70	1.20	0.53	1.13	1.12	0.59	0.44	0.18	0.69	0.33	36.5	69.0	0.00	0.00	0.00
<i>A. texanum</i>	13099	0.39	0.63	0.99	0.74	0.31	0.68	0.36	0.43	1.05	0.53	1.15	1.26	0.67	0.41	0.32	0.69	0.51	35.0	59.0	0.00	0.00	0.00
<i>A. texanum</i>	13104	0.40	0.67	1.06	0.64	0.25	0.51	0.29	0.74	0.95	0.57	1.42	1.16	0.71	0.48	0.45	0.71	0.40	39.0	53.0	0.00	0.00	0.00
<i>A. texanum</i>	13101	0.39	0.67	0.98	0.76	0.29	0.62	0.35	0.78	1.00	0.57	1.32	1.24	0.71	0.40	0.40	0.85	0.38	36.0	79.0	0.00	0.00	0.00
<i>A. texanum</i>	13102	0.36	0.63	0.99	0.69	0.22	0.50	0.28	0.81	1.00	0.56	1.28	1.09	0.61	0.45	0.30	0.70	0.29	43.0	67.0	0.00	0.00	0.00
<i>A. rosacrum</i>	32507	0.45	0.65	1.11	0.37	0.25	0.59	0.32	0.12	1.13	0.54	1.17	1.17	0.63	0.67	0.44	0.63	0.27	12.0	61.0	0.00	0.00	0.00
<i>A. rosacrum</i>	32506	0.30	0.70	1.07	0.40	0.27	0.54	0.30	0.11	0.82	0.55	1.23	1.17	0.65	0.55	0.47	0.67	0.27	28.0	71.0	0.00	0.00	0.00
<i>A. rosacrum</i>	32505	0.46	0.69	0.97	0.51	0.26	0.61	0.31	0.46	0.92	0.52	1.07	1.18	0.61	0.55	0.39	0.73	0.24	21.0	74.0	0.00	0.00	0.00
<i>A. t. agrinum</i>	31462	0.42	0.66	0.92	0.52	0.27	0.61	0.34	0.49	0.80	0.56	1.27	1.05	0.59	0.64	0.50	0.61	0.30	13.0	69.0	0.00	0.00	0.00
<i>A. t. agrinum</i>	32513	0.41	0.68	0.97	0.49	0.28	0.61	0.32	0.46	0.74	0.54	1.11	1.01	0.53	0.53	0.31	0.65	0.36	39.0	73.0	0.00	0.00	0.00
<i>A. t. agrinum</i>	32514	0.45	0.65	1.03	0.39	0.29	0.63	0.34	0.40	0.62	0.55	1.23	1.01	0.56	0.54	0.35	0.70	0.33	38.0	74.0	0.00	0.00	0.00
<i>A. t. melanostictum</i>	703	0.44	0.59	0.88	0.40	0.23	0.50	0.26	0.54														

line of origin extends a considerable distance anteriorly along the lateral margin of the ceratohyal. The insertion is also atypical in this species, being attached to the posterior edge of the mandible just lateral to the symphysis. In other ambystomids that are included in this study, the subhyoideus inserts along the dorsal surface of the linea alba and into fascia over the anterior end of the ceratohyal. The fibers fan out slightly so that the insertion is broader than the origin.

This muscle is apparently able to assist in bringing the hyobranchial apparatus forward in feeding.

Geniohyoideus

Originating on the posteroventral surface of the mandible just lateral to the symphysis, this muscle passes caudad as a rather narrow but stout band to insert onto the second basibranchial and onto the tendonous inscription that extends laterally from the base of the second basibranchial. The geniohyoideus can be seen in some specimens beneath the transparent linea alba. In many specimens, the anterior ends of these two muscles are separated, and the ventral portion of the genioglossus can be seen between them at the angle of the chin. The lateral edge of the genioglossus partially overlaps the origin of the geniohyoideus ventrally. In *Dicamptodon*, the two geniohyoideus muscles are not separated anteriorly.

This muscle acts to depress the lower jaw or the entire head. It also advances the second basibranchial cartilage.

Genioglossus

There are two parts to this muscle. The ventral portion fills the angle of the chin and originates on the posteroventral edge of the mandible, beginning at the symphysis and extending laterally for a millimeter or two. The fibers extend posteromesially to form a small triangle-shaped muscle at the point of the chin. These fibers insert into the aponeurosis lingualis which connects the root of the tongue with the first basibranchial cartilage. A few mesial fibers may also continue caudad for a short distance to attach to the anterodorsal edge of the first basibranchial and onto the otoglossal.

The dorsal portion of the genioglossus arises from the posterior edge of the mandible immediately dorsal to the origin of the ventral portion. The geniohyoideus must be removed in order to see the entire muscle since the latter overlaps the dorsal portion. If one were to proceed dorsad from the lateral edge of the ventral por-

tion of this muscle, he would encounter the ventral portion of the genioglossus, the geniohyoideus, and the dorsal portion of the genioglossus. The dorsal portion spreads out as a fan over the floor of the mouth. The medial fibers often pass posteriorly to insert onto the tip of the second radial, while the lateral fibers continue in a posterolateral direction to insert into the sides of the base of the tongue.

Contraction of this muscle helps to pull the tongue out of the mouth. It may also act to compress the glandular tissue of the tongue preparatory to opening the mouth and extending the tongue in feeding.

Subarcualis Rectus I

This muscle originates on the tip of the epibranchial, around which the fibers wrap, forming a muscular sheath. It then extends anteromedially, parallel with the ceratohyal to insert on the expanded anterior end of the latter and, therefore, loosely binds the epibranchial and the ceratohyal together. Along with the subhyoideus, this muscle acts to bring the hyobranchial apparatus forward in feeding.

Rectus Cervicis Superficialis

This muscle originates on the dorsal surface of the sternum and extends dorsal to the anterior end of the sternum, and to the coracoid cartilages. It continues forward as a thin, broad sheet ventral to the pericardium to attach to the second basibranchial and the tendonous inscription from which the geniohyoideus arises. It then continues forward as a thick, narrow band on either side of the midline to insert onto the posterior edge of the medial end of the ceratobranchial and onto the posterior end of the first basibranchial. The portion between the sternum and the second basibranchial has three transverse tendonous inscriptions in all of the specimens that are included in this paper, except for *Rhyacotriton* and *A. talpoideum*, in which there are only two. The omohyoideus is a muscle associated with the rectus cervicis superficialis. It arises from the ventral surface of the scapula and extends to the lateral edge of the rectus cervicis superficialis, attaching to the latter along the margin between the second basibranchial cartilage and the first or second tendonous inscription posterior to the second basibranchial. The deep fibers of the two rectus cervicis muscles intermingle considerably dorsal to the insertion of the omohyoideus. The omohyoideus is not included in the descriptions of each specimen. It is the only muscle of the throat region that links the hyobranchial

apparatus with the cartilages of the pectoral girdle. The omohyoideus serves to brace the rectus cervicis superficialis and to adduct the shoulder girdle (Tammer, 1952: 596).

The mesial fibers of the rectus cervicis superficialis contract to stabilize the second basibranchial, thereby providing a stable attachment for the insertion of the geniohyoideus. The lateral fibers assist the rectus cervicis profundus in retracting the tongue.

Rectus Cervicis Profundus

This muscle is actually a direct forward continuation of the rectus abdominus muscle which originates on the puboischium. The portion under consideration in this paper begins at the level of the sternum and continues forward in a position dorsolateral to the rectus cervicis superficialis. It lies alongside the pericardium and lateral to the second basibranchial. It then becomes thicker and narrower and passes through the space between the ceratobranchial cartilages. In all of the animals included in this paper, it proceeds forward to attach onto the posterior edge of the otoglossal cartilage. Since *Dicamptodon* does not have an annular otoglossal cartilage, this muscle is not attached in the same manner as in the other ambystomids. In this particular case, the forward portion of the rectus cervicis profundus attaches to the posterodorsal surface of the otoglossal plate, the latter forming a continuous structure with the second radial cartilages.

Myological studies of the Salamandridae (Francis, 1934; Özeti and Wake, 1969) indicate that the rectus cervicis profundus lies ventral to the hyoglossus muscle, but it is definitely dorsal to the hyoglossus in the Ambystomidae. In most specimens examined, the rectus cervicis muscle inserts on the otoglossal at a point that is anterior as well as dorsal to the hyoglossus.

When this muscle contracts, the entire hyo-

branchial apparatus is pulled posteriorly as in the retraction of the tongue. It may also function in flexion of the head.

Hebosteoypsiloideus

This muscle is a narrow band that takes its origin on the dorsal surface of one of the myosepta of the rectus cervicis profundus. From its origin, it proceeds anteriorly dorsal to the rectus muscles. It turns mediad at the level of the second basibranchial to insert on its dorsal surface. The function is to assist the rectus cervicis profundus in stabilizing and in retracting the second basibranchial.

Hyoglossus

This tiny muscle originates on the dorsal surface of the anterior end of the first basibranchial cartilage. There may be a few of the anterior-most fibers that also attach to the aponeurosis lingualis. The fibers are directed caudolaterally to insert on the lateral edge of the second radial cartilage. In some specimens there may be a few fibers which continue laterally for a short distance into the substance of the tongue.

These latter fibers may be homologous with the muscle referred to by Drüner (1901) as the basiradialis. In the ambystomids, however, we were unable to detect a separation along the course of the hyoglossus in any of the specimens observed.

As indicated above, this muscle lies ventral to the rectus cervicis profundus. This is in sharp contrast to the report by Francis (1934) for *Salamandra salamandra* in which he states that the rectus cervicis profundus lies ventral to the hyoglossus and that the former must be removed in order to expose the latter.

The contraction of the hyoglossus causes the second radial cartilage to swing in an antero-dorsal direction, thereby elevating and protruding the pad of the tongue.

SPECIES DESCRIPTIONS

PACIFIC GIANT SALAMANDER

Dicamptodon ensatus (Eschscholtz)

Triton ensatus Eschscholtz, Zool. Atlas, Pt. 5, 1833, p. 6, pl. 22. *Dicamptodon*, Strauch, Mem. Acad. Sci. St. Petersburg. Ser. 7, Vol. 16, 1870.

The range of this species is along the humid coastal regions of the Northwest. It extends from Santa Cruz County in California, north to the southern coastal region of British Columbia, and

into northwestern Idaho and the Rocky Mountains of Montana. The ground color of the skin is brown, mottled or marbled with darker brown or black. This is the largest species of the Ambystomidae, transformed adults attaining occasionally a length of 300 mm. The body is stout, and the limbs are large and strong. The head is proportionately not as broad in this salamander as in many of the other ambystomids. There are 12 costal grooves, but they are poorly defined.

Vomerine teeth form a transverse series behind the internal nares and are interrupted by a narrow break at the midline where the series bends anteriorly. The teeth extend to the lateral margin of the internal nares.

HYOBRANCHIAL SKELETON (Fig. 1)

The first basibranchial is not separated from the radials by definite lines of articulation. It is truncate in shape and uniformly, though slightly, mineralized. In fact, the hyobranchium as a whole appears to be of a consistency intermediate between bone and cartilage. The first basibranchial is located in the center of the area circumscribed by the mandible.

This cartilage is shorter in relation to the total length of the hyobranchial skeleton than in any of the other ambystomids (Table 4). This is probably because the radials are especially long in this species. As seen in Table 5, the ratio of the first basibranchial length to first ceratobranchial length in *Dicamptodon* is the shortest of all the species being considered, with the exception of *A. annulatum*, *A. cingulatum*, and *Rhyacotriton*.

Table 4. Average ratios of length of first basibranchial to total length of hyobranchium.

Species	0	.1	.2	.3	.4	.5
<i>Dicamptodon ensatus</i>						
<i>Rhyacotriton olympicus</i>						
<i>Ambystoma annulatum</i>						
<i>Ambystoma cingulatum</i>						
<i>Ambystoma gracile</i>						
<i>Ambystoma jeffersonianum</i>						
<i>Ambystoma mabeei</i>						
<i>Ambystoma macrodactylum</i>						
<i>Ambystoma maculatum</i>						
<i>Ambystoma talpoidum</i>						
<i>Ambystoma opacum</i>						
<i>Ambystoma texanum</i>						
<i>Ambystoma rosaceum</i>						
<i>Ambystoma tigrinum</i>						
<i>Ambystoma tigrinum melanostictum</i>						
<i>Ambystoma tigrinum nebulosum</i>						

The first radial cartilages are long, curved, and jointed a little beyond their midpoint. Their distal ends articulate with the ceratohyals. They contain no distinct centers of ossification. The ratio of length of the first radial to the length of the first basibranchial is much greater in this species than in the other members of this family which we have studied (Table 6).

The second radials join the first basibranchial at their bases without a visible line of articulation, as mentioned above. These structures also unite with the otoglossal plate without any visible joint line. The otoglossal plate extends transversely between the two second radials and is tilted such that its anterior edge is more dorsal than its posterior edge. These structures appear to be composed of heavily calcified cartilage. In cutting into this tissue, one is impressed with the fact that it is denser than ordinary cartilage but less dense than bone.

The first ceratobranchial contains no distinct center of ossification and articulates, as in all of the species being studied in this paper, with the first basibranchial, the second ceratobranchial, and the epibranchial. As mentioned above, the first ceratobranchial is larger in relation to the first basibranchial than in all of the other species except *A. annulatum*, *A. cingulatum*, and *Rhyacotriton*.

No definite centers of ossification are found in the second ceratobranchials. The distal ends of these structures articulate with the first branchial arch at a point posterior to the articulation between the first ceratobranchial and the epibranchial. The ratio of the second ceratobranchial length to first ceratobranchial length is equal to that seen in *Rhyacotriton* and smaller than in the other ambystomids (Table 8).

A large center of ossification exists in the distal ends of the ceratohyals and is the largest percentage of ossification for this cartilage seen in the family (Table 1). The expanded anterior end is mostly cartilage, with a very slight amount of mineralization uniformly present throughout it.

The lateral arms of the second basibranchial are much larger than the anterior arm. No distinct center of ossification exists in this element.

The ratio of mandible length to width is greatest in this species (Table 9).

MUSCULATURE (Fig. 1)

Intermandibularis posterior originates along the dorsomedial edge of approximately the anterior three-quarters of the mandible. After ex-

tending in a transverse direction across the throat, the fibers insert into the linea alba. The posterior portion of this muscle overlaps the interossaquadrata ventrally. The ratio of the anteroposterior length of this muscle to the distance between the mental symphysis and the pectoralis muscle is greater in this species than in any of the others (Table 10).

Interhyoideus posterior originates on the ventrolateral surface of the quadrate, the lateral surface of the tip of the mandible, and the distal end of the squamosal. The fibers run transversely and slightly posteriorly to insert into the midventral line of fascia and into the skin and fascia of the gular fold. The anterior fibers form an almost indistinguishable margin with the posterior fibers of the interossaquadrata. The posterior edge of this muscle (the gular fold) is more posteriorly situated in this species than in other species (Table 11).

Depressor mandibulae originates in this species along the dorsal aspect of the squamosal and on the posteroventral surface of the otic capsule. It also attaches to the fascia cephalodorsalis. The fibers converge ventrally onto the posterior tip of the mandible.

Levator mandibulae is basically the same as that given above in the general statement of throat musculature of the Ambystomidae, except that the levator mandibulae posterior is not covered largely by the levator mandibulae externus. The majority of the latter muscle lies posterior to the levator mandibulae posterior. The tendon of insertion is tougher and larger than that seen in the other species. The overall size of the muscle, in fact, is hypertrophied as compared to other ambystomids, with perhaps the exception of *Rhyacotriton*, in which this particular muscle also appears to be enlarged.

Interossaquadrata originates on the medial aspect of the posterior tip of the mandible and the ventral surface of the quadrate immediately posterior to the mandibuloquadrate articulation. It inserts into the linea alba as the latter continues caudad from the intermandibularis posterior.

Subhyoideus originates on the posterior tip of the ceratohyal and wraps around the latter before proceeding forward parallel to the subarcualis rectus I. This is a thicker muscle than in the other species included in this investigation. It inserts into the dorsal fascia of the intermandibularis posterior. The interossaquadrata blends in with this muscle and overlaps it ventrally along the posterior one-third of its length.

Geniohyoideus takes its origin on the posterior edge of the mandible extending from the

Table 5. Average ratios of length of first basibranchial to length of first ceratobranchial.

Species	0	.1	.2	.3	.4	.5	.6	.7
<i>Dicamptodon ensatus</i>								
<i>Rhyacotriton olympicus</i>								
<i>Ambystoma annulatum</i>								
<i>Ambystoma cingulatum</i>								
<i>Ambystoma gracile</i>								
<i>Ambystoma jeffersonianum</i>								
<i>Ambystoma mabeei</i>								
<i>Ambystoma macrodactylum</i>								
<i>Ambystoma maculatum</i>								
<i>Ambystoma talpoideum</i>								
<i>Ambystoma opacum</i>								
<i>Ambystoma texanum</i>								
<i>Ambystoma rosaceum</i>								
<i>Ambystoma tigrinum</i>								
<i>Ambystoma tigrinum melanostictum</i>								
<i>Ambystoma tigrinum nebulosum</i>								

symphysis laterally for a distance of about 3 mm. The insertion is onto the anterior edge of the second basibranchial and laterally into the tendonous inscription that separates the geniohyoideus from the rectus cervicis superficialis.

Genioglossus is divided into ventromedial and dorsolateral portions as in the other species of this family. However, it appears to be a stouter muscle than in the others. It originates along the posterior edge of the mandible dorsal to the origin of the geniohyoideus. The medial fibers attach to the aponeurosis lingualis, and then proceed caudad to insert onto the anteroventral surface of the otoglossal plate. The lateral fibers overlap the tip of the second radial cartilage ventrally, and then insert into the adjacent fascia.

Subarcualis rectus I wraps around the posterior end of the epibranchial and forms a sheath which encloses the epibranchial. As the fibers pass forward, they follow the ceratohyal and spread out over the latter's expanded anterior end. The insertion is along the anterior edge of the ceratohyal.

Rectus cervicis superficialis originates on the

Table 6. Average ratios of length of first radial to length of first basibranchial.

Species	0	0.5	1.0	1.5	2.0
<i>Dicamptodon ensatus</i>					
<i>Rhyacotriton olympicus</i>					
<i>Ambystoma annulatum</i>					
<i>Ambystoma cingulatum</i>					
<i>Ambystoma gracile</i>					
<i>Ambystoma jeffersonianum</i>					
<i>Ambystoma mabeei</i>					
<i>Ambystoma macrodactylum</i>					
<i>Ambystoma maculatum</i>					
<i>Ambystoma talpoideum</i>					
<i>Ambystoma opacum</i>					
<i>Ambystoma texanum</i>					
<i>Ambystoma rosacum</i>					
<i>Ambystoma tigrinum</i>					
<i>Ambystoma tigrinum melanostictum</i>					
<i>Ambystoma tigrinum nebulosum</i>					

dorsal surface of the sternum and extends forward dorsal to the sternum, dorsal to the coracoid cartilages, and ventral to the pericardium. It attaches to the dorsal surface of the second basibranchial and laterally to the tendonous inscription from which the geniohyoideus arises. The superficial fibers of the portion which extends forward from this point insert into the posterior edge of the first ceratobranchial lateral to, but not inserting onto, the posterior tip of the first basibranchial. The deeper fibers continue forward to insert onto the posterior surface of the otoglossal plate ventral to the insertion of the rectus cervicis profundus.

Rectus cervicis profundus represents a direct anterior continuation of the rectus abdominus. From the level of the sternum, it passes forward along the dorsolateral edge of the rectus cervicis superficialis. It passes ventrally over the second ceratobranchial and dorsally over the first ceratobranchial. It inserts onto the posterodorsal surface of the otoglossal plate dorsal to the attachment of the rectus cervicis superficialis.

Hebosteoypsiloides originates from the dorsal surface of the second myoseptum posterior

to the second basibranchial. The fibers extend forward dorsal to the rectus cervicis profundus and then medially to insert onto the dorsal surface of the second basibranchial. The distal fibers in this species are strongly intermingled with those of the rectus cervicis profundus.

Hyoglossus. We have been unable to find a hyoglossus muscle in this species. The muscle which most nearly occupies the position of the hyoglossus is the posterior portion of the genioglossus, whose fibers extend in an anteroposterior direction for the most part. The lateral fibers of the genioglossus, however, do extend in a posterolateral direction as is seen in the hyoglossus of other salamanders.

OLYMPIC SALAMANDER.

Rhyacotriton olympicus (Gaige)

Ranodon olympicus Gaige, Occ. Papers Mus. Zool. Univ. Mich., No. 40, May 30, 1917, p. 2 pl. 1.

Rhyacotriton Dunn, Proc. N. Engl. Zool. Club, 7:56, 1920.

The Olympic Salamander is found in western Oregon and Washington. It has been collected in small springs and streams and among stones along the banks. This is a small ambystomid, occasionally attaining the size of 130 mm. It is characterized by its large, protuberant eyes, the horizontal diameter of which is equal to or greater than the length of the snout. The ground color is seal-brown with small white flecks distributed over the skin. The belly is yellow or orange in color. The tail is short and the gular fold is strongly developed. Costal grooves number 14 when the one in the axilla and the one in the groin are included. The vomerine teeth are formed into two strongly arched series that are separated at the midline. In the male, these series consist of fewer and larger teeth than in the female, and they extend in the male to a somewhat more lateral position in relation to the internal nares than in the female. The shape of the vent is different in the two sexes, the male being formed into squarish lobes which can readily be seen from either a dorsal or a ventral view, whereas in the female these lobes are considerably reduced in size.

HYOBRANCHIAL SKELETON (Fig. 2)

There is no ossification in the various components of the hyobranchium in this species (Table I).

The first basibranchial is pear-shaped, but narrow. The width-to-length ratio is smaller, in

Levator mandibulae has its origin and insertions essentially the same as that given in the section on general musculature of the family. The size, however, is a departure from the condition seen in the other species. This muscle is hypertrophied as noted by the fact that it can be seen as a bulge behind the eye when viewed from the ventral surface. It can also be seen in *Dicamptodon* from a ventral view, but not to the same extent in the other species included in this study. The depressor mandibulae, which opens the mouth, is not enlarged in *Rhyacotriton* and perhaps closing the jaw with a powerful stroke is relatively more important in this species than opening the mouth, whereas this may not be the case in other species.

Interosssaquadrata originates from the posterior surface of the quadrate, and ventral surface of the articulation between the ceratohyal and the quadrate. The middle fibers are attached, in addition, to the posterior tip of the mandible, and are hypertrophied to form a band of muscle extending directly mesiad. This muscle fans out over the venter of the throat and inserts into the fascia of the linea alba. The fibers from each side do not meet at the midline. It appears to be better developed and more easily separated from the subhyoideus than in other species of Ambystomidae.

Subhyoideus originates along the lateral margin of the ceratohyal beginning at a point about 1.0 mm from the posterior tip of this cartilage and extending forward about three-quarters of the distance to the anterior tip. It is a heavy muscle which is about as thick as the geniohyoideus, lying lateral and nearly parallel with the latter. The insertion is at a point on the posterior surface of the mandible immediately lateral to the origin of the geniohyoideus. This appears to be better developed than the subhyoideus in other species of the family.

Geniohyoideus is attached to the posterior surface of the mandible along a line which begins at the symphysis and extends laterally about 1.0 mm. The lateral fibers proceed directly caudad while the medial fibers are directed slightly mediad before turning in a caudal direction. This is a strong band of muscle, one on each side of the midline and overlapped ventrally by the intermandibularis posterior. It inserts onto the second basibranchial and in the tendonous inscription which separates this muscle from the rectus cervicis superficialis.

Genioglossus has two portions, a ventral part which is much the same as in other species, and a dorsal portion. Both of these appear to be slightly longer than in other species.

The ventral portion originates on the ventral and posterior surfaces of the mandible, beginning about 0.5 mm lateral to the symphysis and extending along this line of origin on the mandible for about 1.0 mm. The fibers converge to insert along the lateral edge of the ventral surface of the anterior end of the first basibranchial. It also sends a few fibers onto the otoglossal. This muscle is longer in this species than in others.

The dorsal portion originates from the same position as the ventral portion just described, except that it is immediately dorsal to the origin of the ventral portion. The lateral fibers pass caudad and slightly laterally to insert into the lateral part of the floor of the mouth dorsal to the subhyoideus belly. The medial fibers insert onto the ventral surface of the first basibranchial and the anterior edge of the first ceratobranchial. This muscle overlaps the radial cartilages ventrally.

Subarcualis rectus I attaches at its origin to the dorsal side of the posterior tip of the epi-branchial, wraps around it, and encloses it in a sheath. The fibers continue obliquely in an anteromesial direction and fan out over the expanded anterior end of the ceratohyal. The insertion of these fibers is along the anterior margin of the ceratohyal. The overall position of this muscle appears to be more posterior than in the other species, the anterior tip not being very far anterior to the posterior tip of the mandible. In addition, these two muscles lie in a position in which the anterior ends tend to point strongly toward each other.

Rectus cervicis superficialis originates medially from the dorsal surface of the sternum and laterally along the tendonous inscription separating this muscle from the rectus abdominus. There are two transverse inscriptions along its length between the sternum and the second basibranchial. A small section of the pericardium is visible between these two muscles at the midline. The fibers that extend forward from the second basibranchial insert along the posterior edge of the medial end of the first ceratobranchial and onto the posterior tip of the first basibranchial. The sternum in this species is reduced to a small triangle with one angle facing anteriorly.

Rectus cervicis profundus originates technically on the puboischium. It is a broad sheet of muscle extending along the ventral body wall and continuing forward at the level of the sternum as a flat band of muscle that is overlapped partially on its medioventral surface by the rectus cervicis superficialis. It turns mediad and

passes through the arch formed by the two ceratobranchials, and then forward dorsal to the first basibranchial to attach to the posterior edge of the otoglossal.

Hebosteoypsiloideus originates from the dorsal surface of the rectus cervicis muscles at the most anterior tendonous inscription of those inscriptions occurring between the sternum and the second basibranchial. It is thin and narrow and extends forward dorsal to the rectus cervicis profundus for a short distance, where it turns mediad across the rectus cervicis superficialis toward the second basibranchial, upon whose dorsal surface it inserts.

Hyoglossus originates on the dorsal surface of the anterior end of the first basibranchial and along the lateral margin of the dorsal surface of this cartilage. This small muscle is situated dorsal to the first basibranchial and ventral to the insertion end of the rectus cervicis profundus. The fibers extend laterally to insert onto the tip of the second radial and into the fascia at the sides of the base of the tongue.

RINGED SALAMANDER.

Ambystoma annulatum Cope

Amblystoma annulatum Cope, Proc. Amer. Philos. Soc., Vol. 23, 1886, p. 525.

This is a strikingly marked salamander with yellow spots and cross bars on a dark brown to black ground color. The cross bars on the trunk extend ventrad to the level of the legs, whereas those on the tail reach the ventral edge. The head is small and the tail long and slender. Total length rarely exceeds 203 mm. There are 15 costal grooves, counting one each in the axilla and groin. The vomerine teeth consist of two short series that lie obliquely forward between the internal nares to form an inverted V. Each consists of three rows of 7 to 11 small, blunt teeth. This species is abundant in parts of Arkansas and Missouri and appears to be a burrower, spending most of the year beneath the surface of the ground..

HYOBANCHIAL SKELETON (Fig. 3)

A definite center of ossification exists in the first basibranchial. This center is located in an anteromedial position, and constitutes a greater percentage of the total volume of the first basibranchial than in any of the other species (Table 1). There are definite lines of articulation between this cartilage and the first radials. These lines do not exist, however, between the first

Table 8. Average ratios of length of second ceratobranchial to length of first ceratobranchial.

Species	0	0.2	0.4	0.6	0.8	1.0	1.2
<i>Dicamptodon ensatus</i>							
<i>Rhyacotriton olympicus</i>							
<i>Ambystoma annulatum</i>							
<i>Ambystoma cingulatum</i>							
<i>Ambystoma gracile</i>							
<i>Ambystoma jeffersonianum</i>							
<i>Ambystoma mabeei</i>							
<i>Ambystoma macrodactylum</i>							
<i>Ambystoma maculatum</i>							
<i>Ambystoma talpoidum</i>							
<i>Ambystoma opacum</i>							
<i>Ambystoma texanum</i>							
<i>Ambystoma rosaceum</i>							
<i>Ambystoma tigrinum</i>							
<i>Ambystoma tigrinum melanostictum</i>							
<i>Ambystoma tigrinum nebulosum</i>							

basibranchial and the second radials. The first basibranchial is shaped like a slightly elongated shield. This structure is situated in a more posterior position in relation to the position of the mandible than in other species (Table 12).

There is no ossification in the first radial cartilages. These structures are thin and taper to a fine point. They do not attach to the anterior end of the ceratohyal and they are not segmented.

The second radials also are entirely cartilaginous. They articulate with the otoglossal cartilage at their distal tips. The otoglossal is a thin bar of cartilage forming an arch which is directed dorsally into the tongue.

The first ceratobranchial is devoid of bone. In relation to the length of the first basibranchial, this structure is exceeded in length only in *Rhyacotriton* and *A. cingulatum* (Table 5).

The epibranchial contains an ossified tip constituting about 12 percent of its total volume (Table 1), the remainder being cartilage. The first ceratobranchial is long in relation to the epibranchial, this ratio being exceeded only in *A. cingulatum* (Table 13). The articulation be-

tween the epibranchial and the first ceratobranchial is almost indistinguishable.

The second ceratobranchial is longer in relation to the length of the first ceratobranchial in this species than in the others (Table 8) and contains no bone.

The ceratohyal shows no ossification. The width of this structure in relation to its length is exceeded only in *Dicamptodon* and *A. texanum* (Table 14).

The second basibranchial has a shape not seen in most other ambystomids. A small, posteriorly directed arm exists in addition to the other three, and the lateral arms are slightly expanded at their tips. More than half of the structure is cartilage, the lateral arms being almost entirely chondrified (Table 1).

The ratio of mandible length to width is exceeded only by *Dicamptodon* and *A. mabeei*, although it is equalled by *A. maculatum* and *A. cingulatum* (Table 9).

MUSCULATURE

Intermandibularis posterior originates along the dorsomedial surface of the mandible. The fi-

bers lie transversely and insert into the broad linea alba at the midline of the throat. The linea alba is wider than in the other species studied. The genioglossus is visible at the point of the chin, as in most other species.

Interhyoideus posterior originates from the fascia which is attached to the lateral edge of the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule. The posterior fibers arise in the fascia cephalodorsalis. The insertion is into the skin and fascia of the gular fold and into the linea alba at the midline. The anterior fibers blend in with the posterior fibers of the interosssaquadrata.

Depressor mandibulae has its origin along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and the fascia cephalodorsalis. The fibers converge into a short, stout tendon which inserts onto the posterior tip of the mandible.

Levator mandibulae corresponds very closely to the description given in the section on general musculature.

Interosssaquadrata originates from the ventral surface of the hyoquadrate ligament and from the quadrate bone immediately anterior to this ligament. The fibers fan out over the ventral surface of the throat, with the anterior fibers extending anteromedially over the ventral surface of the subarcualis rectus I, and the posterior fibers extending posteromedially to parallel the fibers of the interhyoideus posterior. The insertion is into the linea alba.

Subhyoideus originates on the ventrolateral margin of the posterior tip of the ceratohyal. It is thin and delicate, especially at its insertion. The posterior fibers are difficult to distinguish from those of the interosssaquadrata. It lies over the ventral surface of the subarcualis rectus I and inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates along a line on the posterior edge of the mandible beginning at a point just lateral to the symphysis and extending laterally about 1.5 to 2.0 mm. This end is overlapped ventrally by the ventral portion of the genioglossus. The fibers extend directly caudad to insert on the second basibranchial cartilage.

Genioglossus originates along a line on the ventral surface of the mandible beginning at the symphysis and extending laterally over the ventral surface of the origin of the geniohyoideus. The fibers converge medially to form a strong band which contributes to the aponeurosis lingualis. Some of these fibers, in turn, continue distally to attach to the anterior end of the first basibranchial and to the otoglossal. Contraction

Table 9. Average ratios of mandible length to width.

Species	0	0.2	0.4	0.6	0.8	1.0	1.2
<i>Dicamptodon ensatus</i>							
<i>Rhyacotriton olympicus</i>							
<i>Ambystoma annulatum</i>							
<i>Ambystoma cingulatum</i>							
<i>Ambystoma gracile</i>							
<i>Ambystoma jeffersonianum</i>							
<i>Ambystoma mabeei</i>							
<i>Ambystoma macrodactylum</i>							
<i>Ambystoma maculatum</i>							
<i>Ambystoma talpoideum</i>							
<i>Ambystoma opacum</i>							
<i>Ambystoma texanum</i>							
<i>Ambystoma rosacum</i>							
<i>Ambystoma tigrinum</i>							
<i>Ambystoma tigrinum melanostictum</i>							
<i>Ambystoma tigrinum nebulosum</i>							

Table 10. Average ratios of distance between mental symphysis and posterior edge of intermandibularis posterior to distance between mental symphysis and pectoralis.

Species	0	.1	.2	.3	.4	.5	.6
<i>Dicamptodon ensatus</i>							
<i>Rhyacotriton olympicus</i>							
<i>Ambystoma annulatum</i>							
<i>Ambystoma cingulatum</i>							
<i>Ambystoma gracile</i>							
<i>Ambystoma jeffersonianum</i>							
<i>Ambystoma mabeei</i>							
<i>Ambystoma macrodactylum</i>							
<i>Ambystoma maculatum</i>							
<i>Ambystoma talpoideum</i>							
<i>Ambystoma opacum</i>							
<i>Ambystoma texanum</i>							
<i>Ambystoma rosaceum</i>							
<i>Ambystoma tigrinum</i>							
<i>Ambystoma tigrinum melanostictum</i>							
<i>Ambystoma tigrinum nebulosum</i>							

of this muscle therefore serves to advance both of these cartilages. The ventral portion of the genioglossus is large in this species, as compared to the same muscle in most of the other species investigated.

The dorsal portion originates along the mandible just dorsal to the origin of the ventral portion. This muscle spreads out in a fan shape over the floor of the mouth. The medial fibers extend across the dorsal surface of the tips of the first radials and continue distally to insert along the posterolateral edge of the second radials. The lateral fibers insert into the fascia of the floor of the mouth.

Subarcualis rectus 1 originates along the dorsal edge of the tip of the epibranchial. The fibers radiate around this cartilage and enclose it in a sheath. They then continue forward in a medialanterior direction. When they reach the junction between the epibranchial and the second ceratobranchial, they lose their sheath shape and come to lie in a ventral position over the first ceratobranchial and the ceratohyal. Anteriorly, they spread out over the expanded an-

terior end of the ceratohyal and insert along the latter's anterior edge.

Rectus cervicis superficialis originates from the dorsal surface of the sternum. The medial fibers attach to the second basibranchial and the lateral fibers form a thicker, narrower band which runs forward to insert along the posterior edge of the medial end of the first ceratobranchial. There are three transverse tendonous inscriptions in this muscle between the sternum and the second basibranchial.

Rectus cervicis profundus is actually an anterior continuation of the rectus abdominus. At the level of the sternum, this muscle extends anteriorly alongside of, and dorsal to, the rectus cervicis superficialis. Near its middle, the heboosteoypsiloideus can be seen along the border between the two rectus muscles. The rectus cervicis profundus becomes tendonous as it passes through the opening formed by the two ceratobranchials. This thin tendon then continues forward, dorsal to the first basibranchial, to attach to the medial section of the otoglossal. This tendon was seen only in this species and in *A. cingulatum*. The other species have fleshy insertions of this muscle on the otoglossal.

Heboosteoypsiloideus originates as a narrow band of muscle from the dorsal surface of the third inscription of the rectus cervicis profundus posterior to the second basibranchial. Its origin can be seen between the two rectus muscles. From here it extends forward dorsal to the medial edge of the rectus cervicis profundus and then turns medially to insert onto the dorsal surface of the central portion and anterior arm of the second basibranchial.

Hyoglossus originates on the dorsal surface of the anterior end of the first basibranchial and the adjacent fascia. Its fibers extend laterally and slightly posteriorly to attach along the posterior margin of the tip of the second radial. This is a small muscle.

RETICULATED SALAMANDER.

Ambystoma cingulatum Cope

Amblystoma cingulatum Cope, Proc. Ac. Nat. Sci. Phil., 1867, p. 205.

This is a medium-sized species, less than 102 mm in total length. The ground color is black and has many small, gray spots which form a reticulated pattern on the dorsal surfaces of the head, trunk, and tail. Along the sides, these spots are concentrated into narrow vertical lines between the 13-14 costal grooves. Vomerine teeth are found in two short series, one on either side of the midline, and each contains about seven

Table 13. Average ratios of length of first ceratobranchial to length of epibranchial.

Species	0	0.5	1.0	1.5
<i>Dicamptodon ensatus</i>				
<i>Rhyacotriton olympicus</i>				
<i>Ambystoma annulatum</i>				
<i>Ambystoma cingulatum</i>				
<i>Ambystoma gracile</i>				
<i>Ambystoma jeffersonianum</i>				
<i>Ambystoma mabeei</i>				
<i>Ambystoma macrodactylum</i>				
<i>Ambystoma maculatum</i>				
<i>Ambystoma talpoideum</i>				
<i>Ambystoma opacum</i>				
<i>Ambystoma texanum</i>				
<i>Ambystoma rosaceum</i>				
<i>Ambystoma tigrinum</i>				
<i>Ambystoma tigrinum melanostictum</i>				
<i>Ambystoma tigrinum nebulosum</i>				

branchial in a muscular sheath. This sheath continues anteromedially to the level of the ceratohyal where it leaves the first ceratobranchial and spreads out over the ventral surface of the ceratohyal. It inserts along the forward margin of the expanded anterior end of the ceratohyal.

Rectus cervicis superficialis originates on the dorsal surface of the sternum and extends forward ventral to the pericardium forming a thin, broad sheet. Between the sternum and the second basibranchial there are three transverse inscriptions. The portion which continues forward from the second basibranchial is narrower and thicker than the posterior portion. The anterior portion attaches to the anterior edge of the lateral tip of the second basibranchial and the adjacent tendonous inscription, and the fibers proceed anteromedially to insert along the posterior edge of the medial end of the first ceratobranchial and along the lateral edge of the posterior tip of the first basibranchial.

Rectus cervicis profundus lies dorsolateral to the rectus cervicis superficialis, and its shape is essentially the same as the latter. It is actually a continuation of the rectus abdominus, and so the

origin is, technically, the puboischium. The portion extending anteriorly from the second basibranchial is also narrower and thicker than the posterior portion. This anterior portion passes between the ceratobranchials and dorsal to the first basibranchial. At this point, the fibers converge into a thin, narrow tendon which inserts onto the medial section of the otoglossal. The tendon is 1.5 to 2.0 mm in length.

Hebosteoypsiloides originates as a thin, narrow muscle from the dorsal surface of an inscription on the rectus cervicis profundus. The particular inscription is the second one posterior to the second basibranchial. The fibers extend directly anterior at first, and then turn medially, dorsal to the rectus cervicis superficialis, and insert onto the dorsal surface of the second basibranchial.

Hyoglossus is small, being slightly less than 1.0 mm in length. It originates from the dorsal surface of the anterior end of the first basibranchial and extends laterally to insert on the tip of the second radial.

NORTHWESTERN SALAMANDER.

Ambystoma gracile (Baird)

Siredon gracilis Baird, Pacif. R. R. Rep., Vol. 10, Williamson's Route, Pt. 4, No. 4, 1859, p. 13, pl. 44, fig. 2.

The range of this species is from northern California to British Columbia. It is found in damp habitats and has been collected rather frequently under logs and bark, except during the breeding season, at which time it resorts to ponds and slow streams. It is less than 195 mm in total length. Probably the most distinguishing characteristic is the large, raised, kidney-shaped parotid glands behind the eyes. There is also a glandular region along the dorsal ridge of the tail. The color is dark brown; however, the head and tail may be slightly lighter. Some may be marked dorsally with yellow spots or flecks. There are 11 costal grooves, counting one each in the axilla and groin. The legs are large and strong. In contrast to most *Ambystoma* the ventral edge of the tail tends to be knifelike, while the dorsal edge is rounded. Vomerine teeth are in a transverse line which may be broken into three or four series.

HYOBRANCHIAL SKELETON (Fig. 5)

The first basibranchial is a rod-shaped structure lying in the center of the area outlined by the mandible. It contains no bone and has definite lines of articulation with the radials.

The first radials are moderately long and attached to the anterior edge of the ceratohyals by a ligament. They contain no bone.

The second radials are thin, cartilaginous rods that curve dorsally to attach to the annular-shaped otoglossal. Neither the second radial nor the otoglossal cartilages contains bone.

There is also a lack of bone in the first ceratobranchial, the second ceratobranchial, the epibranchial, and the ceratohyal. The only element which is ossified is the second basibranchial, which averages 78 percent bone for the two specimen studied (Table I).

The ceratohyals are wide, being exceeded in a width-to-length ratio only by *Dicamptodon*, *A. annulatum*, *A. mabeei*, and *A. texanum* (Table 14).

The second basibranchial, as mentioned above, is the only ossified portion of the hyobranchium, the cartilage being located on the tips of the two lateral arms. This structure is strongly triradiate, the anterior arm being almost as long as the two lateral ones.

Only in three cases have we found a smaller ratio of mandible length to mandible width than in *A. gracile*. Those three are *A. talpoideum*, *A. t. nebulosum*, and *A. t. melanostictum*, the shortest being found in *A. talpoideum* (Table 9).

MASCULATURE (Fig. 5)

Intermandibularis posterior has its origin along the dorsomedial surface of the rami of the mandible. The fibers extend transversely to insert into the fascia of the linea alba. A small area at the point of the chin is open so that the ventral portion of the genioglossus is visible. The posterior fibers overlap the anterior end of the interossaquadrata. The anterior fibers of this muscle are continuous across the midventral line. They constitute a band that is 2.0 mm wide at the midline.

Interhyoideus posterior originates in fascia that is attached to the posterior tip of the mandible, quadrate, squamosal, and the otic capsule. The posterior fibers arise from the fascia cephalodorsalis. The fibers spread out as they pass obliquely caudomedially to insert along the skin of the gular fold and the midventral line of fascia.

Depressor mandibulae takes its origin from the squamosal bone, attaching along its entire posterolateral surface except for the ventral 1-2 mm. It also arises from the lateral surface of the otic capsule and from the fascia cephalodorsalis. The fibers converge onto the posterior tip of the mandible.

Levator mandibulae corresponds to the description given earlier in the general section on musculature except that the fibers of the levator mandibulae externus and the levator mandibulae posterior intermingle considerably, making it difficult to separate these two portions.

Interossaquadrata originates from the ventral surface of the quadrate just anterior to the hyoquadrate ligament and from the ventral surface of the hyoquadrate ligament itself. A few fibers are also attached to the ventral aspect of the posterior tip of the ceratohyal. The anterior fibers extend anteromedially over the subarcualis rectus I, the medial fibers extend directly medially, and the posterior fibers extend caudomedial. These posterior fibers lie parallel with the anterior fibers of the interhyoideus posterior. It inserts into the median raphe of the throat.

Subhyoideus attaches along the ventrolateral margin of the posterior 2-3 mm of the ceratohyal. It becomes a thin muscle as it fans out over the anterior end of the subarcualis rectus I and is easily removed from the intermandibularis posterior as the deeper layers are exposed. It is readily distinguished from the interossaquadrata

Table 14. Average width to length ratios of ceratohyal.

Species	0	.1	.2	.3	.4
<i>Dicamptodon ensatus</i>					
<i>Rhyacotriton olympicus</i>					
<i>Ambystoma annulatum</i>					
<i>Ambystoma cingulatum</i>					
<i>Ambystoma gracile</i>					
<i>Ambystoma jeffersonianum</i>					
<i>Ambystoma mabeei</i>					
<i>Ambystoma macrodactylum</i>					
<i>Ambystoma maculatum</i>					
<i>Ambystoma talpoideum</i>					
<i>Ambystoma opacum</i>					
<i>Ambystoma texanum</i>					
<i>Ambystoma rosaceum</i>					
<i>Ambystoma tigrinum</i>					
<i>Ambystoma tigrinum melanostictum</i>					
<i>Ambystoma tigrinum nebulosum</i>					

at its origin but blends in with the latter near the insertion. The insertion is by way of the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from the posterior edge of the mandible along a line which begins about 1.5 mm lateral to the symphysis and extends laterally for approximately 1.0 mm. The anterior end of this muscle is overlapped along its medial edge by the ventral portion of the genioglossus. The lateral fibers extend directly caudad, whereas the medial fibers lie in a medio-caudal direction for a short distance before continuing directly caudad. Insertion is onto the second basibranchial cartilage, with the lateral fibers attaching into the tendonous inscription of the rectus cervicis superficialis.

Genioglossus originates in two parts, the ventral portion from the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally about 2.5-3.0 mm. The fibers extend caudomedially for a short distance, overlapping the anteromedial end of the geniohyoideus as indicated above. Insertion is into the aponeurosis lingualis. A few fibers also continue on to the first basibranchial and the otoglossal. This latter portion is undivided.

The dorsal portion of the genioglossus originates along the posterior surface of the mandible from the symphysis to a point about 3-4 mm lateral from the symphysis. The lateral fibers proceed dorsal to the tip of the first radial and attach into the fascia that forms the floor of the mouth. The medial fibers insert onto the posterior edge of the lateral half of the second radial.

Subarcualis rectus I originates along the dorsal edge of the tip of the epibranchial. These fibers form a strong sheath around the epibranchial and then extend forward over the ventral surface of the ceratohyal. The insertion is along the anterior margin of the expanded end of the ceratohyal.

Rectus cervicis superficialis originates along the lateral edge of the dorsal surface of the sternum and from the tendonous inscription which separates this muscle from the rectus abdominus. It inserts onto the dorsal surface of the second basibranchial and then extends forward onto the posterior end of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is actually a continuation of the rectus abdominus. It continues forward at the level of the sternum as a flat band and is situated dorsolaterally with respect to the rectus cervicis superficialis. The fibers turn slightly medially at the level of the second basi-

branchial and then pass through the opening between the ceratobranchials, where they extend dorsal to the first basibranchial and the hyoglossus and finally inserts along the posterior edge of the otoglossal.

Hebosteopsiloideus consists of a narrow band of fibers arising from the dorsal surface of the second myoseptum of the rectus cervicis profundus posterior to the second basibranchial. It lies along the dorsomedial edge of the rectus cervicis profundus and extends forward and medially to insert along the lateral edge of the dorsal surface of the anterior arm of the second basibranchial cartilage. Like *A. talpoideum* it makes no insertion onto the lateral arms of the second basibranchial.

Hyoglossus originates from the dorsal surface of the anterior end of the first basibranchial and along the lateral edge of this cartilage to the base of the second radial. The anterior fibers extend laterally and posteriorly to insert onto the posterolateral edge of the second radial. The posterior fibers extend more directly lateral and insert into the fascia adjoining the second radial.

JEFFERSON'S SALAMANDER.

Ambystoma jeffersonianum (Green)

Salamandra jeffersoniana Green, Contr. Maclur. Lyc., Vol. 1, No. 1, Jan. 1827, p. 4, pl. 1, fig. 1.

This is a rather slender species which may attain a length of 185 mm. Adults have faint bluish markings on the sides. The ground color is dark brown. There are 12 costal grooves and a prominent gular fold. Toes are very long and slender. The vomerine teeth form a transverse line that is interrupted back of the internal nares and occasionally at the midline. The range extends from Hudson Bay south to Virginia. It is found westward to Wisconsin, Illinois, and Arkansas.

HYOBRANCHIAL SKELETON (Fig. 6)

The first basibranchial is shaped like an elongated pear when viewed from a ventrodorsal direction and is a flat oval when viewed in cross section. It contains a central mass of bone amounting to about 37 percent of the total volume (Table 1). Definite lines of articulation exist between this structure and the radials. There are only four other species in which the first basibranchial is more anteriorly located (Table 12).

The first radial cartilages contain no bone and are attached to the anterior tips of the ceratohyals by small ligaments. These radials are

the fascia of the intermandibularis posterior. This muscle is also very delicate and is easily removed inadvertently with the intermandibularis posterior.

Geniohyoideus takes its origin from a short line along the posterior surface of the mandible, the line beginning about 1.5 mm lateral to the symphysis and extending laterally for approximately 2.5 to 3.0 mm. The lateral fibers coming from this line extend directly caudad, whereas the medial fibers extend medially for a short distance and then proceed directly caudad. This muscle appears as a band proceeding between the chin and the second basibranchial into which it inserts. A few fibers also insert laterally into the tendonous inscription alongside of the second basibranchial.

Genioglossus originates in two parts, the ventral along a line on the posterior surface of the mandible. This line begins about 2.0 mm lateral to the symphysis and extends laterally along the mandible for about another 2.0 mm. This origin is immediately ventral to the medial half of the origin of the geniohyoideus. It inserts into the aponeurosis lingualis, with a few fibers continuing on to the first basibranchial and the otoglossal.

The origin of the dorsal portion of the genioglossus is along a line on the posterior surface of the mandible just dorsal to the origin of the geniohyoideus. The fibers extend laterally as well as caudally to insert into the floor of the mouth. The medial fibers extend caudally to the aponeurosis lingualis and then obliquely in a caudolateral direction to attach to the tip of the second radial.

Subarcualis rectus 1 originates on the posterior tip of the epibranchial and forms a sheath around the cartilage. It also extends out onto the ventral surface of the ceratohyal where it inserts along the anterior margin. The two ceratohyals almost touch each other at their anterior ends. They overlap the lateral edge of the anterior half of the first basibranchial, and these muscles, therefore, are also almost touching at that point.

Rectus cervicis superficialis originates on the posterior edge of the dorsal surface of the sternum and from the tendonous inscription which separates this muscle from the rectus abdominus. These fibers extend forward over the pericardium attaching to the second basibranchial and then continuing forward to insert onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial cartilage.

Rectus cervicis profundus extends forward from the sternum as a stout band of muscle

situated alongside of the rectus cervicis superficialis. It partially overlaps the latter dorsally as the two muscles move forward to the level of the second basibranchial. The archway between the two ceratobranchials serves as a passageway for this muscle as it continues forward to finally attach to the posterior edge of the otoglossal.

Hebosteoypsiloideus originates from one of the myosepta of the rectus cervicis profundus. The particular myoseptum is the second one posterior to the second basibranchial, from whose dorsal surface it arises as a narrow band and proceeds directly anteriorly. After a short distance, it turns medially to insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a tiny muscle originating on the dorsal surface and lateral margin of the anterior end of the first basibranchial. It extends laterally to insert on the tip of the second radial cartilage and into the adjoining fascia.

MABEE'S SALAMANDER.

Ambystoma mabeei (Bishop)

Ambystoma mabeei Bishop, Journ. Elisha Mitchell Sci. Soc., Vol. 43, No. 3-4, 1928, p. 157.

This species inhabits rotted logs and bark in moist areas of the Carolinas and Georgia. The color above is deep brown, and the sides are covered with white or grayish flecks which become indistinct as they approach the dorsal surface, where they appear to be overlain with darker pigment. This salamander resembles *A. texanum* in size, color, and shape of the head. It reaches 102 mm in total length. The vomerine teeth form a transverse line that is broken back of the internal nares. There are 13 costal grooves, counting two that come together in the groin and one in the axilla.

HYOBRANCHIAL SKELETON (Fig. 7)

The first basibranchial cartilage in this species is pear-shaped when viewed from its ventral surface. It is a flat oval in cross section. The core is bony and is surrounded on all sides by a layer of cartilage. The average percent of ossification is 37. The first basibranchial is situated in a rather posterior position as compared to its position in other species, being exceeded in this respect only by *A. annulatum*, *A. cingulatum*, and *Rhyacotriton* (Table 12). The length of the first basibranchial as compared to the total length of the hyobranchium is greater in this species than in others except *A. talpoideum*, *A. opacum*, and *Rhyacotriton* (Table 4).

The first radials are entirely cartilaginous and are relatively longer than in the other species ex-

Table 16. Average ratios of epibranchial length to length of first branchial arch.

Species	0	.1	.2	.3	.4	.5	.6
<i>Dicamptodon ensatus</i>							
<i>Rhyacotriton olympicus</i>							
<i>Ambystoma annulatum</i>							
<i>Ambystoma cingulatum</i>							
<i>Ambystoma gracile</i>							
<i>Ambystoma jeffersonianum</i>							
<i>Ambystoma mabeei</i>							
<i>Ambystoma macrodactylum</i>							
<i>Ambystoma maculatum</i>							
<i>Ambystoma talpoideum</i>							
<i>Ambystoma opacum</i>							
<i>Ambystoma texanum</i>							
<i>Ambystoma rosaceum</i>							
<i>Ambystoma tigrinum</i>							
<i>Ambystoma tigrinum melanostictum</i>							
<i>Ambystoma tigrinum nebulosum</i>							

cept *Dicamptodon* and *Rhyacotriton* (Table 6). Their tips are attached to the anterior tips of the ceratohyals by a short ligament, and a definite line exists at their base, indicating the point of articulation with the first basibranchial.

The second radials attach to the sides of the first basibranchial and then taper to a fine point in an anterodorsal direction. These distal tips articulate with the otoglossal, which is an annular-shaped rod of cartilage arched forward and dorsad into the tongue.

There is no bone in the first ceratobranchial. It is flattened dorsoventrally and forms a smooth arch which is continued distally by the epibranchial. The epibranchial averages 58 percent ossification, the bony portion constituting the distal end (Table 1).

The second ceratobranchial is entirely cartilage. Its distal end articulates with the medial side of the epibranchial at a point well posterior to the first ceratobranchial-epibranchial articulation.

The ceratohyal is longer in relation to the total length of the hyobranchium in this species

than in other ambystomids, except for *Rhyacotriton* (Table 19). The average percent ossification for this structure is 6.8 (Table 1).

Only the extreme tips of the lateral arms of the second basibranchial are cartilage. The majority of the volume of this structure (63 percent) is bone. The anterior arm is much shorter than either of the lateral arms.

The ratio of the mandible length to mandible width is exceeded only by *Dicamptodon* (Table 9).

MUSCULATURE (Fig. 7)

Intermandibularis posterior originates on the dorsomedial surface of the mandible, and the fibers extend medially to the linea alba where they insert. The ventral portion of the genioglossus is visible at the point of the chin. The interossaquadrata and subhyoideus muscles are partly overlapped ventrally by this muscle. In contrast to most of the other species, the posterior fibers in this salamander extend almost directly transversely with only a slight deviation caudad.

Interhyoideus posterior is broad in this species, the anterior fibers extending directly medially to the midline. The origin is by way of fascia which attaches to the posterior tip of the mandible, the squamosal, the quadrate, and the otic capsule and is also continuous with the fascia cephalodorsalis. The fibers pass over the mandible tip, cross the middle section of the subarcualis rectus I and insert into the skin and fascia of the gular fold and into the linea alba midventrally.

Depressor mandibulae fibers arise from the fascia cephalodorsalis, dorsal end of the squamosal and the posterior and ventral surfaces of the otic capsule. They converge to a short, tough tendon which inserts onto the posterior tip of the mandible.

Levator mandibulae consists of four portions as outlined in the general section on musculature.

Interossaquadrata originates on the posterior surface of the quadrate and the ventral surface of the ceratohyal-quadrate articulation. The fibers lie in an anteromedial direction. They insert into the fascia of the linea alba as it proceeds posteriorly from the intermandibularis posterior. This muscle is narrower in this species than in the others since there are no fibers extending in a posteromedial direction.

Subhyoideus originates from the ventral surface of the posterior tip of the ceratohyal. The fibers at the origin are dorsal to the interossaquadrata, but they proceed in a more anterior

direction than those of the interossaquadrata, resulting in a side-by-side location of their distal ends. From a point about midway along the length of these muscles, they appear as a single muscle since no definite line of separation is visible between them. The subhyoideus inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from the posterior surface of the mandible along a line that begins at the symphysis and extends about 1.5 mm laterally. The medial fibers pass around the genioglossus at the point where the fibers of the latter converge and pass dorsad. From this point posteriorly, the fibers proceed directly caudad to insert onto the anteroventral surface of the second basibranchial and into the inscription that is continuous with the latter's lateral arm.

Genioglossus originates in two parts. The ventral portion arises along the ventral surface of the mandible, beginning at the symphysis and extending laterally about 1.5 mm. The origin is ventral to the origin of the geniohyoideus. The fibers converge toward the midline where they attach to the aponeurosis lingualis. From this point, they extend directly caudad and, together with the medial fibers of the dorsal genioglossus, form a broad sheet of muscle contributing substantially to the anterior half of the floor of the mouth. The insertion is onto the anterior edge of the first basibranchial and onto the otoglossal.

The origin of the dorsal genioglossus is immediately dorsal to the origin of the ventral portion. The fibers tend to fan out as they proceed caudad and in so doing form the broad sheet of muscle mentioned above. The medial fibers attach to the tip of the second radial. The lateral fibers insert into the fascia of the mouth floor at the base of the tongue.

Subarcualis rectus 1 originates from the dorsal edge of the epibranchial cartilage. The fibers form a sheath of muscle which completely encloses the epibranchial and then moves anteriorly parallel with the ceratohyal. At the level of the articulation between the epibranchial and the second ceratobranchial, the sheath opens up medially to permit the entrance of the second ceratobranchial into the sheath. From this point anteriorly, the muscle gradually loses its sheath-shape and comes to lie on the ventral surface of the ceratohyal. It inserts onto the anterior edge of this cartilage.

Rectus cervicis superficialis originates from the lateral half of the dorsal surface of the sternum and from the tendonous inscription that extends laterally from the sternum. There are three myosepta between the sternum and the second basibranchial. The omohyoideus arises along the

lateral margin of this muscle between the first two of these myosepta. The rectus cervicis superficialis lies dorsal to the coracoids and ventral to the pericardium. A portion of the pericardium can be seen along the midventral line between these two muscles. The medial two-thirds of the fibers attach to the second basibranchial, but only the lateral half of these continues forward together with the remainder of the fibers to insert onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is actually a forward continuation of the rectus abdominus and its origin is, therefore, from the puboischium of the pelvic girdle. There are three myosepta along the course of this muscle between the sternum and the insertion. It is situated in a position dorsal and lateral with respect to the rectus cervicis superficialis. The profundus is basically a thin, broad muscle, but the fibers become compacted into a thicker and narrower muscle belly at the level of the hyobranchium. The medial half of the opening between the ceratobranchials serves as a passageway through which the fibers pass. From this point, they proceed forward, dorsal to the first basibranchial and the second radial. They finally insert onto the otoglossal at a point well anterior to the first basibranchial.

Hebosteoypsiloideus is a narrow muscle which originates from the second tendonous inscription of the rectus cervicis profundus, posterior to the second basibranchial. It extends forward dorsal to the rectus cervicis profundus and then crosses over medially to insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle seemingly hypertrophied in this species, as compared to the same muscle in other species. It originates on the dorsal surface of the anterior end of the first basibranchial and from the dorsal surface of the articulation between the first radial and the first basibranchial. The fibers converge slightly so that the insertion is narrower than the origin. They wrap around the ventral aspect of the tip of the second radial and insert along the latter's posterior edge.

LONG-TOED SALAMANDER.

Ambystoma macrodactylum Baird

Ambystoma macrodactyla Baird, Journ. Ac. Nat. Sci. Phila., Ser. 2, Vol. I, 1849, p. 292.

This species has been found in breeding ponds, beneath rocks that are just above the waterline of these ponds, and beneath the loose bark of fallen trees. It is not unusual to find

to the posterior tip of the mandible just anterior to the insertion of the depressor mandibulae. By way of fascia, this muscle also attaches to the lateral surface of the mandible tip, the lateral surface of the mandibulo-quadrate articulation, and the lateral surface of the ventral end of the squamosal. The fibers fan out over the posterior throat region to insert along the skin of the gular fold and into the midventral line of fascia, the linea alba.

Depressor mandibulae originates from the posterolateral edge of the squamosal except for the ventral 1-2 mm, which attaches to the fascia cephalodorsalis and the lateral surface of the otic capsule. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as that description given in the general musculature section of this paper.

Interossequadrata originates on the posterior surface of the quadrate, the ventral surface of the articulation of the ceratohyal and the quadrate, and from the posterior tip of the mandible. The fibers spread out over the throat with the

anterior fibers directed anteromedially and the posterior fibers in a posteromedial direction. The insertion is into the fascia of the linea alba.

Subhyoideus originates along the anteroventral edge of the posterior tip of the ceratohyal. It fans out as it proceeds forward over the throat and inserts into the dorsal fascia of the intermandibularis posterior. The posterior fibers blend in with those of the interossequadrata so that no border is distinguishable between these two muscles.

Geniohyoideus originates along a line on the posterior surface of the mandible which begins about 1.0 mm lateral to the symphysis and extends laterally about 1.0 additional mm. The fibers pass caudad and mediad, and then directly caudad to form a stout band on either side of the midline. It inserts onto the second basibranchial and in the tendonous inscription that extends laterally from the arms of the second basibranchial.

Genioglossus has a ventral portion which originates on the ventral and posterior surfaces of the mandible, beginning at the symphysis and extending laterally approximately 1.0 mm. The fibers overlap the anterior end of the geniohyoideus and converge medially to attach themselves into the aponeurosis lingualis before continuing to attach to the anterior tip of the first basibranchial and the otoglossal.

The lateral fibers are directed laterally as well as caudad and form a thin sheet of muscle which inserts into the fascia forming the floor of the mouth. These fibers lie in a dorsolateral position with respect to the anterior end of the ceratohyal. The medial fibers proceed directly caudad into the aponeurosis lingualis and then to the tip of the second radial.

Subarcualis rectus I originates on the tip of the epibranchial cartilage, from which its fibers wrap around and enclose the latter in a muscular sheath and then continue forward over the ventral surface of the ceratohyal. The insertion is along the ventral surface of the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates along the dorsal surface of the posterior end of the sternum and the tendonous inscription which separates this muscle from the rectus abdominus. The fibers extend forward ventral to the pericardium. In this species there is a large section of the pericardium which is exposed at the midline between the two rectus cervicis superficialis muscles. The second basibranchial is attached to this muscle and serves as a landmark between the thin, broad portion of the muscle and the anterior portion which becomes thick and nar-

Table 18. Average ratios of anterior to posterior length to second basibranchial to width of second basibranchial.

Species	0	.1	.2	.3	.4	.5	.6
<i>Dicamptodon ensatus</i>							
<i>Rhyacotriton olympicus</i>							
<i>Ambystoma annulatum</i>							
<i>Ambystoma emgulatum</i>							
<i>Ambystoma gracile</i>							
<i>Ambystoma jeffersonianum</i>							
<i>Ambystoma mahoei</i>							
<i>Ambystoma macrodactylum</i>							
<i>Ambystoma maculatum</i>							
<i>Ambystoma talpoidum</i>							
<i>Ambystoma opacum</i>							
<i>Ambystoma texanum</i>							
<i>Ambystoma rosaceum</i>							
<i>Ambystoma tigrinum</i>							
<i>Ambystoma tigrinum melanostictum</i>							
<i>Ambystoma tigrinum nubilosum</i>							

row. This anterior portion inserts onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the ceratobranchial.

Rectus cervicis profundus at the level of the sternum extends forward alongside of and deep to the rectus cervicis superficialis. After passing dorsal to the omohyoideus, it turns slightly mediad and proceeds through the opening between the ceratobranchials to insert onto the posterior edge of the otoglossal.

Hebosteocypsiloides originates as a narrow muscle on the dorsal surface of the rectus cervicis profundus. It is separated from the latter only by careful dissection since the fibers of these two muscles lie parallel with each other. It is from the second myoseptum posterior to the second basibranchial that this muscle arises. It crosses the rectus cervicis superficialis and then inserts onto the dorsal surface of the second basibranchial.

HyoGLOSSUS is a small muscle situated between the dorsal surface of the first basibranchial and the ventral surface of the rectus cervicis profundus. It originates along the dorsolateral

edge of the first basibranchial between the anterior tip and the base of the second radial. The anterior fibers extend obliquely in a posterolateral direction whereas the posterior fibers extend directly laterad and converge with the former to insert onto the posterolateral edge of the second radial as it curves dorsad into the tongue.

SPOTTED SALAMANDER.

Ambystoma maculatum (Shaw)

Lacerta maculata Shaw, Gen. Zool., Vol. 3, Pt. 1, 1802, p. 304.

The spotted salamander is distinguished by a row of large, round, yellow or orange spots occurring on either side of the middorsal line. The ground color is a deep bluish black. Males are usually more slender than females, and the former are readily recognized in the breeding season by the swollen vent. Total length reaches 206 mm. There are usually 12 costal grooves, a prominent gular fold, and, in this species, larger legs. The vomerine teeth extend across the roof of the mouth in a smoothly curved line immediately behind the internal nares. This line is sometimes interrupted at the midline and in back of the internal nares. The geographical range is from Nova Scotia to Wisconsin and southward to Florida, Louisiana, and Texas. They are found in ponds, slow moving streams, or temporary pools which offer spring breeding sites.

Table 19. Average ratios of length of ceratohyal to total length of hyobranchium.

Species	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
<i>Dicamptodon ensatus</i>											
<i>Rhyacotriton olympicus</i>											
<i>Ambystoma umulatum</i>											
<i>Ambystoma cingulatum</i>											
<i>Ambystoma gracile</i>											
<i>Ambystoma jeffersonianum</i>											
<i>Ambystoma mabeei</i>											
<i>Ambystoma macrodactylum</i>											
<i>Ambystoma maculatum</i>											
<i>Ambystoma talpoderum</i>											
<i>Ambystoma opacum</i>											
<i>Ambystoma texanum</i>											
<i>Ambystoma rosaceum</i>											
<i>Ambystoma tigrinum</i>											
<i>Ambystoma tigrinum melanostictum</i>											
<i>Ambystoma tigrinum nebulosum</i>											

HYOBRANCHIAL SKELETON (Fig. 9)

The first basibranchial is a pear-shaped structure when viewed ventrally and has a central core of bone. In cross section it is flat oval in shape. The bone constitutes an average of about 25 percent of its volume (Table I). There are lines of articulation visible between the first basibranchial and the radials.

The first radials are short in relation to the length of the first basibranchial. The only other species with a smaller ratio of length of first radial to length of first basibranchial is *A. cingulatum* (Table 6). No bone is found in these structures.

The second radials articulate with the otoglossal at their distal tips. The otoglossal forms a thin arch of cartilage extending dorsad into the tongue.

The first ceratobranchials are nearly straight, the only prominent curve in the first branchial arch occurring in the anterior half of the epi-branchial. There is no ossification in either ceratobranchial.

The epibranchial is ossified at its tip, the ossification making up an average of 32 percent of the total volume (Table 1). The width of this element is uniform along most of its length except near the tip where it tapers abruptly to a point.

The ratio of the lengths of the second ceratobranchial to the first ceratobranchial is high in this species, being exceeded only by *A. annulatum* (Table 8). This element is unossified.

The posterior tip of the ceratohyal is ossified and constitutes an average of 10.6 percent of the total volume (Table 1). The anterior tips overlap slightly at the midline.

The lateral arms of the second basibranchial are much longer than the anterior arm, and it is on these lateral tips that the cartilage is found. This cartilage constitutes 27 percent of the total (Table 1).

The mandible is longer than it is wide, the ratio of length to width averaging 1.06 for the five specimens of *A. maculatum* used in this study (Table 9).

MUSCULATURE (Fig. 9)

Intermandibularis posterior originates along the dorsomedial surfaces of the rami of the mandible. There is a small opening at the angle of the chin through which the genioglossus can be seen. This muscle overlaps the anterior end of the interossaquadrata and the anterior portion of the subhyoideus. The fibers pass, basically, in a transverse direction to the midventral line where they insert. There is no broad fascial sheet in this species occupying the midventral line as is seen in most other species.

In one of five specimens the anterior fibers of the intermandibularis posterior were continuous across the midline. This band was 0.7 mm wide at the midventral line.

Interhyoideus posterior originates on the fascia cephalodorsalis and on the posterior tip of the mandible immediately medial and anterior to the insertion of the depressor mandibulae. The majority of this muscle attaches by way of a fascial sheet to the lateral surface of the tip of the mandible, the lateral surface of the articulation between the mandible and the quadrate, and the lateral surface of the ventral end of the squamosal. This muscle inserts into the gular fold and midventral fascia of the throat.

Depressor mandibulae originates from the fascia cephalodorsalis, the lateral surface of the otic capsule, and the dorsal half of the lateral surface of the squamosa. The fibers converge to insert onto the posterior tip of the mandible.

Levator mandibulae has its origin and insertion essentially as in the description given in the section on general musculature.

Interossaquadrata originates from the posterior surface of the quadrate and the ventral surface of the articulation between the quadrate and the ceratohyal. The most posterior fibers also attach to the posterior tip of the mandible and lie ventral to the other fibers of this muscle. These ventral fibers extend caudomesially whereas the dorsal fibers extend anteromesially. The insertion is into the linea alba as it continues caudad from the intermandibularis posterior.

Subhyoideus originates from the dorsum of the posterior or distal tip of the ceratohyal and inserts into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates along the posterior surface of the mandible along a line beginning just lateral to the symphysis and extends laterally approximately 3.0 mm, deep to the ventral portion of the genioglossus. This muscle is narrower anteriorly than posteriorly, and consequently the genioglossus is exposed along the midline in this species. There are some deep fibers which attach to the aponeurosis lingualis and extend posteriorly with the remainder of the muscle. The muscle inserts onto the second basibranchial and into the tendonous inscription which separates this muscle from the rectus cervicis superficialis.

Genioglossus has a ventral portion which originates on the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally for about 3.0 mm. The fibers extend in a caudomedial direction to form a small triangular-shaped muscle. This portion of the genioglossus overlaps the anterior end of the geniohyoideus. The insertion is into the aponeurosis lingualis which continues caudad to attach to the anterior end of the first basibranchial cartilage. A few fibers continue along in association with the aponeurosis lingualis and insert onto the otoglossal.

The dorsal portion of this muscle attaches along the posterior edge of the mandible beginning at a point on the mandibular symphysis and extending laterally for about 2.0 mm. The fibers fan out as a thin sheet which contributes to the anterior floor of the mouth. The medial fibers extend caudad to insert onto the posterior edge of the second radial tip, while the lateral fibers continue caudad and laterally to attach into the fascia lateral to the base of the tongue. The aponeurosis lingualis, in this as well as most other species of this family, sends a slip onto the

Table 20. Average ratios of length of first basibranchial to total length of first branchial arch.

Species	0	.1	.2	.3	.4
<i>Dicamptodon ensatus</i>					
<i>Rhyacotriton olympicus</i>					
<i>Ambystoma annulatum</i>					
<i>Ambystoma cingulatum</i>					
<i>Ambystoma gracile</i>					
<i>Ambystoma jeffersonianum</i>					
<i>Ambystoma mabeei</i>					
<i>Ambystoma macrodactylum</i>					
<i>Ambystoma maculatum</i>					
<i>Ambystoma talpoideum</i>					
<i>Ambystoma opacum</i>					
<i>Ambystoma texanum</i>					
<i>Ambystoma rosaceum</i>					
<i>Ambystoma tigrinum</i>					
<i>Ambystoma tigrinum melanostictum</i>					
<i>Ambystoma tigrinum nebulosum</i>					

first ceratobranchial where the latter articulates with the first basibranchial. It also sends fibers onto the dorsal surface of the base of the first ceratobranchial and the lateral portion of the dorsal surface of the posterior end of the first basibranchial.

Rectus cervicis profundus is extended forward alongside and dorsal to the rectus cervicis superficialis. At the level of the second basibranchial, it begins to turn medially and become thicker and narrower. It passes through the archway formed by the two ceratobranchials and continues forward dorsal to the first basibranchial to its insertion on the posterior edge of the otoglossal cartilage.

Hebosteoupsiloides originates from the dorsal surface of the most posterior inscription on the rectus cervicis profundus. It extends forward dorsal to the latter until, at the level of the omohyoideus, it turns medially to cross the rectus cervicis superficialis dorsally and insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a small triangular-shaped muscle which originates on the dorsal surface of the anterior end of the first basibranchial and along the lateral edge of the dorsal surface of this cartilage to the base of the second radial. The fibers converge to insert on the tip of the second radial where the latter turns dorsad to join the otoglossal. A few fibers, in addition, continue laterally to attach to the fascia of the floor of the mouth.

tip of the first radial cartilage and continues on to attach the first radial to the anterior tip of the ceratohyal.

Subarcualis rectus I originates on the tip of the epibranchial cartilage. It wraps around this tip and proceeds forward, medial to the angle of the jaw where it then begins to fan out into a thin sheet over the ventral surface of the ceratohyal. It inserts along the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates from the dorsal surface of the sternum and the tendonous inscription which separates this muscle from the abdominal muscles posteriorly. It passes forward ventral to the pericardium. The medial fibers attach to the second basibranchial, which is actually partly imbedded in this muscle. The lateral fibers end on the tendonous inscription which extends outward from the lateral arms of the second basibranchial. At this point, the muscle continues forward again to become a thick band which inserts onto the hyobranchial skeleton. It inserts onto the posterior tip of the first basibranchial and the posterior edge of the

MOLE SALAMANDER.

Ambystoma talpoideum (Holbrook)

Salamandra talpoidea Holbrook, N. Amer. Herp., Ed. 1, Vol. 3, 1838, p. 117, pl. 29.

This is a small species with a broad, depressed head, a rounded body, and a short tail. Total length ranges up to 97 mm. It has 10 costal grooves, counting one each in the axilla and groin. Vomerine teeth form three distinct series, the middle one being situated some distance posterior to the internal nares. The lateral series begin a short distance behind the internal nares and extend a short distance laterally. The ground color is dark brown dorsally, becoming bluish gray along the lower sides. Small bluish white flecks are scattered over the surface of the skin, becoming numerous enough on the lower sides to form large patches. The range of this species is along the Southeast and Gulf Coasts of the United States from North Carolina to Louisiana and northward to Illinois. It has also been found in Oklahoma, Arkansas, and Texas.

HYOBRANCHIAL SKELETON (Fig. 10)

The ossification center which makes up the core of the first basibranchial amounts to an average of 32.6 percent of the total volume. This structure is pear-shaped when viewed from the ventral surface, and the cross sectional area is a flat oval. The lines of articulation with the radials are distinct. The first basibranchial is long compared to the total length of the entire hyobranchium and as compared to the length of the first ceratobranchial (Tables 4 and 5).

There is no bone in the radials. The first pair is free from the ceratohyals and unjointed. The second pair attaches to the tips of the otoglossal. The otoglossal cartilage is a smoothly curved rod of cartilage which arches into the tongue from below.

The first ceratobranchial is a slightly curved, unossified, rod of cartilage. It is flattened dorso-ventrally. The major bend in the first branchial arch occurs in the anterior half of the epibranchial. The latter is also unossified. The epibranchial length in relation to the length of the entire first branchial arch and in relation to the length of the first ceratobranchial is greater than in any other species (Tables 13 and 16).

The second ceratobranchial is an unossified, slightly curved rod of cartilage articulating at its proximal end with the tip of the first basibranchial and with the anterior end of the epibranchial at its distal end.

The ceratohyal was ossified in one specimen and unossified in the other two. In the specimen with ossification, this amounted to 11 percent of the total volume (Table 1). Only in *A. mabeii*, *A. t. melanostictum*, and *Rhyacotriton* is the ratio of ceratohyal length to total hyobranchial skeleton length greater than in this species (Table 19).

The lateral arms of the second basibranchial are longer than the anterior arm, and the former contain cartilage on their tips. The average ossification is 76 percent.

The ratio of mandible length to mandible width is much smaller than in other species (Table 14), indicating a short mandible.

MUSCULATURE (Fig. 10)

Intermandibularis posterior originates along the dorsomedial margin of each mandibular ramus. The fibers extend transversely and slightly posteriorly to attach to the fascia of the linea alba. It covers more than three-quarters of the area between the rami of the mandible. The anterior portion at the point of the chin is missing, and the genioglossus can be seen in that position.

Interhyoideus posterior originates from fascia which attaches to the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule. The posterior fibers originate in the fascia cephalodorsalis. The origin overlaps the insertion of the depressor mandibulae on the tip of the mandible. The insertion is into the mid-ventral raphe. The anterior fibers blend in with those of the interossequadrata.

Depressor mandibulae originates along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and along the fascia cephalodorsalis, the fibers of this muscle converge onto the posterior tip of the mandible where they insert as a short, stout tendon. There are also a few short fibers which extend from the ventral surface of the quadrate to the posterior tip of the mandible.

Levator mandibulae corresponds closely to the description that is given in the section on general musculature. There is considerable intermingling of fibers between the levator mandibulae posterior and the levator mandibulae externus.

Interossequadrata is a fan-shaped muscle which originates from the ventral surface of the quadrate anterior to the hyoquadrate ligament, from the articulation of the ceratohyal and the quadrate, and from the ventral surface of the posterior tip of the ceratohyal. The anterior fibers, arising from the quadrate, lie dorsal to the posterior fibers and are directed in an antero-medial direction. The posterior fibers, which arise from the ceratohyal tip, extend transversely and slightly posteriorly. The fibers form a delicate fan which adheres to the dorsal surface of the intermandibularis posterior and blends in well with the subhyoideus. The insertion is into the fascia of the dorsal surface of the intermandibularis posterior.

Subhyoideus originates from the ventral surface of the posterior tip of the ceratohyal immediately medial to the origin of the interossequadrata and the insertion blends in with the latter before inserting into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates from a line on the posterior edge of the mandible beginning at the symphysis and extending laterally about 1.5 mm. The fibers extend directly caudad to form two bands of muscle lying side by side along the venter of the throat. The thin fascia of the linea alba overlaps this muscle ventrally. The insertion is onto the second basibranchial cartilage and the tendonous inscription that extends laterally from the arms of the second basibranchial.

Genioglossus has two parts. The ventral portion originates along a line on the posterior edge

of the mandible. The line in this case lies immediately ventral to the origin of the geniohyoides and extends from the symphysis to a point about 2.0 mm lateral to the symphysis. The fibers extend caudomesially to insert into the aponeurosis lingualis and onto the otoglossal. This is a large muscle in this species and is thicker and broader than in the other species investigated.

The origin of the dorsal portion of the genio-glossus is from a line along the mandible immediately dorsal to the origin of the geniohyoides. The fibers spread out as they pass distally over the throat and become almost indistinguishable from the fascia of the floor of the mouth. It is into this fascia that these fibers finally insert at a position lateral to the second radial cartilage. The tip of the first radial is overlapped by the fibers of this muscle, and the medial fibers also attach to the posterior edge of the tip of the second radial cartilage as the latter turns dorsad to articulate with the end of the otoglossal.

Subarcualis rectus I attaches at its origin to the dorsal edge of the posterior tip of the epibranchial. The fibers wrap around and enclose the epibranchial and the lateral portion of the ceratobranchial in a sheath. There is an opening in the sheath which faces medially and into which the second ceratobranchial passes on its way to articulate with the epibranchial. The fibers lie parallel with the ceratohyal and spread out over the latter's anterior expanded end. The insertion is along the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates along the lateral margin of the dorsal surface of the sternum and along the transverse tendonous inscription which separates it from the rectus abdominus. It passes forward as a thin, broad band to the level of the second basibranchial, which is partially imbedded in this muscle. The portion of this muscle up to this point has only two tendonous inscriptions crossing it. The portion running anterior from the second basibranchial is thicker and narrower than the posterior portion. This anterior portion inserts onto the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is a direct forward continuation of the rectus abdominus, arising at the level of the sternum and passing forward alongside of the pericardium and both dorsal and lateral to the rectus cervicis superficialis. At the level of the second basibranchial, it is directly dorsal to the rectus cervicis superficialis. It continues forward from this point to lie in a posi-

tion dorsal to the first basibranchial and the hyoglossus. The two rectus cervicis profundus muscles together are about as wide as the first basibranchial. This muscle inserts on the posterior edge of the otoglossal.

Hebosteoypsiloides is a narrow muscle which arises from the dorsal surface of one of the myosepta of the rectus cervicis profundus. In *Ambystoma talpoideum*, this muscle originates from the second myoseptum posterior to the second basibranchial. The fibers extend forward dorsal to the rectus cervicis profundus and then cross the rectus cervicis superficialis to attach to the dorsal surface of the anterior arm of the second basibranchial.

Hyoglossus is a thick, well-developed muscle which originates from the dorsal surface of the base of the first radial and the adjacent surface of the first basibranchial. The insertion is laterad along the tip of the second radial.

MARBLED SALAMANDER.

Ambystoma opacum (Gravenhorst)

Salamandra opaca Gravenhorst, Vergl. Uebers. Zool. Syst., 1807, p. 421.

The geographical range extends along the Atlantic Coast of the United States from Massachusetts to Florida and westward to Texas, Arkansas, Missouri, Indiana, Illinois, and Wisconsin. This species is found in drier habitats than most of the other species of the genus. It is often collected in sandy areas bordering ponds and slow-moving streams. The females are slightly larger than the males, the total length ranging up to 120 mm. The ground color is black and is interrupted by light markings in the form of transverse bands. These bands are narrow dorsally and widen as they approach the upper sides of the body, where they may unite with the ends of adjacent bands to enclose a series of regular black spots along the midline of the back. Males have bright white transverse bands, while those of the females are grayish in color. The body is thick, short, and cylinder shaped. The gular fold is prominent, and there are 12 costal grooves if the one immediately above the foreleg is counted. The vomerine teeth form a transverse line which is interrupted both at the midline and at a point just back of the internal nares. Most species of this genus deposit their eggs in the springtime in ponds or slow-moving streams. The Marbled Salamander, however, deposits its eggs in the fall under logs, pieces of bark, or other materials on the surface of the ground. These laying sites are subsequently flooded by the last summer or fall rains.

HYOBRANCHIAL SKELETON (Fig. 11)

The average amount of bone in the first basibranchial for the four specimens was 41 per cent. The basibranchial-radial articulations are seen as definite lines. When the length of the first basibranchial is compared with the total length of the hyobranchial apparatus or with the length of the first ceratobranchial, it is seen to be greater than in any of the other species (Tables 4 and 5).

The first radials do not connect with the anterior tip of the ceratohyals. The radials are wholly cartilaginous and are intermediate in length between the extremes seen in other members of the family.

The second radials are directed in a dorso-lateral direction while gradually tapering to a fine point which articulates with the otoglossal. The otoglossal is arched dorsally into the tongue and is entirely cartilaginous.

The boneless first ceratobranchial forms a smooth arch that continues with the epibranchial to form a quarter circle of cartilage.

The second ceratobranchial is a thin cartilaginous rod only slightly curved and articulating on the epibranchial well posterior to the first ceratobranchial-epibranchial articulation.

The ceratohyal is unossified except in two specimens, in which a small ossification center is found in the posterior tip of each of these structures.

The second basibranchial is unossified except in one specimen, and is shaped as an inverted V.

MUSCULATURE (Fig. 11)

Intermandibularis posterior originates along the dorsomedial edge of the rami of the mandible and passes transversely over the venter of the throat to insert into the linea alba. There is no subdivision of this muscle into parts. The ventral portion of the genioglossus can be seen in the angle of the chin inasmuch as the intermandibularis posterior does not completely cover the intermandibular space at that point. The posterior fibers extend slightly caudad and overlap the interossaquadrata.

Interhyoideus posterior originates from the fascia which is attached to the lateral aspect of the tip of the mandible, the quadrate, the squamosal, the otic capsule, and from fibers which attach to the fascia cephalodorsalis. The fibers spread out as they move distally and medially until they form a thin sheet which inserts into the skin of the gular fold and the midline fascia. The anteriormost fibers are blended with

those of the interossaquadrata near their insertion.

Depressor mandibulae originates from the squamosal bone of the skull, attaching along its entire posterolateral surface except for the ventral 1 to 2 mm. It also arises from the fascia cephalodorsalis and the lateral surface of the otic capsule. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same in its origins and insertions as that description which has been given previously in the section on general musculature.

Interossaquadrata originates on the posterior surface of the quadrate and from the ventral surface of the articulation between the quadrate and the tip of the ceratohyal. A few fibers also arise from the posterior tip of the mandible. The anterior fibers extend anteromedially, while the posterior ones are in a posteromedial direction. It inserts into the midventral raphe of the throat. This is a thin, fan-shaped muscle.

Subhyoideus originates along the anteroventral edge of the posterior end of the ceratohyal and then fans out slightly as it proceeds forward over the throat. It lies ventral to the subarcualis rectus I and inserts into the dorsal fascia of the intermandibularis posterior. The latter covers the anterior portion of this muscle ventrally. The insertion end is displaced slightly lateral from the subarcualis rectus I.

Geniohyoideus originates from the posterior edge of the mandible along a line which begins about 1.5 mm lateral to the symphysis and extends laterally about 1.0 mm. The anteromedial end of this muscle is overlapped ventrally by the ventral portion of the genioglossus. The lateral fibers extend directly caudad, while the medial fibers are in a medio-caudal direction for a short distance before continuing directly caudad. The insertion is onto the second basibranchial cartilage, with the lateral fibers attaching into the tendonous inscription of the rectus cervicis superficialis.

Genioglossus has a ventral portion which originates from the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally about 2 to 3 mm. From this area of origin, the fibers extend caudo-medially to form a small triangle which overlaps the anteromedial end of the geniohyoideus. This ventral portion is divided into two portions by a separation in the fibers. It inserts into the aponeurosis lingualis. A few fibers continue along in this ligament to attach to the first basibranchial and to the otoglossal.

The dorsal portion of the genioglossus originates along the posterior edge of the mandible

from the symphysis to a point about 1.5 mm lateral from the symphysis. The medial fibers insert onto the posterior edge of the lateral half of the second radial, while the lateral fibers extend beyond this point and attach into the fascia, forming the floor of the mouth.

Subarcualis rectus 1 originates on the dorsal edge of the tip of the epibranchial. The fibers wrap around and enclose this end of the epibranchial in a sheath and extend forward parallel with the ceratohyal. After spreading out over the ceratohyal's expanded anterior end, these fibers insert along the ventral edge of the anterior margin of this cartilage.

Rectus cervicis superficialis originates from the dorsal surface of the lateral half of the sternum. Lateral fibers originate on the tendonous inscription which separates this muscle from the rectus abdominus. After passing forward from the second basibranchial, the medial fibers insert onto the posterior end of the first basibranchial, whereas the lateral fibers insert onto the posterior surface of the medial end of the first ceratobranchial.

Rectus cervicis profundus constitutes a direct forward continuation of the rectus abdominus, arising at the level of the sternum. It is situated in a dorsolateral position with respect to the rectus cervicis superficialis. The fibers pass ventral to the second ceratobranchial and dorsal to the first ceratobranchial. It continues forward dorsal to the first basibranchial and the hyoglossus to insert onto the posterior edge of the otoglossal.

Hebostcoypsiloides is a narrow muscle which originates from a more posterior position than in most of the other species. It arises from the third tendonous inscription posterior to the second basibranchial and extends anteriorly and then medially to insert onto the dorsal aspect of the second basibranchial.

Hyoglossus originates from the aponeurosis lingualis and the lateral edge of the dorsal surface of the anterior end of the first basibranchial. The fibers converge toward the insertion to form a small, triangular-shaped muscle that attaches laterally to the posterolateral edge of the second radial cartilage as the latter curves dorsad to join the end of the otoglossal. There are also a few fibers which extend laterally to attach to the fascia at the base of the tongue.

TEXAS SALAMANDER.

Ambystoma texanum (Matthes)

Salamandra texana Matthes, Allg. deutsche naturh., Zeitschr., N. S. Vol. 1, 1855, p. 266.

The Texas Salamander is dark brown in color with grayish, irregular, lichenlike blotches. Total length may reach 153 mm. A slender head and small mouth are characteristic of this species. The vomerine teeth are very slender and are arranged in a transverse line that is entirely between the internal nares and is interrupted at the midline. There are usually 14 costal grooves. It is found in Iowa, Ohio, Indiana, and Illinois in the north and westward to Nebraska and Kansas. It extends southward to Texas and Louisiana and has also been reported from North and South Carolina, Tennessee, Kentucky, and West Virginia.

HYOBRANCHIAL SKELETON (Fig. 12)

The first basibranchial is a shield-shaped structure with a large core of bone averaging 38 percent of the total volume (Table 1). The lines of articulation with the radials are distinct. The first basibranchial is situated posteriorly as compared to its position in most of the other species. Only in *A. annulatum*, *A. cingulatum*, *A. mabeei*, and *Rhyacotriton* is the first basibranchial in a more posterior position (Table 12). This structure is wider in this species in relation to its length than in any of the others, except *A. cingulatum* (Table 15).

The first radials are long and curved, and they are attached to the tips of the ceratohyals by a short ligament. Their length in relation to the first basibranchial is exceeded only by *Rhyacotriton*, *A. mabeei* and *Dicamptodon* (Table 6).

The bases of the second radials overlap the medial end of the first ceratobranchial ventrally. These radials are also without ossification. They articulate with the tips of the otoglossal, a dorsally curved rod of cartilage.

The first ceratobranchial is cartilage. It is a gradually curved rod whose medial end is fused to the first basibranchial.

The epibranchial is devoid of bone and moderate in length (Table 16).

The second ceratobranchial is longer than the first ceratobranchial and, in fact, the ratio of the length of the second ceratobranchial (the second branchial arch) to the length of the first branchial arch (the first ceratobranchial plus the epibranchial) is greater than in the others except *A. annulatum* and *A. cingulatum* (Table 17). The second ceratobranchial is entirely cartilaginous.

In three of the five specimens, the ceratohyals contained ossification centers in the posterior tips. The other specimens were unossified in the ceratohyals. This lack of consistency in ossification between these five specimens cannot be at-

tributed to size differences since they were all approximately equal in this respect. There may have been an age difference between the five specimens, although they all were collected on the same day and in the same location, and all five were completely transformed adults.

The second basibranchial is shaped like an inverted V and contains cartilage on the two tips. The average ossification is 65.1 percent.

MUSCULATURE (Fig. 12)

Intermandibularis posterior originates along the dorsomedial edge of the mandible. The fibers extend transversely to insert into a broad midline of fascia, the linea alba of the throat. A small area is opened at the point of the chin through which the ventral portion of the genioglossus can be seen. The posterior portion of the intermandibularis posterior overlaps the anterior end of the interosssaquadrata ventrally.

Interhyoideus posterior is attached at its origin to several bony and fascial surfaces, arising from the posterior tip of the mandible, the lateral surface of the quadrate, the lateral surface of the squamosal, and from the fascia cephalodorsalis. It inserts into the gular fold and into the median ventral raphe which is a posterior continuation of the fascial material into which the intermandibularis posterior and the interosssaquadrata insert.

Depressor mandibulae originates along the upper squamosal, the ventral and posterior surfaces of the otic capsule, and posteriorly from the fascia cephalodorsalis. The fibers of this muscle insert onto the posterior tip of the mandible where they function to depress or lower the mandible.

Levator mandibulae in *Ambystoma texanum* is essentially the same as the description given previously in the section on general musculature.

Interosssaquadrata originates along the ventral surface of the articulation between the ceratohyal and the quadrate. The insertion is into the dorsal side of the median fascia into which the intermandibularis posterior inserts. The fibers extend medially to a point somewhat short of the midline and, consequently, this muscle overlaps ventrally the lateral half of the genioglossus.

Subhyoideus originates along the anteroventral edge of the posterior end of the ceratohyal. It extends dorsal to the interosssaquadrata at its origin end. The fibers are directed more medially in this species than in most of the others, and consequently the insertion end overlaps the venter of the subarcualis rectus 1 medially rather

than laterally. It fans out to insert into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates on the posterior surface of the mandible. More precisely, the origin is along a line extending laterally from the mandibular symphysis for a distance of 1.5 to 2.0 mm. The fibers run caudad to insert onto the second basibranchial and into the tendinous inscription of the rectus cervicis superficialis that extends laterally at that point.

Genioglossus has a ventral portion which originates along the posterior edge of the mandible immediately ventral to the medial portion of the origin of the geniohyoideus. The fibers extend caudomedially and overlap the medial anterior end of the geniohyoideus. They insert into the aponeurosis lingualis at about the level of the anterior edges of the ceratohyals, and a few fibers continue in the aponeurosis lingualis to the first basibranchial and to the otoglossal.

The dorsal portion originates along the same line on the mandible as the ventral portion, but the fibers extend caudolaterally. The medial fibers are dorsal to the geniohyoideus, and they insert onto the anterior edge of the second radial near its tip. The lateral fibers insert into the fascia of the tongue at its base and contribute to the floor of the mouth.

Subarcualis rectus 1 originates on the dorsal side of the posterior tip of the epibranchial, from which the fibers proceed forward, wrapping around and enclosing the epibranchial in a sheath of muscle. These fibers continue forward parallel with the ceratohyal to insert onto the latter's expanded anterior end along the anterior margin.

Rectus cervicis superficialis originates on the dorsal surface of the posterior end of the sternum. The fibers extend dorsal to the anterior part of the scapula and dorsal to the coracoids. It lies on the ventral surface of the pericardium. These fibers insert onto the medial end of the first ceratobranchial just before the latter articulates with the first basibranchial. It also inserts onto the point of articulation of these two cartilages and onto the posterior tip of the first basibranchial. The medial three-fourths of this muscle also attaches to the second basibranchial.

Rectus cervicis profundus passes forward alongside the pericardium and is both dorsal and lateral to the rectus cervicis superficialis. It continues forward through the opening formed by the two ceratobranchial cartilages and finally inserts onto the posterior edge of the otoglossal.

Hebosteocypsiloides originates from the dorsal surface of a myoseptum of the rectus cervicis profundus. The particular myoseptum in this case is the second one posterior to the second

basibranchial. This narrow muscle extends forward dorsal to the rectus cervicis profundus. At the level of the second basibranchial, it turns medially and crosses the rectus cervicis superficialis to attach along the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle situated between the first basibranchial ventrally and the rectus cervicis profundus dorsally. It originates from the dorsal surface of the anterior end of the first basibranchial and along the lateral margin of the dorsal surface of this cartilage. From this point, the fibers extend caudolaterally to wrap around and insert onto the posterolateral edge of the tip of the second radial cartilage. There are also a few fibers which continue for a short distance into the sides of the base of the tongue.

CHIHUAHUA SALAMANDER.

Ambystoma rosaceum Taylor

Ambystoma rosaceum Taylor, Copeia 1941 (3): 143-144, figs. 1a and 1b.

This species has a uniform dark brown ground color with a lighter brown ventrally. Along the chin and tail there are light, indistinct spots which may also continue along the sides of the body in a somewhat linear pattern. There are usually 11 costal grooves, counting one each in the axilla and groin. Vomerine teeth are divided into two groups of 26 each, separated by a midline diastema. The tail is compressed laterally and has a small dorsal tail fin. There are glands scattered over the body, becoming prominent along the proximal third of the dorsal ridge of the tail and also forming a parotid gland. These glandular areas are similar to but not as well developed as in *A. gracile*. Total length may reach 165 mm. These salamanders are found in the mountains of the Sierra Madre Occidental from El Salto, Durango, to northern Chihuahua and northeastern Sonora.

HYOBRANCHIAL SKELETON (Fig. 13)

The first basibranchial is shield-shaped when viewed from the ventral aspect. In cross section, it is a flat oval. The core of this structure is bone, constituting an average of 28 percent of the total volume (Table 1). The articulation lines separating this structure from the radials are distinct. The first basibranchial is situated anteriorly with respect to the position of the mandible. Only *A. t. nebulosum* has a more anteriorly situated first basibranchial (Table 12).

The first radials are sharply curved laterally and entirely cartilaginous. They are long, as in-

dicated by the fact that the ratio—radial I length to basibranchial I length—is greater in this species than in the others, with the exception of *A. mabeii*, *A. texanum*, *Rhyacotriton*, and *Dicamptodon* (Table 6).

The second radials are bent in a slightly posterior direction when in a resting position. They are wholly cartilaginous and attach to the ends of the annular otoglossal.

No bone is found in the first ceratobranchial, and they are rather straight, the major curve in the first branchial arch occurring at the anterior end of the epibranchial.

In one of the three available specimens, the epibranchials and ceratohyals were devoid of bone in their posterior tips. The other two specimens had well-developed ossification centers in these structures. The average ossification for the three specimens was 36 percent for the epibranchials and 4.8 percent for the ceratohyals.

The ratio of ceratohyal width to ceratohyal length is equalled in *A. t. melanostictum* and exceeded in all of the others (Table 14).

The totally cartilaginous second ceratobranchial is long when analyzed by the ratio of length of second ceratobranchial to length of first ceratobranchial (Table 8).

The lateral arms of the second basibranchial contain cartilage on their tips, the cartilage constituting an average of 31 percent of the total volume (Table 1).

The mandible length compared to the mandible width is a rather high ratio in this species, being exceeded only by four others—*Dicamptodon*, *A. annulatum*, *A. mabeii*, *A. maculatum*, and *A. cingulatum* (Table 9).

MUSCULATURE (Fig. 13)

Intermandibularis posterior originates on the dorsomedial surface of the mandible and extends medially to the linea alba. It is seen immediately under the skin of the throat and overlaps the more dorsally situated intercrossaquadrata and subhyoideus muscles. The posterior fibers are directed obliquely caudomedial, while the majority of the fibers are transverse.

Interhyoideus posterior originates from fascia which is in turn attached at several points, the lateral aspect of the posterior tip of the mandible, the quadrate, the squamosal, the otic capsule and the fascia cephalodorsalis. The fibers spread out as they extend in a caudomesial direction to insert into the gular fold and the midventral fascia.

Depressor mandibulae originates on the dorsal end of the squamosal, the ventral and posterior surfaces of the ear capsule and along the

fascia cephalodorsalis. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as the description which is given in the earlier section on general musculature.

Interossequadrata originates on the ventral surface of the quadrate, anterior to the hyoquadrate ligament and from the hyoquadrate ligament itself. This is a delicate muscle which is easily lifted along with the intermandibularis posterior. It is fan-shaped, the anterior fibers lying in an anteromesial direction and the posterior fibers in a posteromesial position. It inserts into the median raphe into which the intermandibularis posterior and the interhyoideus posterior also insert.

Subhyoideus originates from the ventrolateral margin of the posterior end of the ceratohyal. The posterior fibers of this thin muscle blend in with those of the interossequadrata, making separation of these two muscles difficult at their insertion ends. This is also a delicate muscle that is easily disrupted when the intermandibularis posterior is lifted. The insertion end overlaps laterally part of the ventral surface of the subarcualis rectus I. It inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from a short line on the posterior surface of the mandible. This line runs laterally for about 3.0 mm from a point about 1.5 mm lateral to the symphysis. The fibers extend caudad to form a band of muscle which inserts onto the second basibranchial and onto the tendonous inscription lateral to the second basibranchial. This muscle appears to be rather narrow in this species.

Genioglossus originates along a line beginning at the mandibular symphysis and extends laterally about 2.0 mm along the posterior surface of the mandible. The fibers extend caudomesiad to form a small triangle. The insertion is into the aponeurosis lingualis, and a few fibers continue on to the anterior edge of the first basibranchial. A few fibers also attach to the otoglossal cartilage.

The broader lateral portion originates immediately dorsal to the origin of the ventral portion but extends laterally from the symphysis for a distance of 3 to 4 mm. The fibers fan out and extend posterolaterally to insert into the fascia of the floor of the mouth at about the level of the second radial tip.

Subarcualis rectus I originates along the dorsal edge of the posterior end of the epibranchial, wraps around this cartilage, and extends forward over the ventral surface of the ceratohyal. The

fibers fan out and insert along the anterior margin of this cartilage.

Rectus cervicis superficialis originates on the dorsal surface of the sternum and the tendonous inscription extending laterally from the sternum. It extends dorsal to the coracoid cartilages and ventral to the pericardium. The second basibranchial is partially enveloped by this muscle as it continues anteriorly. It then becomes narrower and thicker and turns medially to insert onto the posterior tip of the first basibranchial and onto the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus appears at the level of the sternum as a flat band extending forward alongside and dorsal to the rectus cervicis superficialis. At the level of the omohyoideus, it begins to turn medially. Forward from the second basibranchial, it is a thick, narrow band which lies dorsal to the rectus cervicis superficialis. The fibers pass ventral to the second ceratobranchial and dorsal to the first ceratobranchial. From this point forward, it leaves the rectus cervicis superficialis and inserts onto the posterior edge of the otoglossal.

Hebosteoypsiloides originates from one of the myosepta of the rectus cervicis profundus. The particular myoseptum is the second one posterior to the second basibranchial. It is a narrow muscle which at first extends directly forward dorsal to the rectus cervicis profundus. After a short distance, it turns across the dorsal surface of the rectus cervicis superficialis and inserts onto the dorsum of the second basibranchial.

Hyoglossus is a small muscle extending from the first basibranchial to the tip of the second radial. It is triangular in shape, with the base of the triangle situated along the dorsal surface of the anterior end of the first basibranchial and along the lateral margin of this cartilage to the base of the second radial. The point of the triangle is the insertion end which attaches onto the tip of the second radial and out into the adjoining fascia.

TIGER SALAMANDER.

Ambystoma tigrinum Green

Salamandra tigrina Green, 1825, Jour. Acad. Nat. Sci. Phil., (1), 5:116.

EASTERN TIGER SALAMANDER.

Ambystoma tigrinum tigrinum (Green)

Salamandra tigrina Green, Journ. Ac. Nat. Sci. Phila., Vol. 5, 1825, p. 116.

This subspecies ranges extensively throughout most of the United States, from New York to northern Florida and westward to Texas in the south and Minnesota and parts of Ontario in the north. It is a burrower and spends most of the year underground. Its burrowing habit is abandoned only during the breeding season, during which time it can be found in ponds and slow streams. This is the largest species of the genus *Ambystoma*, attaining a length of 254 mm in some individuals. It is a stout-bodied salamander with 12 costal grooves when those in the axilla and groin are counted. The gular fold is prominent, and the vomerine teeth are usually in a continuous series, although there is occasionally a break in this series at the midline. Males are usually larger than females, and the tail and hind legs are also usually longer in male specimens. Ground color is dark brown or dull black. The venter is olive yellow in color. Brownish olive or brownish yellow blotches are scattered over the dark ground color. These blotches may fuse somewhat between the costal grooves to form short bands along the sides of the trunk.

NORTHWESTERN TIGER SALAMANDER.

Ambystoma tigrinum melanostictum (Baird)

Siredon lichenoides melanostictum Baird, 1860
Expl. Surv. R. R. Miss. Pacific, 12, pt. 2, p. 306.

This subspecies is characterized by extreme development of the light colored areas of the skin. These areas converge greatly such that the darker ground color persists as irregular patches. The light areas are pale yellow and the ground color is brown to black. There are usually 13 costal grooves when one in the axilla and two that converge in the groin are counted. There may be three series of vomerine teeth which form a forward arching line in front of the internal nares; however, the central series is occasionally interrupted at the midline. Adults may reach a total length of 219 mm. Adult specimens are sometimes found in damp situations under logs or stones; whereas, during the breeding season, they may be abundant in the mountain lakes and ponds throughout their range. They are found in British Columbia, Alberta, Washington, Oregon, Idaho, Montana, Wyoming, North Dakota, South Dakota, and Nebraska.

CLOUDED TIGER SALAMANDER.

Ambystoma tigrinum nebulosum Hallowell

Ambystoma nebulosum Hallowell, Proc. Acad. Nat. Sci. Phila., 6, p. 209.

This subspecies of tiger salamander is characterized by having black spots on a dark ground color of olive green or dark gray. It has a well developed gular fold and usually 13 costal grooves when the one in the axilla and the two that run together in the groin are counted. The line formed by the vomerine teeth tends to arch forward between the internal nares and may or may not form a continuous series. When not continuous, the tooth line will be interrupted just medial to the inner margin of the naris and also at the midline. Males tend to be slightly larger than females. Total length may reach 230 mm. During the breeding season the swollen vent is characteristic of the male. These salamanders are found commonly in the mountain lakes and ponds and also occasionally beneath logs and stones. Their range extends over western Colorado, northwestern New Mexico, northern Arizona, the inner basin of Utah, and the Colorado Plateau in Utah.

The anatomical descriptions which follow are based upon a study of the above three subspecies of Tiger Salamander.

HYOBRANCHIAL SKELETON (Fig. 14-16)

The first basibranchial is shield shaped and has a central core of bone. The percentages of ossification of the first basibranchial are similar for *A. t. melanostictum* and *A. t. tigrinum* (Table 1).

The relative position of the first basibranchial along the anteroposterior axis of the throat is very similar for these three subspecies and, as a group, their first basibranchials are more anterior than they are in the other species (Table 12).

The first radials attach to the tips of the ceratohyals by a short ligament. These radials are moderate in length and unossified.

The second radials also contain no bone and are curved dorsally where their distal ends articulate with the ends of the otoglossal. The otoglossal is unossified and arched dorsally into the tongue.

The first ceratobranchials are entirely cartilaginous and moderate in length. They are uniform in width and thickness throughout their length and are flattened dorsoventrally.

The epibranchials were ossified in all 10 of the specimens examined. The amount of ossification was notably different, however, in *A. t. nebulosum* from that found in the other two subspecies (Table 1). This, however, is based on a limited number of specimens.

The average first ceratobranchial length, when compared to the length of the epibranchial

chial, was shorter for *A. t. melanostictum* and *A. t. nebulosum* than all of the others except *A. talpoideum* (Table 13).

The second ceratobranchial compared to the first ceratobranchial has a smaller ratio in the *tigrinum*-group than in other species except for *Dicamptodon* and *Rhyacotriton* (Table 8).

Two of the subspecies were found to have ossification centers in the ceratohyal tips. The third, *A. t. melanostictum*, has no bone in the ceratohyals. The average percent ossification of the ceratohyals in *A. t. nebulosum* and *A. t. tigrinum* was 8 and 5 respectively (Table 1). The ceratohyal length in relation to the total length of the hyobranchium is shorter in *A. t. tigrinum* than in the other two tiger salamander subspecies (Table 19). This ratio is moderate for the *tigrinum* group as a whole.

The second basibranchial in the *tigrinum* group is triradiate in shape, with the anterior arm being considerably shorter than the lateral arms. The anteroposterior length of this element is greater in *A. t. tigrinum* in relation to the side-to-side length than in the other two subspecies (Table 18). This ratio is also moderate compared with all the other species.

As a group, the *tigrinum* subspecies have a broad head compared with the other species. The ratio—mandible length to mandible width—is smaller in *A. t. tigrinum* than in the others except for the mole salamander, *A. talpoideum* (Table 9).

MUSCULATURE (Fig. 14-16)

Intermandibularis posterior originates on the dorsomedial surface of the mandible. The direction of the fibers is transverse for the most part, except for the posterior fibers which are directed caudomedially. It inserts into the linea alba of the throat.

Interhyoideus posterior originates from fascia which is attached to the lateral part of the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule, with some posterior fibers originating from the fascia cephalodorsalis. It inserts into the skin and fascia of the gular fold and into the midventral line. The anterior fibers blend imperceptibly with those of the *interosaquadrata*. The posterior edge of this muscle (the gular fold) is more anteriorly situated in *A. t. nebulosum* than in any of the other specimens included in this study (Table 11).

Depressor mandibulae attaches along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and in the fascia cephalodorsalis. The insertion is onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as the description given in the earlier section on general musculature.

Interosaquadrata originates from the ventral surface of the quadrate anterior to the hyoquadrate ligament and from the ligament itself. The anterior fibers extend anteromedial and ventral to the subarcualis rectus I, whereas the posterior fibers lie parallel with those of the *interhyoideus posterior*. The insertion is in the median raphe into which the *intermandibularis posterior* and *interhyoideus posterior* also insert.

Subhyoideus originates on the ventrolateral margin of the posterior 2 to 3 mm of the ceratohyal. It is a thin muscle, the posterior fibers of which blend in closely with those of the *interosaquadrata*. The fibers lie parallel with the subarcualis rectus I; and, in fact, if the *intermandibularis posterior* is removed carefully, the *subhyoideus* can be seen lying against the ventral surface of the subarcualis rectus I. The insertion end overlaps the venter of the subarcualis rectus I laterally. This muscle inserts into the dorsal fascia of the *intermandibularis posterior*.

Geniohyoideus originates from a short line along the posterior surface of the mandible. This line begins at a point about 1.5 mm lateral to the symphysis and extends laterally about 3.0 mm. The fibers pass caudad and slightly medial to insert onto the second basibranchial. A few of the lateral fibers also insert onto the tendonous inscription of the *rectus cervicis superficialis* that extends laterally from the arms of the second basibranchial.

Genioglossus has a ventral portion which originates along a line beginning at the mandibular symphysis and extending laterally about 2.0 mm. The fibers extend caudomedially and form a small triangle that is seen between the anterior ends of the *geniohyoideus*. The insertion is into the aponeurosis lingualis which connects the root of the tongue with the first basibranchial and with the otoglossal.

The lateral portion is a broader muscle which originates along a line immediately dorsal to the origin of the ventral portion but extends laterally from the symphysis for a distance of 3 to 4 mm. These fibers extend posterolaterally to insert into the base of the tongue. The medial fibers attach to the tips of the second radials.

Subarcualis rectus I originates from the dorsal side of the posterior end of the epibranchial cartilage. The fibers radiate around and enclose this end of the epibranchial, forming a sheath at the posterior end of the muscle with the opening of the sheath facing medially and into which the ceratobranchial passes. The fibers lie parallel with the cartilage and insert on the ventroante-

rior border of the expanded anterior end of the ceratohyal.

Rectus cervicis superficialis originates from the posterior two-thirds of the dorsal surface of the sternum. The fibers of this muscle extend forward dorsal to the sternum, dorsal to the coracoids, and ventral to the pericardium to insert onto the dorsal surface of the second basibranchial and into the tendonous inscription from which the geniohyoideus arises. The part anterior to the second basibranchial inserts onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial cartilage.

Rectus cervicis profundus is a direct forward continuation of the rectus abdominus. At the level of the sternum, it passes forward along the side of the pericardium and both dorsal and lateral to the rectus cervicis superficialis. It is ventral to the second ceratobranchial and dorsal to the first ceratobranchial and inserts finally on

the posterior edge of the otoglossal cartilage.

Hcbosteoypsiloideus is a narrow muscle originating from the dorsal surface of one of the myosepta of the rectus cervicis profundus. In this species it arises from the second myoseptum posterior to the second basibranchial, extends dorsal to the rectus cervicis profundus, turns medially for a short distance dorsal to the rectus cervicis superficialis, and inserts on the dorsal surface of the second basibranchial.

Hyglossus is a small muscle which lies ventral to the rectus cervicis profundus and originates from the dorsal surface of the anterior end of the first basibranchial cartilage and along the lateral margin of the dorsal surface of this cartilage. The fibers extend caudolaterally to wrap around the tip of the second radial cartilage. The point of insertion is on the posterolateral edge of the second radial, although a few of the posterior fibers extend laterally to insert into the sides of the base of the tongue.

DISCUSSION

The foregoing descriptions of comparative morphology have been condensed to 48 characters which we have used in a cluster analysis using the method of Wishart (1969). We believe that the use of this method, together with the methods of descriptive morphology, provides for an analysis of the data which is more precise than is possible by use of descriptive morphology alone.

A character analysis produced by statistical methods concerning relationships between the various species of the Ambystomidae provides useful information for the deduction of a phylogeny. It must be kept in mind, however, that the basis for these relationships, as used in this study, is comparative morphology of the hyobranchium and throat musculature. It is entirely possible that these results could be different using information derived from different sources, such as the skull or external morphology.

It is not known whether the individual characters are evolving as independent units or whether they are parts of larger integrated systems. We suspect that some are related to the development of the feeding and/or breathing mechanisms.

The characters used in the cluster analysis are of two types—numeric and binary. The former are recorded as the length of a particular structure, the ratio of lengths of two different structures, or as a percentage of ossification of a structure. Binary characters are expressed as

either the presence or absence of a particular structure, and are recorded in the data as 0 or 1 for absence and presence, respectively.

The numbered paragraphs which follow contain explanations of each of the 48 characters. Some of the binary characters contain two or three different attributes so that the total number of attributes amounts to 63 (22 numeric and 41 binary). The number of each paragraph corresponds to the character and/or attribute number. (See Tables 2 and 3 for the specific characters for each individual.)

1. The ratio of the distance between the mental symphysis and the posterior edge of the intermandibularis posterior to the distance between the mental symphysis and the anterior edge of the pectoralis.

2. The ratio of the distance between the mental symphysis and the gular fold to the distance between the mental symphysis and the anterior edge of the pectoralis.

3. The ratio of mandible length to mandible width.

4. The ratio of the distance between the mental symphysis and the anterior edge of the first basibranchial to the length of the mandible.

5. This ratio is a comparison of the length of the first basibranchial with the total length of the hyobranchial apparatus. The basibran-

chial length is taken as the distance between the anterior edge of the first basibranchial and a line drawn between the posterior edges of the medial ends of the first two ceratobranchials. The latter point was chosen rather than the extreme posterior tip of the first basibranchial because the articulation between the first basibranchial and the second ceratobranchial was often indistinct.

6. The ratio of the length of the first basibranchial to the length of the first ceratobranchial.

7. The ratio of the length of the first basibranchial to the total length of the first branchial arch.

8. This ratio compares the width of the first basibranchial to its length.

9. The ratio of the length of the first radial to the length of the first basibranchial.

10. This character is expressed as the ratio of the length of the first ceratobranchial to the total length of the first branchial arch.

11. The ratio of the length of the first ceratobranchial to the length of the epibranchial.

12. The ratio of the length of the second ceratobranchial to the first ceratobranchial.

13. The ratio of the length of the second ceratobranchial to the length of the first branchial arch.

14. The ratio of the length of the hyobranchium to the distance between the mental symphysis and the sternum.

15. The ratio of the anteroposterior length of the second basibranchial to its side-to-side width.

16. The ratio of the length of the ceratohyal to the length of the entire hyobranchium.

17. The ratio of the width of the ceratohyal to its length.

18-22. These characters are the percentages of ossification of the first basibranchial, second basibranchial, first ceratobranchial, ceratohyal, and epibranchial, respectively.

23. This binary character is the absence or presence of a definite line of articulation between the first radial and the first basibranchial.

24. The absence or presence of a definite line of articulation between the second radial and the first basibranchial.

25-27. This is a binary character with three different attributes. Each first basibranchial either is or is not truncate, pear shaped,

or shield shaped. Column 25 on Table 3 indicates whether or not it is truncate; column 26 indicates whether or not it is pear shaped; and column 27 indicates whether or not it is shield shaped.

28. The absence or presence of a joint midway along the first radial cartilage.

29. A binary character based on whether or not the first radial tip attaches to the ceratohyal.

30-31. This binary character has two attributes—whether the otoglossal is or is not annular in shape and whether it is or is not platelike in shape.

32. This character is whether the otoglossal is lightly ossified, as in *Dicamptodon*, or completely cartilaginous. The ossified condition is designated with a 1 on Table 3, and the cartilaginous condition is designated with a 0.

33. This binary character is whether or not the otoglossal is fused with the second radials.

34-35. The posterior tip of the second ceratobranchial articulates with the first branchial arch at a point either directly on the joint between the first ceratobranchial and the epibranchial or at a point slightly posterior to that point. The first attribute of this character is whether or not the point of articulation is posterior to the joint. The second attribute is whether or not it is directly on the joint.

36-38. This binary character has three attributes. The second basibranchial either is or is not triradiate, it either is or is not 4-radiate, and it either is or is not an inverted V.

39. This is a binary character concerned with hypertrophy or lack of hypertrophy of the levator mandibulae.

40-42. This character has three attributes concerned with the insertion of the rectus cervicis superficialis—whether this muscle does or does not insert only on the first basibranchial, whether it does or does not insert only on the first ceratobranchial, and whether it does or does not insert on both the first basibranchial and the first ceratobranchial.

43-45. The heboosteopsiloides originates on one of the three myosepta posterior to the second basibranchial. These three attributes are whether or not this muscle originates on the first, second, or third myoseptum.

46. This character is the absence or presence of the hyoglossus.

47. This character is whether or not there is an opening in the intermandibularis posterior at the point of the chin.

48. This is a binary character concerned with the width of the linea alba. If it is a thin line running down the midline of the throat, it is designated with a 1. If it is wider than this, it is designated with a 0.

49-50. This character deals with the number of inscriptions on the rectus cervicis superficialis. Each animal has either two inscriptions or three inscriptions.

51-52. The insertion of the rectus cervicis profundus is either fleshy or tendonous. Attribute 51 is either fleshy or not fleshy, and attribute 52 is either tendonous or not tendonous.

53-54. This character is whether the joint between the first ceratobranchial and the epibranchial is distinct or indistinct.

55. A binary character concerned with whether or not the anterior end of the geniohyoideus is overlapped ventrally by the genioglossus.

56. This character is whether or not the intermandibularis posterior is divided.

57. This is the presence or absence of parotid glands and a glandular ridge on the tail.

58-59. This character has two attributes—either the ventral edge of the tail is rounded or it is thin.

60. This is whether the genioglossus does or does not insert on the first ceratobranchial.

61. This character is whether the subhyoideus inserts on the mandible or not.

62-63. In *Dicamptodon* the majority of the hyobranchium is uniformly, but lightly, ossified or mineralized. In all of the other species the majority of the elements of this structure are cartilage. This character is whether the hyobranchium is like that of *Dicamptodon*, or whether it is mostly cartilaginous.

The numeric characters were tested for homogeneity of variance using Bartlett's Test (Dixon and Massey, 1969). Unfortunately, there was for each character in the cluster analysis at least one species in which the variance was great enough to cause heterogeneity. For this reason the numeric characters were of little use in the deduction of a phylogeny. In other words, the variation between individuals of a single species with reference to a given numeric character was so excessive that the use of this character to separate species was invalid. There is

considerable individual variation in the lengths and widths of the separate components of the hyobranchial skeleton. Other workers have used a few of these dimensions for studies at the generic level (Özeti and Wake, 1969); however, this study has shown that they are of little use in separating species or subspecies.

There were 26 binary characters used in the cluster analysis. The dendrograms for this analysis are shown in Figures 18 and 19. A brief discussion and summarization of the results of the binary characters is as follows:

Dicamptodon remains separate from the others in this analysis. It is the only species with a segmented radial, a platelike otoglossal, a fused otoglossal-second radial, no hyoglossus, no opening in the intermandibularis posterior at the chin, and a uniformly, but lightly, ossified hyobranchium.

Rhyacotriton has a totally cartilaginous hyobranchial skeleton. This is probably an advanced condition associated with terrestrial feeding habits (Regal, 1966). A cartilaginous hyobranchium is more flexible than a bony one, and in the act of feeding is a more pliable part of the tongue apparatus enabling the tongue to be extended with more speed and precision than could be done with a hyobranchium of bone. Bony hyobranchial elements are characteristic of primitive aquatic salamanders.

Another advanced trait found in *Rhyacotriton* is the reduced number of myosepta on the rectus cervicis superficialis. The number is two in this case as compared to the usual three. A trait peculiar to *Rhyacotriton* is the long subhyoideus. In all of the other species investigated this muscle is attached to the anterior end of the ceratohyal, whereas in *Rhyacotriton* it extends forward beyond that point to reach the mandible. In most of the others, the subhyoideus is so reduced as to be difficult to detect upon dissection. It has been completely overlooked by some anatomists, as pointed out above. The genioglossus is also longer than in other species, extending as far posterior as the first ceratobranchial.

The affinity between *Dicamptodon* and *Rhyacotriton* which has been suggested by numerous workers is based on data other than throat morphology. Dunn (1940) says that these two genera are related to each other and differ from *Ambystoma* in their skull features. Tihen (1958) suggested, on the other hand, that *Dicamptodon* and *Rhyacotriton*, based on the osteology of their skulls, were derived independently from the proto-ambystomatid stock and that they are different from each other and from the remainder of the family. Noble (1927), in attempting to support the idea that *Dicamptodon* and

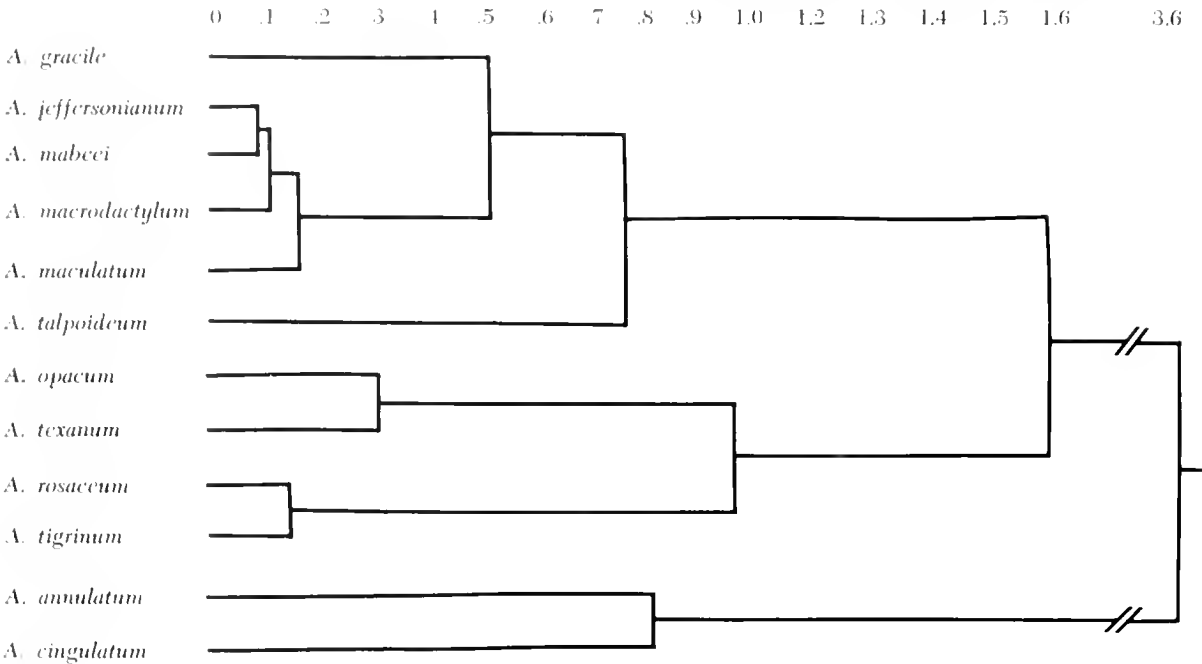


Fig. 18. Dendrogram for the Genus *Ambystoma*.

Rhyacotriton are related, has pointed to the fact that these two genera have stream-type larvae in contrast to the pond-type larvae of *Ambystoma*. We can add to this the fact that the adults of these two stream-type genera have hypertrophied levator mandibulae muscles which are apparently of great value in grasping and swallowing the elusive types of food items present in a fast-moving stream. It is also noteworthy that in the mouth of one of the *Rhyacotriton* specimens was found a winged insect the size of a small bee. Furthermore, the geographical distributions are basically the same. They are found in the Pacific Northwest and nowhere else. In addition, the long subhyoideus in *Rhyacotriton* is a primitive trait. In spite of this, however, our studies have verified the fact that these two genera are different from each other and from the genus *Ambystoma*. Not only is *Rhyacotriton* distinct from *Ambystoma*, but it is also different from *Dicamptodon* in its wholly cartilaginous hyobranchium, fewer transverse insertions in the rectus cervicis muscles, unsegmented radials, annular otoglossal, and presence of the hyoglossus. We believe, therefore, that there is a preponderance of evidence for an independent derivation of *Dicamptodon* and *Rhyacotriton* from the proto-ambystomatid stock.

A. annulatum and *A. cingulatum* consistently remained together throughout the analyses. They share several characters. They are the only species in which the second basibranchial is 4-ra-

diated and they alone have tendonous insertions of the rectus cervicis profundus. They and *Dicamptodon* are the only species in which the first ceratobranchial-epibranchial point is indistinct. It is interesting to note that Cope (1887) considered *A. annulatum* and *A. lepturum* (*cingulatum*) to be a distinct and separate group from the other ambystomids.

As expected, the *tigrinum* group remained together, but it is of interest that *A. rosaceum* is aligned closely with them. This is a confirmation of the idea which others have expressed concerning the close relationship between *A. rosaceum* and *A. tigrinum* (Anderson, 1961). We definitely believe that *rosaceum* separated early from the *tigrinum* group and became a mountain type of tiger salamander. With the dispersion after the recent ice age salamanders of the *tigrinum* group (or their ancestral stock) in the southern areas, particularly those of the Rio Concha and other smaller drainage basins flowing into the Rio Grande, moved up the streams to become mountain inhabitants. Such a dispersal produced mountain islands of isolation with wide desert flats to insure the separation. *Ambystoma rosaceum* is also similar to some of the subspecies of *tigrinum* in its basic habitus, color (light spots or with light mottling as seen in specimens from the border states) and is a burrower. On the basis of our data this salamander should perhaps be realigned as a subspecies of *A. tigrinum*.

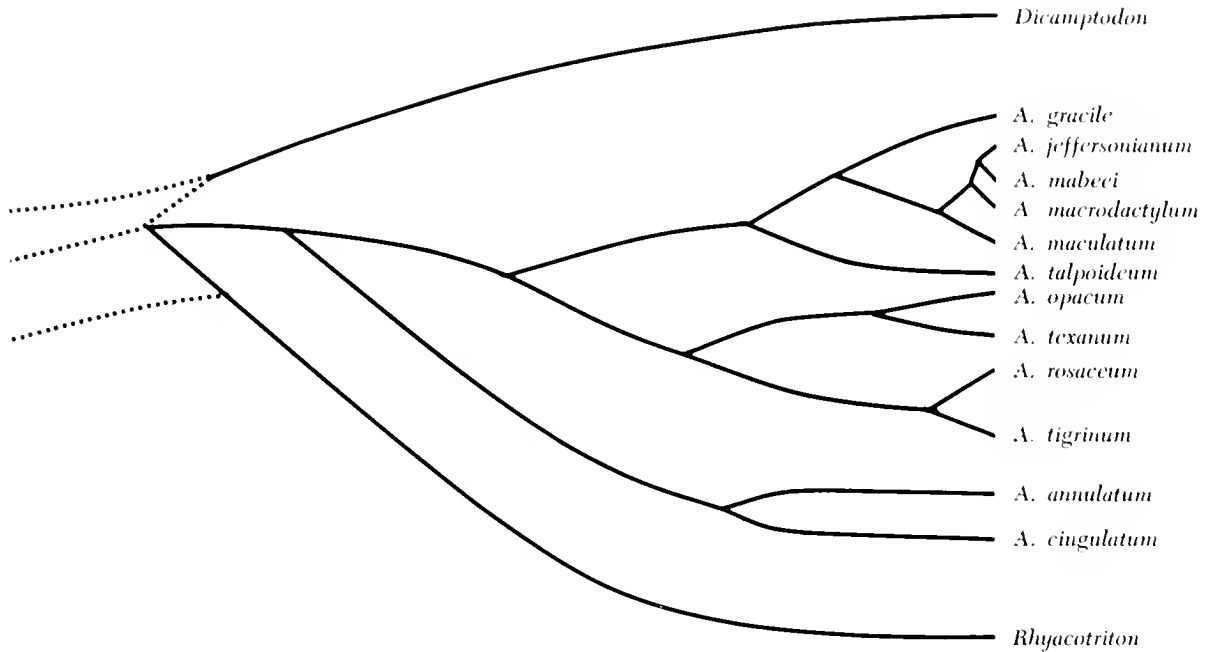


Fig. 19. Possible phylogeny for the Ambystomidae of the United States and northern Mexico.

A. opacum and *A. texanum* show a closer relationship to each other on the basis of their throat anatomy than they do to other members of the family. They differ from each other in only two characters, and for the one character (the shape of the second basibranchial) they are different from all of the others. The nearest association of the *opacum-texanum* group is with the *rosaceum-tigrinum* group at .991 (Fig. 18).

A. jeffersonianum, *A. mabeei*, and *A. macrodactylum* differ in none of the binary characters. However, *A. macrodactylum* can be separated from *A. jeffersonianum* and *A. mabeei* by the fact that it contains no ossification in the epibranchial tips in fully transformed adults. *A. jeffersonianum* and *A. mabeei* can be separated by the shapes of their otoglossal cartilages (Fig. 6 and 7). *A. maculatum* differs from the others in the width of the linea alba. *A. gracile* is associated with this same cluster, differing from them in the shape of the first basibranchial and in having a divided intermandibularis posterior.

A. talpoideum is aligned more closely with the *gracile-jeffersonianum-mabeei-macrodactylum-maculatum* group than with the *opacum-texanum-tigrinum* group. This is based primarily on the shape of the first basibranchial. The former group, like *A. talpoideum*, all have pear-shaped first basibranchials, whereas this structure in the latter group is shield shaped.

When the binary characters concerned with muscles are masked from the analysis, the alignment of the species is unchanged from that de-

scribed above. This then, represents an arrangement based on the hyobranchial skeleton. The hyobranchial skeleton characters were also masked, and the analysis produced thereby is one based on information concerning muscles. In this case *A. opacum* and *A. texanum* are more widely separated from each other than in the former method, and *A. rosaceum* becomes more widely separated from the *tigrinum* group. Otherwise, the cluster arrangement is the same. Such confirming data derived from two anatomical sources add considerable weight to a phylogenetic conclusion and seems to us to be of utmost importance.

There is considerable similarity between the alignment of the species of the genus *Ambystoma* as presented here and that suggested by Tihen (1958). There is agreement in the placement of *A. rosaceum* in the *tigrinum* group, and in the placement of *A. gracile*, *A. jeffersonianum*, *A. macrodactylum*, and *A. maculatum* in the *maculatum* group. He has also aligned *A. annulatum* and *A. cingulatum*. We disagree in the placement of *A. talpoideum*, *A. mabeei*, and *A. texanum* (compare Figure 18 with Tihen's groups in the introduction).

Tihen's classification is based on skull morphology, whereas ours is based on the hyobranchial apparatus. Inasmuch as the hyobranchial apparatus is more directly involved with those anatomical structures associated with the processes of breathing and feeding than is the skull, this apparatus provides, we believe, a more sensitive

indicator of the evolution that has occurred in these salamanders.

Some interesting evidence with regard to interfamilial relationships has come to light in the course of this investigation. Most workers are of the opinion that the ambystomids gave rise to the salamandrids and that the salamandrids in turn gave rise to the plethodontids. Regal (1966), in considering feeding mechanisms, affirms that the free-tongue condition seen in the plethodontids is an advanced condition and that the tongue of the Salamandridae, which is attached and less protrusible, is a correspondingly less advanced condition. He further concludes that in primitive salamanders the tongue, being firmly attached at its base and along its sides, is not capable of extension outside of the mouth cavity. This latter type is an aquatic structure—a "water tongue"—whereas the free-tongue condition is found in terrestrial salamanders which feed upon more elusive prey. For the most part the Ambystomidae have a tongue which is attached in a primitive manner. The flexible hyobranchium of *Rhyacotriton*, however, enables this advanced ambystomid to utilize terrestrial feeding more so than it would appear to occur in most of the other members of the family. The long subhyoidus and genioglossus muscles have assumed an important role in propelling the tongue forward.

The epibranchial cartilage was found in all of the ambystomids dissected. The absence of this cartilage in some of the salamandrids would appear to be evidence for the advanced nature of the Salamandridae with respect to the Ambystomidae.

Further evidence for this relationship is found in the fact that there were two pair of radials present in all of the ambystomid specimens. Some salamandrids have only one pair, and Bogoljuskij (1924) has confirmed that the two-pair condition is primitive. The otoglossal cartilage was also present in all of the ambystomid specimens, whereas it is lacking in both Salamandridae and Plethodontidae (Dunn, 1926). Figure 17 illustrates those changes which have occurred in the otoglossal and the radials. The primitive ambystomid, *Dicamptodon*, has a platelike otoglossal which is fused to the second radials. The more advanced condition in Ambystomidae consists of an annular otoglossal which articulates with the tips of the second radials. The salamandrid condition shows complete loss of the otoglossal and in some genera a loss also of the second radial. The otoglossal is absent in Plethodontidae as illustrated in Figure 17, and there is likewise a noticeable reduction in the radial cartilages. As the tongue has become more flexible and freed from the floor of the mouth in

advanced salamanders, it would appear that there has been a tendency toward reduction and even loss of the otoglossal as well as a rearrangement of teeth over the roof of the mouth. The rearrangement consists of a shifting of the teeth posteriorly to lie directly above the tongue pad rather than more anteriorly to correspond in position above the otoglossal as in the ambystomids. In the more terrestrial salamandrids and plethodontids, the tongue has become increasingly freed from the floor of the mouth and functions more effectively in the capture of insects. Captured insects are manipulated by the tongue and forced up against the numerous teeth located on the roof of the mouth. Ambystomids, on the other hand, have a much less flexible tongue, and have retained the otoglossal cartilage apparently as an aid in forcing food up against the vomerine teeth, which form a transverse row directly opposite the otoglossal.

The epibranchial is longer with respect to the ceratobranchial in Salamandridae (Özeti and Wake, 1969) than in the Ambystomidae studied. Tanner (1952) illustrated these extremely long cartilages in the Plethodontidae.

The second basibranchial is present in all of the ambystomids studied. It is lost in most salamandrids (Özeti and Wake, 1969) and is probably completely missing in plethodontids (Dunn, 1926; Tanner, 1952).

All of the foregoing facts support the hypothesis that the ambystomids are primitive to the salamandrids and that the latter are in turn primitive to the plethodontids. There is reason, however, to consider another alternative. If ossification of the hyobranchium is to be considered a primitive character, then with respect to this character the Salamandridae would be primitive to the Ambystomidae and the Plethodontidae. The ceratohyal, for example, is from 30 to 50 percent ossified in most salamandrids (Özeti and Wake, 1969), whereas it is much less than this in Ambystomidae (Table 1) and in the Plethodontidae (Tanner, 1952; Wake, 1966). The first ceratobranchial is totally unossified in the Ambystomidae and well ossified in most Salamandridae. However, there are salamandrids with totally cartilaginous hyobranchial skeletons, and, therefore, since this high level of ossification is not consistent throughout the family, the use of percentages of ossification as an index of phylogenetic relationships between families seems to be unjustified. In fact, there is considerable variation within each family with respect to percentages of ossification, and, moreover, an interesting parallelism seems to have occurred in each family. The advanced members of a particular family seem to be more capable of terrestrial

feeding habits, and in these salamanders there has been a reduction in the amount of calcification in the hyobranchium, thereby making it more flexible to facilitate the capture of prey through tongue pad flipping. The highly advanced free-tongued plethodontids studied by Tanner (1952) were shown to have no ossification whatever in the hyobranchium, whereas the more primitive plethodontids as reported by Wake (1966) did have definite centers of bone in the hyobranchium. The ambystomid which is most terrestrial in its feeding habits, *Rhyacotriton*, has a completely bone-free hyobranchium; and the terrestrial feeders among the Salamandridae (*Salamandra*, *Chioglossa*, and *Salamandrina*) are likewise equipped with more cartilage in the hyobranchium than the other presumably more primitive members of the family (Özeti and Wake, 1969). It would appear, therefore, that the percentage of ossification of the hyobranchium may have some value as an index to phylogeny, but is of limited value if one wishes to study interfamilial phylogeny. Thus, the percentage of ossification has importance in determining the degree of adaptation toward a terrestrial habitat.

An investigation of the muscle adaptations is also important and of interest in an assessment of development toward the more terrestrial type of feeding. An examination of the more advanced plethodontids indicates a greater development of the anterior transverse muscles. Except for the genus *Thorius* those genera of free-tongued plethodontids studied by Tanner (1952) possessed a large anterior development of the intermandibularis. According to his analysis, this represents the intermandibularis anterior, a muscle thought by Piatt (1935) to be lost at metamorphosis. This must yet be demonstrated by an embryological investigation; however, the fact still remains that in these plethodontids there is a relatively large mass of transverse muscle which ties the anterior part of the mandibular area together and which is not interrupted by the linea alba. The development anteriorly is also accompanied by a reduction in the size and extent of the transverse muscles in the more posterior areas of the throat.

If we examine other related but more primitive families (salamandrids and ambystomids), we do not see the same types of muscle development; but we do see in the more terrestrial forms of these families a development of the more anterior transverse muscles. In the Salamandridae, for example, the genera in which terrestrial feeding is best developed are *Salamandra*, *Chioglossa*, and *Salamandrina*; and, furthermore, these three genera tend to have a greater degree of

elaboration of the anterior portions of the throat musculature than other genera in the family (Özeti and Wake, 1969). There is also a concomitant reduction in the posterior parts of the throat musculature in these land feeders. The three genera of salamandrids noted above all have experienced a reduction in myosepta of the rectus cervicis superficialis as compared to the other members of the family, and a corresponding reduction in rectus cervicis superficialis myosepta has occurred in *Rhyacotriton* of the *Ambystomidae*.

In the plethodontidae there is also a reduction of the myosepta in the rectus series. Tanner (1952) figures this reduction and also indicates a reduction and finally a complete loss of the omohyoideus muscle, which in the less advanced species ties the rectus throat muscles to the pectoral girdle (scapula). There is also a gradual reduction in the size of the second basibranchial (os thyroideum) until it is lost in the free-tongued plethodontids. These reductions and deletions have also served to increase the flexibility of the longitudinal throat muscles and have produced an uninhibited band of muscle from the pelvis to the hyobranchium providing a mechanism for rapid tongue retraction.

An analysis of the myology and osteology of the hyobranchium of the families Ambystomidae, Salamandridae, and Plethodontidae provides evidence to support the conclusion that there has been a degree of parallel development leading toward a terrestrial development of feeding and perhaps breathing. In all three families, we note a reduction in the ossification of the skeletal elements of the hyobranchium depending, we believe, on the degree of the terrestrial type feeding achieved by members of a generic or specific group within these families. The flexibility of the hyobranchium achieved by the free-tongued plethodontids is most remarkable and has virtually eliminated in some species that type of feeding in which jaws are used as the grasping or food-getting device. One is caused to wonder if the development of the tongue as an almost exclusive food-getting device is the ultimate type of development to be achieved in the process of adaptive radiation in terrestrial salamanders and perhaps also in lizards (Chamaeleonidae).

The conversion of the skeletal elements into a flexible cartilaginous structure and the reduction in size and deletion of some elements has been accompanied by modifications in the myology. As indicated above, there have been basic modifications in the muscles which have in effect reduced the heavy musculature of the throat area. Associated with this reduction, there has

been a specialization in both the transverse and longitudinal muscle series. A specialization of particular interest to us is the development of the most anterior transverse muscles in certain groups of each family in which the muscle fibers extend uninterrupted across the midline. Tanner (1952) referred to these as the intermandibularis anterior and based his conclusions on the fact that in the plethodontids studied there was a small tendinous fascia tying each end of the muscle to the opposing mandible. A comparison of this muscle in those ambystomids and salamandrids in which fibers extend across the linea alba suggests that in these families those continuous fibers represent the anterior fibers of the intermandibularis posterior which have been modified to strengthen the anterior area of the now changing food-getting mechanism. We have found no indication that the intermandibularis anterior is retained in any members of the latter two families. This anterior myological specialization suggests that there is a definite convergence leading toward a terrestrial type of feeding which involves an increasing use of a more flexible tongue.

If we examine the posterior transverse muscles, we note a reduction in size and mass with an increase in the width of the central fascia as the entire structure becomes more flexible. The longitudinal series has also been effected to the extent that they have become more elongate (in some plethodontids the rectus cervicis series are actually folded, Tanner, 1952, plate 73, Fig. G). Özeti and Wake (1969) indicate a reduction in the numbers of myosepta in the rectus series of such genera as *Salamandra*, *Chioglossa*, and *Salamandrina*. We particularly note a similar change in *Rhyacotriton* in which the myosepta of the rectus series have been reduced to two. In *Rhyacotriton* the genioglossus has been extended beyond the first radii of the first basibranchial and reaches posterior to insert on and in fascia attached to the first ceratobranchial. This adaptation provides for a longer muscle and permits a greater length of contraction in pulling the hyobranchium anteriorly in the extending of

the tongue. Although we note that different structures have been altered, the general effect appears to be the same, namely, that terrestrial groups in each family have modified the hyobranchium to provide for greater flexibility and have increasingly involved the tongue as an evermore important food-getting organ.

We have found the musculature of the Ambystomidae to be more advanced in some respects than previous workers have reported. Contrary to Piatt's findings, the ambystomids do have a subhyoideus, and therefore this character cannot be used to separate the families as it has been in the past. Piatt further reported that the transverse ventral throat muscles posterior to the intermandibularies posterior are the interhyoideus posterior in Cryptobranchidae, Amphiumidae, and Ambystomidae and that these two muscles remain in the adults in an essentially unchanged condition. We have found the interhyoideus posterior to be the same as the larval muscle. In the Plethodontidae, this muscle becomes divided into the gularis and the quadratopectoralis. The interhyoideus of the larva, however, becomes divided into subhyoideus and interossequadrata in the adults of Ambystomidae and Salamandridae.

This new information on myology does not answer the question with regard to the relationship between Ambystomidae and Salamandridae except that it does make the ambystomids appear more advanced than they were previously thought to be. The preponderance of evidence still seems to support the concept that the Ambystomidae are primitive to both the Salamandridae and the Plethodontidae.

In the past it has been assumed that the order of phylogeny is from the Ambystomidae to the Salamandridae to the Plethodontidae. However, based on the findings of this study there is a second distinct possibility that the ambystomids may have given rise independently to both the salamandrid and plethodontid families. These two possibilities are presented in Figure 20.

SUMMARY

1. The hyobranchial skeleton is mostly cartilaginous with a few isolated areas of bone located in certain components. Only in *Dicamptodon* is ossification widespread throughout the hyobranchium, although this ossification is not heavy. In only a few areas in *Dicamptodon*, such

as the tips of the ceratohyals, is the ossification heavy.

2. The first basibranchial is shield-shaped, pear-shaped or rod-shaped and usually has a central core of bone. Bone is completely absent in *Rhyacotriton* and in *A. gracile*.

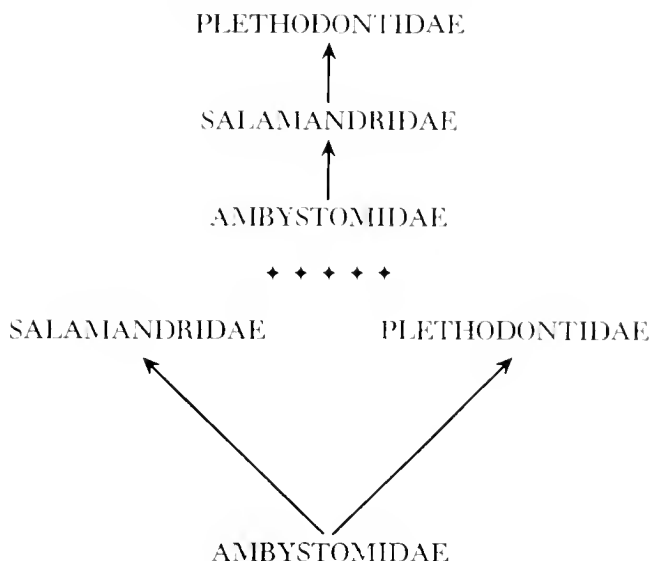


Fig. 20. Diagrams depicting the possible phylogenetic relationships between the Ambystomidae, Salamandridae, and Plethodontidae.

3. The first radial cartilages are entirely cartilaginous. They are usually long, slender rods that may or may not unite with the tips of the ceratohyal; although in *A. cingulatum* they are very short and rounded. In *Dicamptodon* there is a joint midway along the length of the first radial.

4. The second radial cartilages are always unossified and curve dorsally to meet the otoglossal. *Dicamptodon* has a fusion of the second radials and the otoglossal plate to form a single platelike structure.

5. There is usually no ossification in the first ceratobranchial. One specimen of *A. cingulatum* contained a spot of bone in the medial end of this structure which represented 11 percent of the total volume of the first ceratobranchial.

6. The second ceratobranchial is always unossified and articulates with the first branchial arch either at the joint between the first ceratobranchial and the epibranchial or immediately posterior to that joint.

7. There is an epibranchial cartilage in all species included in this study. However, in some the articulation of this structure with the first ceratobranchial is indistinct. This is the case in *Dicamptodon*, *A. annulatum*, and *A. cingulatum*.

8. The ceratohyal is often ossified on its posterior or distal tip.

9. The second basibranchial is present in all species. Its shape is 3-radiate, 4-radiate, or an inverted V. Usually, the central portion is ossified with the tips of the lateral arms remaining cartilaginous. In *Dicamptodon*, *Rhyacotriton*,

and *A. opacum*, the entire structure is cartilaginous.

10. The linea alba is usually wide at the level of the intermandibularis posterior. In *A. maculatum* it is a very thin line.

11. The fibers of the intermandibularis posterior insert into the linea alba of the throat; although, in *Rhyacotriton*, *A. cingulatum*, and *A. gracile*, a few of the anterior fibers extend all the way across the midline without being interrupted by the linea alba.

12. The levator mandibulae is hypertrophied in *Rhyacotriton* and *Dicamptodon*. This may be associated with their stream feeding habit, which requires a more aggressive behavior than used by the other members of the family (genus *Ambystoma*) in their pond habitats.

13. Contrary to the reports of earlier workers, the subhyoideus is found in all species studied. It is derived from the larval interhyoideus which at metamorphosis divides into the subhyoideus and the interosssaquadrata. It is usually small and delicate and extends forward only as far as the anterior edge of the ceratohyal. In *Rhyacotriton*, however, it is longer, extending all the way forward to the mandible. In *Dicamptodon*, this muscle is not as long as in *Rhyacotriton*, but it is thick and heavy when compared with other species.

14. The genioglossus is divided into a ventral and dorsal portion in all species. Only in *Rhyacotriton* does this muscle extend as far posteriorly as the first ceratobranchial.

15. A hyoglossus is present in all species ex-

cept *Dicamptodon*. The posterior portion of the genioglossus in *Dicamptodon* lies in the position occupied by the hyoglossus in the other members of the family, and it appears likely that the hyoglossus is derived from the genioglossus by specialization of the posterior part of the muscle.

16. There are usually three transverse inscriptions on the rectus cervicis superficialis. In *Rhyacotriton* and *A. talpoideum*, however, there are only two.

17. The rectus cervicis profundus usually attaches to the otoglossal cartilage by a fleshy rather than a tendinous insertion. In *A. annulatum* and *A. cingulatum* this insertion is by way of a thin tendon.

18. The heboosteopsiloideus originates on the second myoseptum of the rectus cervicis profundus posterior to the second basibranchial in all species except *A. annulatum* and *A. opacum*, in which it arises from the first inscription.

19. The variation in ratios of dimension of hyobranchial skeleton elements that is found within a given species is excessive beyond that which would allow this information to be of value in species differentiation. Whereas these dimensions have been used successfully by other workers in the phylogenetic alignment of salamanders at the generic level, this study indicates they are not equally usable in studies at the species level.

20. The 16 species and subspecies are placed into six groups according to their throat morphology as follows: The *Dicamptodon* group, the *Rhyacotriton* group, the *A. annulatum*-*A. cingulatum* group, the *A. gracile*-*A. jeffersonianum*-*A. mabeei*-*A. macrodactylum*-*A. maculatum* group, the *A. talpoideum* group, the *A. opacum*-*A. texanum* group, the *A. rosaceum*-*A. t. tigrinum*-*A. t. melanostictum*-*A. t. nebulosum* group.

21. *Dicamptodon* appears to be the most

primitive group, and *Rhyacotriton*, the most specialized.

22. Based on the morphology of the throat region, it is suggested that *A. rosaceum* be placed in the tiger salamander group as a subspecies of *A. tigrinum*.

23. The binary characters when applied separately to the hyobranchial skeleton and the hyobranchial musculature produce essentially the same phylogenetic results.

24. In comparing the hyobranchium and throat myology in different families of salamanders, there appears to have developed a parallelism within each family with respect to adaptations toward terrestrial feeding. These adaptations include the reduction and even complete loss of bone in the hyobranchium. The elaboration of the anterior throat musculature to provide a mechanism for rapid tongue pad flipping has resulted in a reduction in the size of muscles and in the number of myosepta in the posterior throat musculature. These adaptive changes seem to have occurred as the need for sucking action and jaw movement seen in aquatic salamanders are replaced by rapid tongue protrusion and retraction in the terrestrial forms.

25. The results of this investigation support the hypothesis that Ambystomidae is primitive to Salamandridae and to Plethodontidae. The findings which have led to this conclusion are based upon the protrusibility of the tongue and upon the structure and presence of the epibranchial, otoglossal, second radial, and second basibranchial cartilages of the three families. The muscles which have added information concerning these interfamilial relationships are the intermandibularis posterior, levator mandibulae, subhyoideus, genioglossus, hyoglossus, rectus cervicis profundus, rectus cervicis superficialis, and heboosteopsiloideus.

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**Brigham Young University
Science Bulletin**

**UNDERSTORY CHARACTERISTICS
RELATED TO SITE QUALITY
FOR ASPEN IN UTAH**

by

James H. Warner

and

K. T. Harper



BIOLOGICAL SERIES — VOLUME XVI, NO. 2

APRIL 1972

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TABLE OF CONTENTS

INTRODUCTION	1
LITERATURE REVIEW	2
METHODS	3
Location of Study Areas	3
Tree Samples	5
Herb Layer	5
Soil Studies	5
LABORATORY METHODS	7
Plant Species	7
Environmental Factors	7
Data Analysis	7
RESULTS	7
Stand Distribution	7
Prevalent Species	7
Species Associated by Chi-Square	8
Site-Quality Determinations	11
Environment	14
DISCUSSION	14
ACKNOWLEDGMENTS	18
LITERATURE CITED	19

tion. Undoubtedly, a large part of the neglect is attributable to the fact that the species was considered a "weed" tree for many decades by resource managers. At the present time, the literature pertaining to aspen in the West consists of numerous notes and peripheral studies considering individual facets of the species' ecology; but Baker's study (1925) is the sole attempt to interpret the general ecology of this forest-type. Even Baker's classical study largely ignores characteristics of the understory vegetation and details of the soil environment. Thus, at the present time when new and often conflicting demands are being made on the aspen-type, western resource managers find themselves confronted with a bewildering array of ecological questions for which there are few, well-documented answers.

LITERATURE REVIEW

Baker's paper (1925) stands as the only intensive consideration of the ecology of quaking aspen in the West, although several other investigators have studied individual facets of aspen ecology. Age and height values for aspen growing in association with different understory types in Montana have been reported by Lynch (1955). Alder (1969) has reported on the age structure of aspen forests of Utah. A recent popularized account of aspen ecology in the West was published by Cottam (1963), Langenheim (1962), working in western Colorado, and Ream (1963), in the Wasatch Mountains of Utah and Idaho, drew general conclusions about the relative position of aspen in the environmental complex in their respective areas. Heinselman and Zasada (1955), Strotham and Zasada (1957), and Fowells (1965) have attempted to integrate published reports of the behavior and use of quaking aspen throughout North America.

Compositional characteristics of the understory in aspen forests have been more thoroughly investigated in the West than has the tree itself. Numerous papers have contributed to our knowledge of the understory vegetation associated with aspen. Lynch's studies (1955) provide a useful understanding of the understory vegetation of aspen in northern Montana. The nature of the understory in Wyoming is set forth by J. Reed (1952), R. Reed (1969), and Hoff (1957). For Colorado, papers by Costello (1944), Hoff (1957), Langenheim (1962), and Morgan (1969) give useful data for the aspen-type. In Utah, Allan (1962) and Ream (1963) provide data on the understory of aspen in the Wasatch Mountains, and Ellison and Houston (1958) dis-

This study was designed to provide a better understanding of the relationship between understory composition and site-quality for aspen itself. An attempt is made to devise a scheme for predicting site-quality from understory vegetation. Also, some preliminary correlations between gross characteristics of the understory and height-over-age relations of aspen are made.

Inasmuch as a major portion of the acreage of aspen in western America is confined to the states of Colorado and Utah, it was considered desirable to conduct the study within that area. Preliminary work indicated that a broad range in site-quality and understory characteristics could be found in aspen forests of Utah and northern Arizona. Accordingly, all field work was confined to that area to minimize travel time.

cuss the production of herbaceous material under the canopy and in treeless openings of aspen forests of central Utah. Houston (1954) published a "condition" guide for aspen ranges in the Intermountain Region which gives some idea of the impact livestock have had on the type. In none of the foregoing papers, however, has there been an attempt to relate the performance of individual species or groups of species to specific characteristics of the abiotic environment or to the performance of aspen itself.

There is clear evidence that many aspen forests throughout the West are currently being replaced by conifers in the course of natural succession (Baker, 1918 and 1925; Daubenmire, 1943; Hall, 1953; Oosting, 1956; Hoff, 1957; and Cottam, 1963). There are numerous indications in the literature, however, that the successional processes are extremely slow or nonexistent in many parts of western America (Fetherolf, 1917; Reed, 1952; Lynch, 1955; Marr, 1961; Langenheim, 1962; Julander et al., 1964; Morgan, 1969; and Reed, 1969). A more thorough knowledge of the successional process would seem to be needed if the best management procedures possible are to be implemented.

The nature of aspen forests can also be greatly modified by the influence of domestic grazers (Baker, 1918; Sampson, 1919; Houston, 1945; Coles, 1965; Hutchins, 1965; and Lucas, 1969) and big game (Coles, 1965 and Alder, 1969). It seems possible that aspen can actually be eliminated from a site if animals are permitted to repeatedly browse off the trees' reproduction (Alder, 1969 and Lucas, 1969).

The most conspicuous deficiency in all of the foregoing studies lies in their failure to study the abiotic environment in detail. The soil studies of Lynch (1955) are not presented in a form suitable for interpretation of the performance of individual plant species. Likewise, a detailed study of the influence of topographic position on the behavior of aspen has never appeared in the literature. Crowther and Harper (1965) have studied the influence of parent material on aspen forest development in Utah, but the study was confined to a single watershed and a narrow range of parent materials. A useful study by Jones (1967a) considers the influence of various combinations of climatic, topographic, and edaphic characteristics on height growth of aspen stands in Colorado, New Mexico, and Arizona. Additional studies of this type are needed in other parts of the Mountain West.

Disease appears to play a key role in the dynamics of aspen forests in the West. Meinecke (1929), Mielke (1957), Hinds (1962), and Krellbill (1971) discuss the major diseases attacking western aspen. The influence of ecological conditions on distribution and severity of important diseases is still largely unknown, however.

Attempts to utilize understory species as indicators of site potential for either tree growth or herbage production as advocated by early ecologists (Korstian, 1917 and Riggs, 1929) have not usually been successful (Kittredge, 1938 and Driscoll, 1963). However, a few workers have used understory species as indicators of site potential for tree growth with success (Rowe, 1956; Gadnon and MacArthur, 1959; Hills and Pierpont, 1960; Daubenmire, 1961; and Orloci, 1962), but methods employed have not usually been well quantified.

METHODS

In this study, an attempt is made to develop a simplified and completely quantitative approach to the use of understory species as indicators of site-quality. Statistical reliability of indicators will be verified and a straightforward technique for integrating response of many indicators devised. Once the indicators are identified, any person with the ability to identify those species should be able to derive the index for any given site.

The 49 stands employed in this study were initially ordered according to site indices derived from tree height-over-age data using Jones's (1967b) natural site index curves. The statistical relationship between Jones's natural site index for each of the several stands and the index values derived by the use of understory species for the same stands was determined by simple correlation.

LOCATION OF STUDY AREAS

Study sites extend along the mountainous backbone of Utah from Logan Canyon on the north to Fish Lake on the south. Six additional stands are located in northern Arizona on the Kaibab Plateau (see Fig. 1 and Table 1).

All stands selected were approximately 0.04 hectare (0.1 acre) in size and satisfied the following criteria: (1) tree density appeared average for the particular site (very sparse and very dense stands were avoided); (2) aspen contributed 100 percent of the tree canopy; (3) average tree age was in excess of 30 years; (4) area

sampled was well buffered on all sides by similar aspen forest; and (5) aspect, soil, topo-

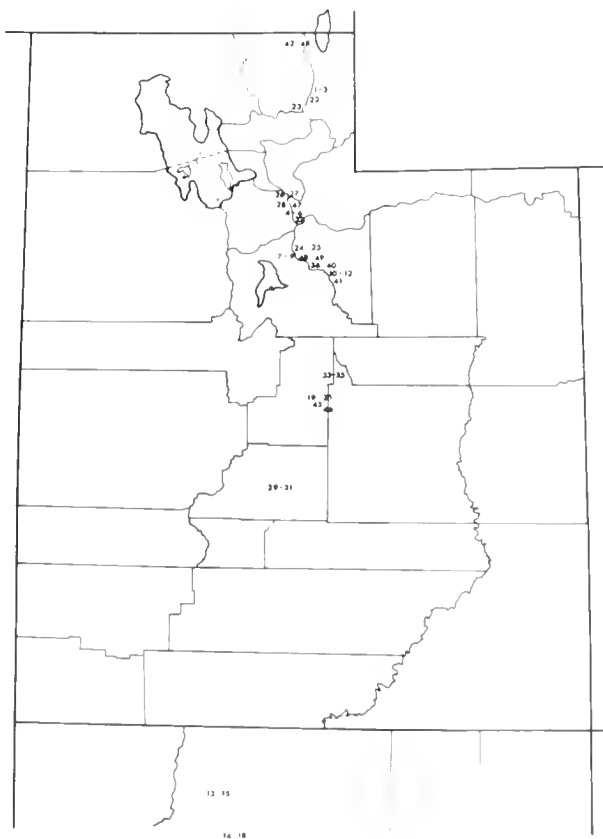


Figure 1. Distribution of stands.

Table 1. Location of stands and the gross environmental characteristics of each.

Stand No.	Elev. (m)	% Slope	Exposure ^o	Township-Range Section	Natl. Forest	Area Name
1	2469	12	20	T8N R4E S21	Cache	Squaw Flats
2	2469	15	295	T8N R4E S21		
3	2499	19	23	T8N R4E S21		
4	2667	47	190	T2S R3E S26	Wasatch	Big Cottonwood Canyon
5	2301	53	180	T2S R3E S17		
6	2865	36	158	T2S R3E S25		
7	2435	6	115	T4S R3E S33	Wasatch	Aspen Grove (Mt. Timpanogos)
8	2408	43	47	T4S R3E S33		
9	2423	13	105	T4S R3E S33		
10	2591	11	0	T3S R12W S24	Uinta	Mud Creek (Strawberry Reservoir)
11	2591	14	325	T4S R12W S24		
12	2591	13	348	T4S R12W S24		
13	2789	20	50	T35N R3E S34	Kaibab	Jacob Lake Arizona
14	2576	29	100	T38N R2E S20		
15	2667	8	70	T37N R2E S34		
16	2515	5	120	T33N R2E S4	Grand Canyon Natl. Park	North Rim
17	2499	7	35	T33N R2E S4		
18	2545	29	150	T32N R3E S5		
19	2652	14	200	T17S R4E S20	Manti-LaSal	Great Basin Exp. Sta. (Ephraim)
20	2682	10	113	T17S R4E S20		
21	2743	32	225	T17S R4E S20		
22	2134	7	270	T8N R4E S20	Cache	Ant Flats
23	2438	17	260	T8N R4E S20		
24	2377	27	90	T4S R3E S33	Wasatch	Aspen Grove
25	2377	15	280	T4S R3E S33		
26	2057	31	315	T1N R3E S20	Wasatch	Red Butte Canyon
27	2073	40	315	T1N R3E S20		
28	2316	NA	195	T1S R3E S31	Wasatch	Mill Creek Canyon
29	2758	8	10	T24S R3E S24	Fish Lake	Cold Springs
30	2774	30	75	T24S R3E S24		
31	2743	31	120	T24S R3E S24		
32	2323	30	210	T2S R3E S26	Wasatch	Big Cottonwood
33	2435	11	150	T14S R6E S34	Manti-LaSal	Scad Valley
34	2591	16	95	T14S R6E S26		
35	2438	48	150	T14S R6E S26		
36	2731	18	70	T6S R6E S7	Uinta	Wallsburg Road (Daniels Canyon)
37	2792	21	60	T6S R6E S7		
38	2481	20	347	T5S R5E S36		
39	2408	12	145	T5S R6E S26		
40	2522	9	40	T5S R6E S26		
41	2234	6	60	T3S R12W S35	Uinta	Bryants Fork
42	2408	13	160	T13N R3E S7	Cache	Tony Grove (Logan Canyon)
43	2385	27	150	T13N R3E S7		
44	2469	48	180	T13N R3E S8		
45	2347	43	345	T17S R4E S23	Manti-LaSal	Willow Creek
46	2713	8	300	T17S R5S S28	Manti-LaSal	Thistle Flats
47	2286	NA	200	T1S R3E S31	Wasatch	Mill Creek Canyon
48	2432	NA	NA	T4S R3E S33	Wasatch	Aspen Grove
49	2408	NA	NA	T4S R3E S33		

* In degrees, clockwise from north
 NA = Data not available

graphic position, slope, and vegetational pattern were uniform throughout the area sampled. Stands were almost exclusively grazed by deer and/or domestic sheep. The three stands on the Kaibab National Forest are now grazed by cattle but have had a long history of sheep use until the recent past. All sampling, except for soil temperature, was completed during the summers of 1965 and 1966.

Stands were selected on a variety of sites supporting pure aspen forests (i.e., to the extent possible, seral stands were avoided). An attempt was made to include stands on the full range of site conditions within the defined area (see Fig. 1). For ease of accessibility all stands were located within national forests and national parks. Detailed maps were drawn of each stand and its surroundings so that the exact location could be easily located on return visits. Stands were square-shaped and marked at each corner with orange surveyor's tape.

For each stand, the following data were recorded: (1) location, (2) elevation, (3) aspect, (4) slope, (5) description of landscape, and (6) nature of any disturbing influence.

TREE SAMPLES

A tree is here interpreted as any woody stem having a diameter in excess of 10 cm (4 in) at breast height (dbh). All trees within the borders of each stand were measured and the following data recorded: (1) dbh, (2) height (using an optical range finder), and (3) evidence of disease, fire, or animal damage. In addition, cores from the 10 tallest trees were taken at breast height with an increment borer for subsequent aging in the laboratory. An attempt was made to locate stand boundaries so that all trees of the stand were of the same clone. When it could be determined, the sex of the clone was recorded.

HERB LAYER

The herb layer was sampled immediately following establishment of the stand boundary in order to minimize the effect of trampling. Twenty-five square quadrats, each 0.25 m² in area (1/16,000 acre), were uniformly distributed throughout the stand for frequency data. Above ground, current year production to a height of 1.8 m (6 ft) was taken in 42 stands between July 15 and August 15 of the years of study. Production was estimated on 36 quadrats (0.89 m² or 9.6 ft²) per stand. Accuracy of the estimate was regularly checked by clipping and weighing. Field weights were converted to air dry weights

by use of conversion factors obtained by drying vegetational samples from each study area.

A list of all vascular plants present within the boundaries of each stand was prepared (Warner, 1971). Species were classified into broad life-form and longevity classes (Table 2). A degree of arbitrariness was involved in the assignment of perennial forbs to height classes. *Osmorhiza chilensis* and *Valeriana occidentalis*, for instance, occasionally grow to a height in excess of 30 cm (the breaking point between short and tall forbs); but since their photosynthetic surface is almost wholly developed close to the ground, we have classified these species as short forbs.

SOIL STUDIES

In each stand, soil samples were collected and soil temperature measured. Soil profile data were obtained from a pit dug to the depth of 1.5 m (60 in) or to bedrock, whichever was shallower. Samples were taken from each horizon of the profile with a bulk density sampler of 750 cc capacity. For each horizon, the occurrence of mottling or gleying and physical properties such as structure, color (by Munsell soil color chart), percent by volume of rock over 2 mm diameter, and the amount of rooting were recorded. Soil samples from each horizon were placed in plastic bags and returned to the laboratory, where they were dried at 105° C for at least 24 hours.

Soil temperatures were taken at the center of each stand at the following depths: 13, 25, and 38 cm (5, 10, and 15 in), using a steel-stem, dial-type thermometer. Soil temperatures were taken in all stands during a two-week period in mid-August 1968.

Following drying, the portion of soil samples passing a 2 mm sieve was analyzed for the following characteristics: (1) texture, (2) bulk density, (3) pH, (4) exchangeable calcium, and (5) "available" phosphorus. Soil extracts for determination of the nutrient elements were prepared by washing 3 g of sieved soil with 60 ml of 0.2 N acetic acid for one hour. Calcium was measured by flame photometry (Jackson, 1958) and phosphorus by spectrophotometry (Goldenberg and Fernandez, 1966). The results are expressed as mg of substance per g of soil.

Soil texture was analyzed by a hydrometric method as described by Bouyoucos (1928). The pH was determined by preparation of a slurry consisting of a soil-water mixture in a ratio of 1:1. Readings were made with a glass electrode pH meter.

The weight of a standard volume of rock-free soil was used to compute the bulk density of the various horizons of the soil profiles. When aver-

age values for whole profiles were calculated for pH, phosphorus, calcium, and texture, values for individual horizons were weighted by horizon

depth (reduced by a quantity equal to the percent volume of rock in the horizon) and bulk density.

Table 2. Prevalent species list. The letters in parentheses following the scientific names designate the "life-form" class of the species. Life-form abbreviations are as follows: T, tree; S, shrub; TF, tall forb; SF, short forb; AF, annual forb; and G, graminoid.

Species	Common Name	Pres. %	Avg. Freq.	P x F Index
1. <i>Stellaria jamesiana</i> (SF)	Tuber Starwort	80	64	5120
2. <i>Bromus polyanthus</i> (G)	Mt. Brome	84	59	4956
3. <i>Lathyrus lauszwertii</i> (SF)	Peavine	78	56	4368
4. <i>Galium bifolium</i> (AF)	Twinleaf Bedstraw	78	55	4290
5. <i>Collomia linearis</i> (AF)	Collomia	61	59	3599
6. <i>Nemophila breviflora</i> (AF)	Nemophila	51	67	3417
7. <i>Collinsia parviflora</i> (AF)	Blue-eyed Mary	63	48	3024
8. <i>Elymus glaucus</i> (G)	Blue Wildrye	69	43	2967
9. <i>Osmorhiza chilensis</i> (SF)	Sweetroot	73	39	2847
10. <i>Agropyron trachycaulum</i> (G)	Slender Wheatgrass	71	39	2769
11. <i>Polygonum douglasii</i> (AF)	Douglas Knotweed	69	38	2622
12. <i>Vicia americana</i> (TF)	American Vetch	67	36	2412
13. <i>Descurainia californica</i> (AF)	California Tansymustard	67	36	2412
14. <i>Poa curta</i> (G)	Bluegrass	57	37	2109
15. <i>Thalictrum fendleri</i> (TF)	Fendler's Meadow Rue	78	27	2106
16. <i>Viola nuttallii</i> (SF)	Nuttall Violet	57	36	2052
17. <i>Taraxacum officinale</i> (SF)	Dandelion	61	32	1952
18. <i>Poa pratensis</i> (G)	Kentucky Bluegrass	51	35	1785
19. <i>Chenopodium fremontii</i> (AF)	Fremont Goosefoot	74	24	1776
20. <i>Hackelia floribunda</i> (TF)	Stickseed	63	26	1638
21. <i>Achillea millefolium</i> (SF)	Yarrow	84	19	1596
22. <i>Valeriana occidentalis</i> (SF)	Western Valerian	41	36	1476
23. <i>Populus tremuloides</i> (T)	Aspen	100	14	1400
24. <i>Symphoricarpos oreophilus</i> (S)	Mt. Snowberry	78	17	1326
25. <i>Phacelia heterophylla</i> (SF)	Vari-leaf Phacelia	49	23	1127
26. <i>Rudbeckia occidentalis</i> (TF)	Niggerhead	61	18	1098
27. <i>Mertensia arizonica</i> (TF)	Arizona Bluebell	33	33	1089
28. <i>Smilacina stellata</i> (TF)	Starry False Solomon Seal	31	34	1054
29. <i>Hydrophyllum capitatum</i> (SF)	Waterleaf	55	18	990
30. <i>Aster engelmannii</i> (TF)	Engelmann Aster	45	21	945
31. <i>Silene menziesii</i> (SF)	Menzies Silene	37	25	925
32. <i>Pachistima myrsinites</i> (S)	Mt. Lover	16	54	864
33. <i>Stipa columbiana</i> (G)	Columbia Needlegrass	43	17	731
34. <i>Berberis repens</i> (S)	Oregon Grape	29	24	696
35. <i>Carex occidentalis</i> (G)	Western Sedge	42	16	672
36. <i>Agastache urticifolia</i> (TF)	Nettleleaf Gianthyssop	55	12	660
37. <i>Senecio scrra</i> (TF)	Butterweed Groundsel	41	16	656
38. <i>Delphinium occidentale</i> (TF)	Western Tall Larkspur	41	16	656
39. <i>Senecio uintahensis</i> (SF)	Uintah Groundsel	12	51	612
40. <i>Osmorhiza occidentalis</i> (TF)	Sweet Anise	43	12	516
41. <i>Melica bulbosa</i> (G)	Onion Grass	45	10	450
42. <i>Floerkea proserpinacoides</i> (AF)	False Mermaid	14	31	434
43. <i>Cayophytum ramosissimum</i> (AF)	Groundsmoke	12	32	384
44. <i>Heracleum lmatum</i> (TF)	Cowparsnip	22	17	374
45. <i>Helenium hoopesii</i> (SF)	Sneezeweed	14	27	378
46. <i>Polemonium foliosissimum</i> (TF)	Leafy Jacobsadder	41	8	328
47. <i>Erysimum argillosum</i> (SF)	Wallflower	20	14	280
48. <i>Ligusticum porteri</i> (TF)	Porter Ligusticum	8	32	256
49. <i>Castilleja rhexifolia</i> (TF)	Splitleaf Painted Cup	6	40	240
50. <i>Bromus ciliatus</i> (G)	Fringed Brome	14	17	238
51. <i>Epilobium angustifolia</i> (TF)	Fireweed	14	14	196
52. <i>Aconitum columbianum</i> (TF)	Monkshood	10	18	180
53. <i>Scrophularia lanceolata</i> (TF)	Lanceleaf Figwort	22	8	176

LABORATORY METHODS

PLANT SPECIES

All species of the study were ranked in descending order based on a presence X frequency (P X F) index (Anderson, 1954; and Curtis, 1959) utilizing percent presence in the several stands and average frequency in *stands of occurrence* in the 0.25 m² quadrats. It should be noted that this method of calculation departs from the method used by the foregoing authors who based average percent frequency on *all stands* and not on stands of occurrence only. However, by basing average frequency on stands of occurrence only, the index becomes a probability statement of the likelihood of finding a species in any quadrat placed within the spectrum of stands sampled. This advantage was the motive for the change in manner of calculation. Species selected for detailed study were those with the highest P X F indices. A total of 53 species were used in the initial analyses.

The occurrence of positive or negative association among 42 prevalent understory species was evaluated by chi-square analysis of joint and independent occurrences of all possible combina-

tions of species in the 1,225 quadrats used to sample the herb layer of the 49 stands.

Plant nomenclature follows Holmgren and Reveal (1966).

ENVIRONMENTAL FACTORS

The following factors were tested for environmental differences among stands grouped according to site-quality of aspen: (1) slope, (2) aspect, (3) altitude, (4) soil temperature at three depths, (5) values for pH, calcium, phosphorus, sand, silt, clay, and bulk density in the A₁ horizon, and (6) average values for pH, calcium, phosphorus, sand, silt, clay, and bulk density for whole profiles. These same environmental factors were correlated with each other in all possible combinations by simple statistical correlation to determine the interrelatedness of the several environmental variables (Warner, 1971).

DATA ANALYSIS

All analysis was made by computer, using programs designed and tested by Dennis Powell, University of Utah.

RESULTS

STAND DISTRIBUTION

The stands are distributed over a range of more than 5 degrees of latitude (from 36° 13' at the North Rim of the Grand Canyon to 41° 45' in Logan Canyon, Utah). Elevation varies from 2,059 to 2,867 m (6,750 to 9,400 ft) above sea level. Average elevation for all stands is 2,500 m (8,198 ft). Stands were selected in six national forests and one national park (Table 1).

PREVALENT SPECIES

A list of the 53 most important species in the study is shown in Table 2; species are listed in decreasing magnitude of the P X F indices. An average of 36 vascular plant species was found per 0.04 ha stand.

The species listed in Table 2 include but a single tree (aspen) and only three shrubs, of which snowberry (*Symphoricarpos oreophilus*) is the most common. The remaining species include 40 forbs (23 percent of which are annuals) and 9 graminoides. Roughly two-thirds of the perennial forbs grow to a height in excess of 30 cm (1 ft). On the basis of the P X F index,

which may be viewed as a kind of ubiquity index, Table 3 demonstrates that the flora of the aspen type is dominated by forbs (almost 75 percent of the index sum). Shrubs are unimportant, and grasses and grasslike plants contribute only about one-fourth as much as forbs to the sum. The large contribution of annuals appears to be related to excessive grazing pressure from domestic animals. Stands grazed only by deer rarely support an abundance of annuals. The an-

Table 3. Contribution of various life-form groups to the sum of the P x F indices of the 53 species listed in Table 2.

Group	Sum P x F Indices	% of Total
Tree	1,400	1.7°
Shrubs	2,886	3.6
Perennial forbs - tall (>30 cm)	14,580	18.0
Perennial forbs - short (<30 cm)	23,723	29.2
Annual forbs	21,958	27.0
Graminoides	16,677	20.5
Total	81,224	100.0

*The tree layer is dominated by aspen, but this value considers occurrences of aspen stems in the herb layer quadrats only.

nials involved all appear to be native to the Mountain West.

SPECIES ASSOCIATION BY CHI-SQUARE

A number of coefficients have been developed to measure the degree of association between species based on presence-absence data. These have been widely used and adequately reviewed by Cole (1949, 1957) and Hurlbert (1969). For the purposes of this study, it was considered desirable to be able to identify species which were either positively or negatively associated to a significant degree; but the degree of association was not considered essential. Accordingly, significant associations among all possible combinations of understory species were determined by chi-square analysis of joint and independent occurrences of the specified species pairs in the 1,225 quadrats taken in the herb layer. The results are reported in Fig. 2. This figure shows in matrix form the relationship between species, the level of significance of the chi-square values, and whether a relationship is positive or negative.

It is possible to graphically summarize the association data in many ways. Kershaw (1964) demonstrates several techniques by which species "constellations" based on significant positive associations only can be constructed. Sokal and Sneath (1963) discuss numerous ways in which entities may be "clustered" using all values of interspecific association. We have drawn association "constellations" as suggested by Kershaw (1964) and considered various "clustering" techniques. The pair-group clustering method based on simple averages (see Sokal and Sneath, 1963) was finally adopted, since it has the theoretical advantage of employing all association values (negative and positive, significant and nonsignificant) in construction of the association diagram. Furthermore, its synthesis of the data seemed to square with field observations better than those based on other techniques.

As shown in Fig. 3, the 15 species on the extreme left form a highly associated group of annual and perennial herbs. The group includes the most common species of the array of stands sampled and seems to represent those understory species that distinguish modal aspen areas in the region sampled. Many of these species are also known (Hutchins, 1965) to be increasers on heavily grazed aspen areas. The nine species at the extreme right in the figure are known, on the basis of our own unpublished work, to be most abundant in aspen forests that are prone to rapid displacement by conifers. Species intermediately positioned between these two extreme

groups are apparently characteristic of specialized microhabitats of aspen forests. Within that group, dandelion and Kentucky bluegrass are perennial exotics that invade moist, disturbed sites. Yarrow and oregon grape also occur on such sites.

Fringed brome and Columbia needlegrass were positively associated to a significant degree with each other but with no other species. This pattern is related to the fact that only those species among the 42 considered in Fig. 3 were abundant in the six Arizona stands.

Figure 2. Association by chi-square among 42 important understory species in aspen forests of Utah and northern Arizona. The summation chi-square value for the association test of each species pair is reported in the box formed by the intersection of the row and column of the two species compared. Negative associations are designated by a minus sign. Significance levels are as noted in the figure. Species abbreviations appear below.

Species	Abbreviation
<i>Achillea millefolium</i>	Ala
<i>Agastache urticifolia</i>	Aur
<i>Agropyron trachycaulum</i>	Atr
<i>Aster engelmannii</i>	Aen
<i>Berberis repens</i>	Bre
<i>Bromus polyanthus</i>	Bca
<i>Bromus ciliatus</i>	Bei
<i>Carex occidentalis</i>	Coe
<i>Cheopodium fremontii</i>	Cal
<i>Collinsia parviflora</i>	Cpa
<i>Collomia linearis</i>	Ch
<i>Delphinium occidentale</i>	Doc
<i>Descurainia californica</i>	Dea
<i>Elymus glaucus</i>	Egl
<i>Galium bifolium</i>	Gbi
<i>Haekelia floribunda</i>	Hfl
<i>Hydrophyllum capitatum</i>	Hea
<i>Lathyrus lanszucertii</i>	Lla
<i>Melica bulbosa</i>	Mbl
<i>Mertensia arizonica</i>	Mar
<i>Nemophila breviflora</i>	Nbr
<i>Osmorhiza chilensis</i>	Och
<i>Osmorhiza occidentalis</i>	Ooe
<i>Pachistima myrsinites</i>	Pmy
<i>Phacelia heterophylla</i>	Phc
<i>Poa curta</i>	Peu
<i>Poa pratensis</i>	Ppr
<i>Polygonum douglasii</i>	Pdo
<i>Rudbeckia occidentalis</i>	Roc
<i>Senecio serra</i>	Sse
<i>Senecio utahensis</i>	Sui
<i>Silene menziesii</i>	Sme
<i>Smilacina stellata</i>	Sst
<i>Stellaria jamesiana</i>	Sja
<i>Stipa columbiana</i>	SCO
<i>Symphoricarpos oreophilus</i>	Sor
<i>Taraxacum officinale</i>	Tof
<i>Thalictrum fendleri</i>	Tfe
<i>Valeriana occidentalis</i>	Voe
<i>Vicia americana</i>	Vam
<i>Viola nuttallii</i>	Viu

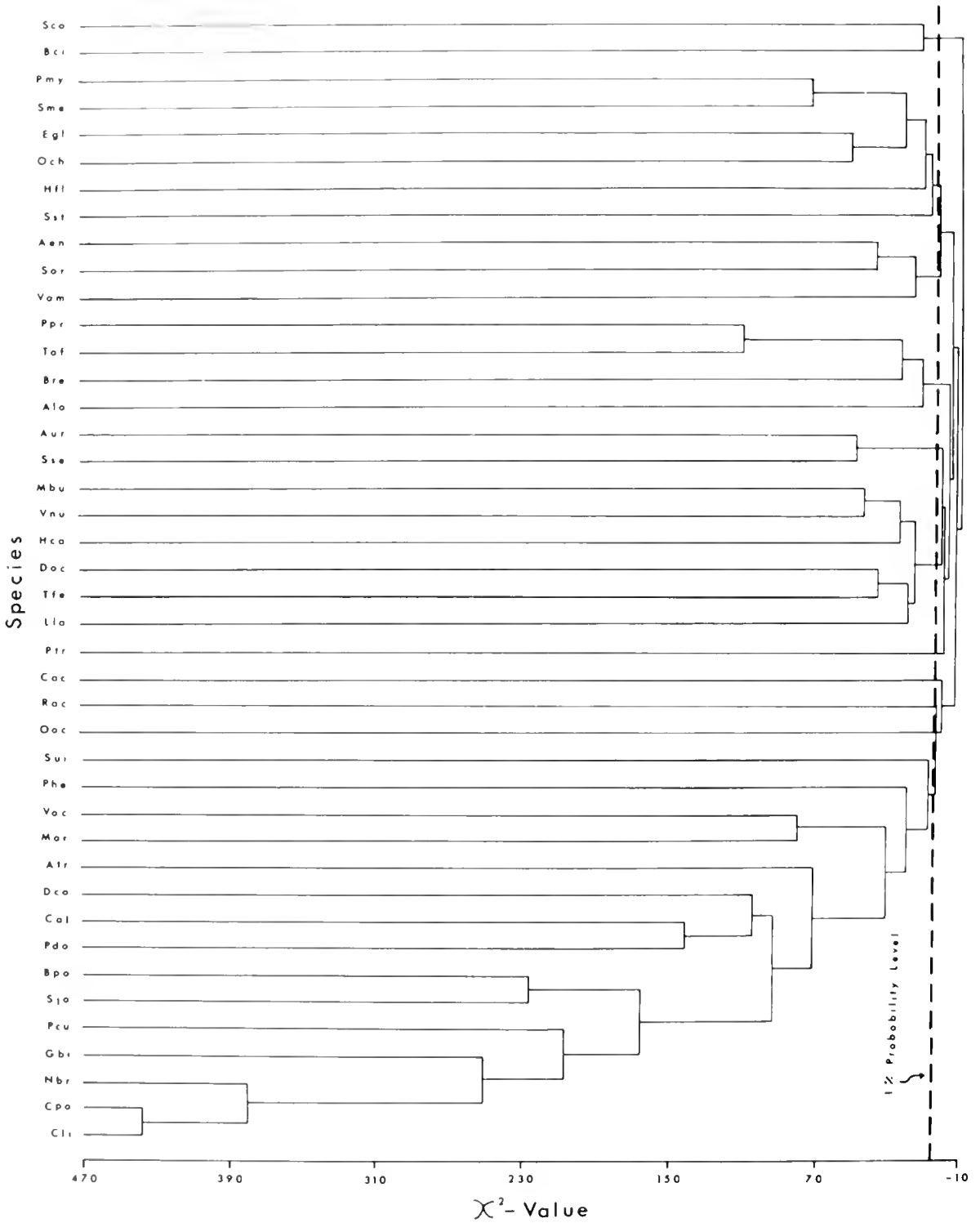


Figure 3. Results of the "cluster" analysis of interspecific association values among 42 species. Species abbreviations are as in Fig. 2, except for *Achillea millefolium* (Ami), *Bromus polyanthus* (Bpo), and *Melica bulbosa* (Mbu).

As noted earlier, species "constellations" based on significant positive associations were also drawn utilizing indices of interspecific association obtained by correlation and chi-square analysis (Snedecor and Cochran, 1967). See Warner (1971) for results of these analyses.

SITE-QUALITY DETERMINATIONS

Site-quality was determined for 43 stands, using the natural site index curves of Jones (1967b). The 6 stands in Northern Arizona were not used in this phase of the study because of basic compositional differences in the understory. Almost none of the dominants of those stands corresponded with dominants of the Utah stands. An index value was obtained for each of the stands used by extrapolation from the natural site index curves which are derived from height-over-age at breast-height data. Height and age values used in this study were the averages for height and age (in years) of the 10 tallest trees in each of the stands tested (Warner, 1971). Using these values, stands were ordered according to Jones's site index.

Forest characteristics of the several stands are shown in Table 4. Excluding the Arizona stands (which are not used in site-quality analyses), average tree density is 1,005 per ha (407/acre); aspen reproduction (individuals having dbh less than 10 cm) density averages just over 4,200 individuals per ha (1,707/acre). Average stand age (based on the 10 tallest trees per stand) is 74 years, with a range running from 42 to 111 for individual stands. Average site index is 15.8 m (52 ft) at 80 years of age.

In order to identify understory species significantly associated with stands of high or low site-quality, average quadrat frequency of understory species of the top 16 stands on the site-quality gradient, based on Jones's index, was tested against the average frequency of the same species in the last 16 stands of that gradient. Average quadrat frequency was calculated for each of the 53 herbaceous species in those two groups of stands. Of those species, 15 were found to be significantly (at the .05 level or better) more or less abundant on the better quality aspen sites (Table 5).

An index value was calculated for each of the 15 indicator species. The derivation of this index was as follows: (1) the mean difference between quadrat frequencies of all species on excellent as opposed to poor site-quality stands was used to rank the 15 species, (2) all of the positive differences were divided by the smallest positive difference, (3) the same procedure was used for the negative differences, and finally,

(4) all values were adjusted so that there were no negative values (Table 5).

The aspen stand site indices were then determined for each stand using such indicator species as occurred in the stand and the following equation:

$$\text{Understory site index} = \frac{\sum(\text{species index value} \times \text{species \% frequency})}{\sum \% \text{ frequency of indicator species}}$$

Table 4. Stand characteristics of the 49 forests sampled.

Stand No.	Aspen Trees Ind/ha	Aspen Reproduction Ind/ha	Understory Production kg/ha	Avg. Age (years)	Avg. Ht (m)	Jones Index
1	1458	1483	374	47	12.5	52
2	544	6259	649	86	13.1	43
3	815	12190	489	111	20.7	57
4	1334	4119	763	68	14.3	52
5	840	4945	720	66	14.6	56
6	1112	9392	235	60	12.5	50
7	741	1483	2237	62	17.1	66
8	519	4942	1354	83	18.3	59
9	815	2308	1658	75	21.0	70
10	568	7416	1246	67	14.6	54
11	791	2634	911	63	15.2	58
12	914	1814	657	78	15.5	53
13*	2372	329	29	70	12.5	44
14*	1483	1317	132	75	23.8	70
15*	544	2471	NA	85	16.5	53
16*	1359	329	75	66	15.2	57
17*	1112	1154	98	67	16.8	60
18*	1063	166	80	86	18.3	57
19	1211	494	500	75	8.5	30
20	865	329	1221	83	16.8	53
21	815	1646	879	42	9.4	48
22	717	1648	331	94	15.2	46
23	593	1979	175	73	12.2	40
24	1581	0	582	78	14.6	48
25	618	3128	659	71	15.8	56
26	1878	329	776	61	12.2	45
27	NA	NA	NA	59	8.8	35
28	NA	NA	NA	65	9.1	34
29	1211	3625	558	80	19.2	62
30	1260	7744	745	78	18.0	60
31	1211	6096	416	96	18.3	54
32	1112	10791	NA	75	11.6	37
33	1236	988	418	100	19.5	58
34	766	4942	823	98	20.7	60
35	1606	9224	525	68	14.0	50
36	840	5105	462	74	18.3	60
37	1038	5108	409	88	18.6	58
38	544	3128	379	67	11.6	42
39	1236	5271	429	66	11.9	43
40	988	4611	188	84	14.3	46
41	1754	1317	1699	52	17.7	75
42	1532	8402	381	69	15.5	55
43	964	2965	392	80	17.4	58
44	1137	13344	321	63	12.2	46
45	939	494	693	76	16.2	55
46	272	3128	399	95	16.5	48
47	840	3951	NA	47	8.5	37
48	NA	NA	NA	67	14.9	54
49	NA	NA	NA	69	18.3	66

*Stands not used in site-quality analyses
 NA - Data not available

Table 5. Comparative frequency of understory species in aspen stands of contrasting height growth. Only species of significantly different abundance in the two groups are listed. Derivation of the indicator index is also demonstrated.

Species	Average Frequency			Indicator Index ^a	Indicator Index ^b (transformed)
	16 High Site-Quality Stands	16 Low Site-Quality Stands	Difference		
<i>Elymus glaucus</i>	46	23	23	4.68	8.3
<i>Lathyrus lanszwertii</i>	54	33	21	4.47	8.1
<i>Viola nuttallii</i>	28	7	21	4.42	8.0
<i>Poa curta</i>	27	11	16	3.37	7.0
<i>Mertensia arizonica</i>	16	2	14	2.84	6.5
<i>Floerkea proserpinacoides</i>	11	0	11	2.26	5.9
<i>Thalictrum fendleri</i>	19	11	8	1.74	5.4
<i>Heracleum lanatum</i>	7	0	7	1.53	5.2
<i>Helenium hoopesii</i>	6	0	6	1.21	4.8
<i>Aconitum columbianum</i>	5	0	5	1.00	4.6
<i>Gayophytum ramosissimum</i>	0	9	-9	-1.00	2.6
<i>Symphoricarpos oreophilus</i>	7	16	-9	-1.03	2.6
<i>Aster engelmannii</i>	3	16	-13	-1.30	2.3
<i>Pachistima myrsinites</i>	4	20	-16	-1.76	1.9
<i>Polygonum douglasii</i>	16	40	-24	-2.62	1.0

^a Positive differences were divided by the smallest positive difference and the negative differences by the smallest negative difference.
^b The largest negative index was adjusted to a value of +1.00 and all other indices were adjusted to the new base by adding the factor used to adjust the largest negative index.

Table 6 illustrates the method of computing the understory site-index, using stand 34 as an example.

The degree of correspondence between Jones's natural site-index values and the understory site-index values for the 43 stands was evaluated by simple correlation. The correlation coefficient for the test is +0.70. The r-value is significant at the 1 percent level. The coefficient of determination (r^2) for this relationship is 0.49. Thus approximately half of the variation in height growth can be accounted for by the linear regression of Jones's natural site index on understory site index. Figure 4 illustrates the results.

The use of simple presence of indicator species, rather than frequency values, was also tested. If site indices could be predicted with reasonable accuracy using simple occurrence of indicator species, sampling and associated expenses in time and money could be saved. In this case, site values were determined using the following formula:

Stand index =

$$\frac{\sum \text{index values for indicators present}}{\sum \text{indicator species present}}$$

The degree of correspondences between Jones's natural site-index values and the understory site-index values based on indicator presence only was also evaluated by simple correlation for the 43 stands. The correlation coefficient for the test is +0.64 and is significant at the

one percent level. The coefficient of determination (r^2) for this relationship is 0.41. The r^2 for indices based on frequency is thus slightly higher than that for indices based on presence data only, but the difference is not great. In view of the greater simplicity of the latter method, one may be willing to accept slightly less precision in estimates in exchange for savings in labor and time.

The average species composition of low, intermediate, and high site-quality stand-groups

Table 6. Calculation of the understory site index for aspen stand 34.

Species	Index Value	Species % Freq.	Species Index
<i>Elymus glaucus</i>	8.3	80	664.0
<i>Lathyrus lanszwertii</i>	8.1	88	712.8
<i>Viola nuttallii</i>	8.0	100	800.0
<i>Poa curta</i>	7.0	32	224.0
<i>Mertensia arizonica</i>	6.5	16	104.0
<i>Floerkea proserpinacoides</i>	5.9	0	0
<i>Thalictrum fendleri</i>	5.4	48	259.2
<i>Heracleum lanatum</i>	5.2	0	0
<i>Helenium hoopesii</i>	4.8	8	38.4
<i>Aconitum columbianum</i>	4.6	0	0
<i>Gayophytum ramosissimum</i>	2.6	0	0
<i>Symphoricarpos oreophilus</i>	2.6	4	10.4
<i>Aster engelmannii</i>	2.3	0	0
<i>Pachistima myrsinites</i>	1.9	0	0
<i>Polygonum douglasii</i>	1.0	0	0
Total		376	2812.8

Understory site index = $\frac{\sum (\text{Species index value} \times \text{species \% freq.})}{\sum \% \text{ frequency of all indicator species}} = 7.48$

according to Jones's index is shown in Table 7. It can be seen that several species have similar average frequency in all site classes. *Bromus polyanthus*, *Collomia linearis*, *Collinsia parviflora*, *Descurainia californica*, *Hackelia floribunda*, *Polemonium foliosissimum*, *Senecio serra*, and *Stellaria jamesiana* are representative of such

Table 7. Average understory composition of low, intermediate, and high site-quality-stand groups.

Species	Average Frequency		
	16 High Site-Quality Stands	11 Intermediate Site-Quality Stands	16 Low Site-Quality Stands
<i>Achillea millefolium</i>	11	19	15
<i>Aconitum columbianum</i>	5	0	0
<i>Agastache urticifolia</i>	6	1	4
<i>Agropyron trachycaulum</i>	23	32	31
<i>Aster engelmannii</i>	3	10	16
<i>Berberis repens</i>	6	3	4
<i>Bromus ciliatus</i>	0	3	3
<i>Bromus polyanthus</i>	58	41	51
<i>Carex occidentalis</i>	5	54	0
<i>Castilleja nuxifolia</i>	0	0	3
<i>Chenopodium fremontii</i>	21	16	28
<i>Collomia linearis</i>	36	43	41
<i>Collinsia parviflora</i>	33	33	35
<i>Delphinium occidentale</i>	11	6	0
<i>Descurainia californica</i>	23	28	23
<i>Elymus glaucus</i>	46	25	23
<i>Epilobium angustifolium</i>	3	0	2
<i>Erysimum argillosum</i>	1	0	4
<i>Floerkea proserpinacoides</i>	11	1	0
<i>Galia bifolium</i>	54	53	40
<i>Gayophytum ramosissimum</i>	0	0	9
<i>Hackelia floribunda</i>	14	18	10
<i>Helenium hoopesii</i>	6	7	0
<i>Heraclum lanatum</i>	7	1	0
<i>Hydrophyllum capitatum</i>	8	23	6
<i>Lathyrus lanszwertii</i>	54	47	33
<i>Ligusticum porteri</i>	6	0	0
<i>Melica bulbosa</i>	4	8	2
<i>Mertensia arizonica</i>	16	19	2
<i>Nemophila breviflora</i>	12	43	29
<i>Osmorhiza chilensis</i>	40	20	24
<i>Osmorhiza occidentalis</i>	6	6	4
<i>Pachistima myrsinites</i>	4	0	20
<i>Phacelia heterophylla</i>	8	7	13
<i>Poa curta</i>	27	31	11
<i>Poa pratensis</i>	17	10	12
<i>Polemonium foliosissimum</i>	1	1	1
<i>Polygonum douglasii</i>	16	22	40
<i>Populus tremuloides</i>	14	15	11
<i>Budbeckia occidentalis</i>	13	3	8
<i>Scrophularia lanceolata</i>	0	1	1
<i>Senecio serra</i>	6	3	5
<i>Senecio uintahensis</i>	7	0	11
<i>Silene menziesii</i>	8	8	12
<i>Smilacina stellata</i>	12	5	8
<i>Stellaria jamesiana</i>	55	49	51
<i>Stipa columbiana</i>	3	6	3
<i>Symphoricarpos orcophilus</i>	7	12	16
<i>Taraxacum officinale</i>	18	8	22
<i>Thalictrum fendleri</i>	19	16	11
<i>Valeriana occidentalis</i>	15	20	6
<i>Vicia americana</i>	25	36	23
<i>Viola nuttallii</i>	28	30	7

rather uniformly distributed species. Other species appear to prefer stands of intermediate site-quality. Such species as *Achillea millefolium*, *Carex occidentalis*, *Hydrophyllum capitatum*, *Valeriana occidentalis*, and *Vicia americana* are representative of this latter group. Species that are most abundant in stands of high or low site-quality have already been identified in Table 5. Perhaps the most striking thing about understory composition in the three site-quality groups of Table 7 is the floristic uniformity that exists among groups.

Understory production (current year, above-ground growth to a height of 6 ft) is significantly correlated with Jones's site-quality index for the 42 stands for which production data are available ($r = +0.45$). Average understory production in these stands was 621 kg/ha (554 lbs/acre) with the range running from 29 to 2,237 kg/ha. As shown in Table 8, the contrast in production between selected stands of low as opposed to high site-quality is marked. Also, stands of low site-quality are relatively more shrubby than tall stands. On the average, understories of tall stands tend to be more heavily dominated by forbs than do those of short stands; but individual values were too variable in our sample to yield statistically significant differences.

Tree and tree reproduction density values reported in Table 8 would seem to indicate that the greater understory production of tall stands is not attributable to lower stocking rates and consequent better lighting of the forest floor. Tree and reproduction densities do not differ significantly in the two stand groups.

Table 8. Comparison of average values for various vegetational parameters from the 7 shortest as opposed to the 7 tallest aspen stands for which data for all parameters are available. Stand numbers of the short stands are: 2, 13, 19, 23, 26, 38, and 39. Tall stands used are numbers 7, 9, 29, 30, 34, 36, and 41.

Parameter	Site Quality Group	
	Short	Tall
Understory production (kg/ha)	419	1169*
% composition of understory (by wt)		
Shrubs	19.7*	4.2
Graminoides	35.5	36.4
Perennial forbs	44.7	59.2
Annual forbs	3.7	2.8
Aspen trees (no./ha)	1196	1055
Age of 10 tallest trees (years)	71	74
Tree site quality (Jones Index)	41	65*
Aspen reproduction (no./ha)	2540	3788

*Value is significantly (0.05 level or better) larger than that with which it is paired.

ENVIRONMENT

Mean values were calculated for various environmental variables in the two stand groups previously used for the identification of herbaceous species associated with high or low site-quality aspen stands (Table 5). As shown in Table 9, only two environmental variables (soil

reaction and exposure) differ significantly between the two stand groups. Better sites were consistently more acidic than were sites of low quality for aspen. Exposure was shown to differ at the 0.1 level of significance only. In general, the better sites had an easterly exposure, while poor sites were more common on westerly exposures.

DISCUSSION

The desire to predict site-quality for aspen using understory species occurring on the sites stems from the fact that aspen is a fire-follower. As such, the species may become dominant on large acreages previously controlled by another forest type. If the tree itself is to provide the estimate of site potential for aspen on such areas, one must wait from two to three decades before an accurate estimate is possible (Graham, Harrison, and Westell, 1963). Obviously, better management alternatives would be possible if a prediction of potential tree production could be made earlier.

Predicting aspen site-quality from understory vegetation may also prove easier than us-

ing tree height-over-age techniques as predictors. Aspen increment cores are normally difficult to age and require mounting, drying, sanding, and staining before accurate counts are possible (Alder, 1969). Prediction based on understory vegetation would require only field samples of relative simplicity. Furthermore, predictions based on understory species can reveal much about quality and quantity of forage in the forest understory. Predictions based on understory parameters could thus have value for multiple-use decisions.

The test of validity of the index developed in this study admittedly includes a strong element of circular reasoning, inasmuch as 32 of

Table 9. Environmental characteristics of stand groups of contrasting site quality for aspen. Averages are based on 16 stands in each group.

Characteristics	Low Site-Quality Group	High Site-Quality Group	Significance of Difference
Altitude (feet)	8283	8115	n.s.
Slope (%)	20.5	20.8	n.s.
Exposure ^a	.72	1.39	•
PO ₄ ^b (mg/g)	.250	.208	n.s.
Ca ^{++b} (mg/g)	3.62	5.54	n.s.
pH ^b	6.02	6.13	n.s.
bulk den. ^b (g/cc)	1.31	1.32	n.s.
Sand (%) ^b	32	30	n.s.
Clay (%) ^b	33	33	n.s.
Silt (%) ^b	35	37	n.s.
PO ₄ (A ₁) (mg/g)	.026	.038	n.s.
Ca ⁺⁺ (A ₁) (mg/g)	3.55	3.50	n.s.
pH (A ₁)	6.20	5.60	••
bulk den. (A ₁) (cc/g)	1.10	1.05	n.s.
Sand (%) (A ₁)	36	35	n.s.
Clay (%) (A ₁)	24	25	n.s.
Silt (%) (A ₁)	40	40	n.s.
Soil temp. (5" depth) (F)	50.7	47.6	n.s.
Soil temp. (10" depth) (F)	46.8	46.0	n.s.
Soil temp. (15" depth) (F)	46.1	45.6	n.s.

^a Exposure values are a sine transformation of direction of slope in azimuth degree clockwise from north using the formula of Beers, Dress, and Wense (1960). This formula gives southwest exposures a value of zero and those of northeast 2, all others receive intermediate values.

^b Mean value for entire soil profile. Obtained by weighting values for separate horizons by horizon depth.

• Significant at 0.1 level

•• Significant at 0.01 level

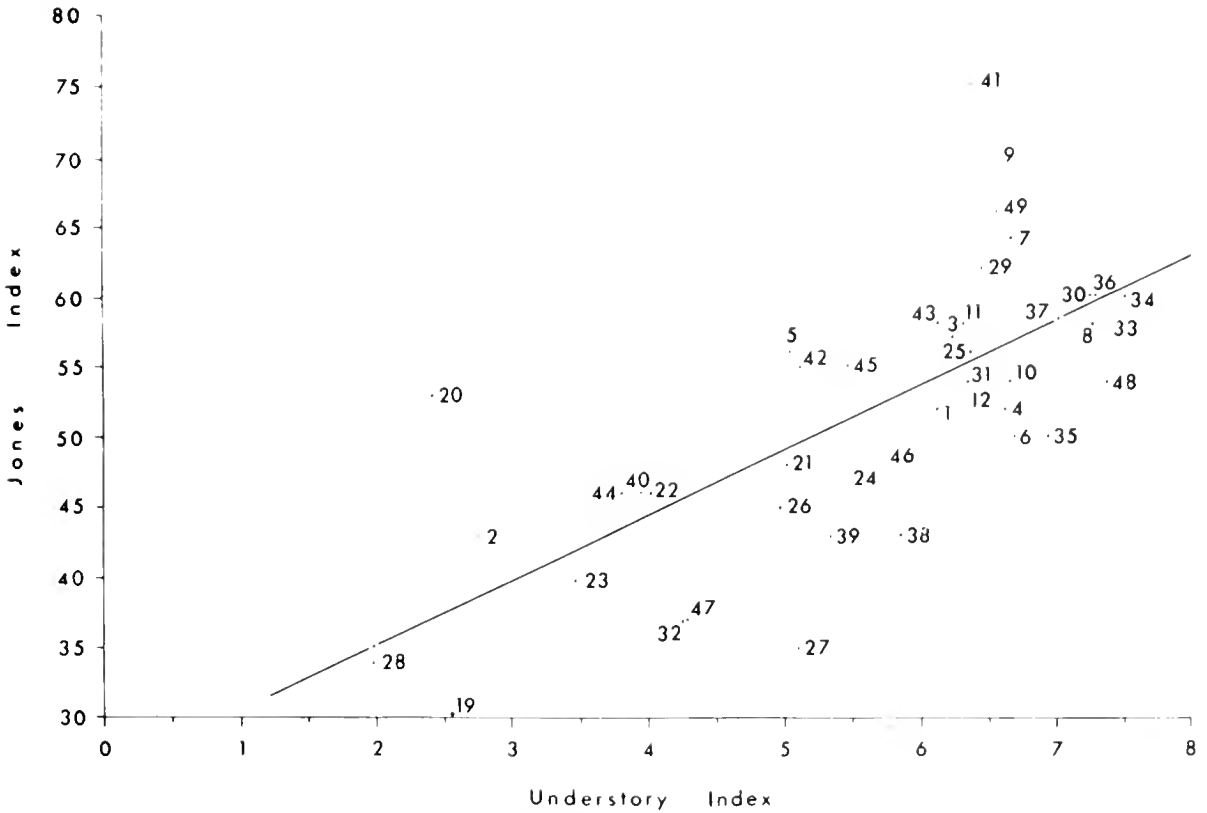


Figure 4. Computed regression line of Jones's Index on the Understory Index. Dots represent individual stand locations. Equation for the regression line is: Understory Index = 4.62 (Jones's Index) + 25.96.

the 43 stands used in the validity test illustrated in Fig. 4 were previously used to identify indicator species, a strong positive correlation between Jones's index and the understory index is to be expected. Ideally, the derived index should have been tested on an independent sample of aspen forests from the same region. Unfortunately, such a set of data was not available.

Several different lines of evidence suggest, however, that the understory index does have real validity for Utah aspen forests. One such evidence stems from analysis of the interspecific association values for understory indicators of sites of high as opposed to low quality. Ten of the 15 indicators identified in Table 5 appear in the matrix of interspecific association values shown in Fig. 4. *Floerkea proserpinacoides*, *Heraclium lanatum*, *Aconitum columbianum*, and *Gayophytum ramosissimum* were omitted from Fig. 4 because all occurred with low frequency, even in stands of occurrence. Six of the 10 indicators represented in Fig. 4 are indicators of better sites, while the other 4 are indicative of poor sites.

Inasmuch as the association data (Fig. 2) are based on presence or absence in individual quadrats of all 49 stands, those results are, at

least partially, independent of responses reported for the same indicators in Table 5 which are based on percent frequency data from only 32 of the stands. Yet, as shown in Table 10, indicators of good sites still tend to hang together as a group with 80 percent of the possible interspecific associations being significantly positive. The four indicators of poor sites form a less homogeneous group but still are significantly positive in their association in one-third of the possible comparisons. If, however, indicators of good sites are compared with indicators of poor sites, it will be noted that only 8 percent of the comparisons are significantly positive, and 42 percent become significantly negative. Average chi-square value for all possible comparisons between species of the two groups drops to +3.2, a value far smaller than that obtained when all possible association values within groups are averaged.

Another bit of evidence supporting the validity of the indicator species selected is furnished by the index based on presence only of indicators. Indicators were initially selected on the basis of average frequency in stand groups of contrasting site-quality. The fact that a highly significant correlation exists between the Jones

Table 10. Summary of interspecific associations among the 10 indicator species of Table 5 that also appear in Fig. 2.

	Interrelationships among Indicators of:		Interrelationships between Indicators of High vs. Low Site Quality
	High Quality Sites	Low Quality Sites	
No. indicators studied	6	4	10
No. interspecific comparisons made	15	6	24
Avg. chi-square value for the interspecific comparisons (from Fig. 2)	+18.3	+11.4	+3.2
% chi-square values that are significantly positive	80	33	8
% chi-square values that are significantly negative	0	17	42
Coefficient of variation ^o for the ave. chi-square value for interspecific comparisons (%)	85	245	452

^oStandard deviation \times 100 = C.V.
mean

index and the presence index indicates again that the selected species do have real value as predictors.

A final evidence for validity of the indicators is presented in Fig. 5. Here the understory index is plotted against the Jones index for 15 stands. The 15 stands include the 11 intermediate

stands of Table 7 (none of which were used in identification of the indicator species) and the two tallest and the two shortest stands shown in Fig. 4. Thus, 73 percent of these stands provide independent evidence concerning the validity of the index. The two tall and the two short stands were added to the analysis to lend length to the

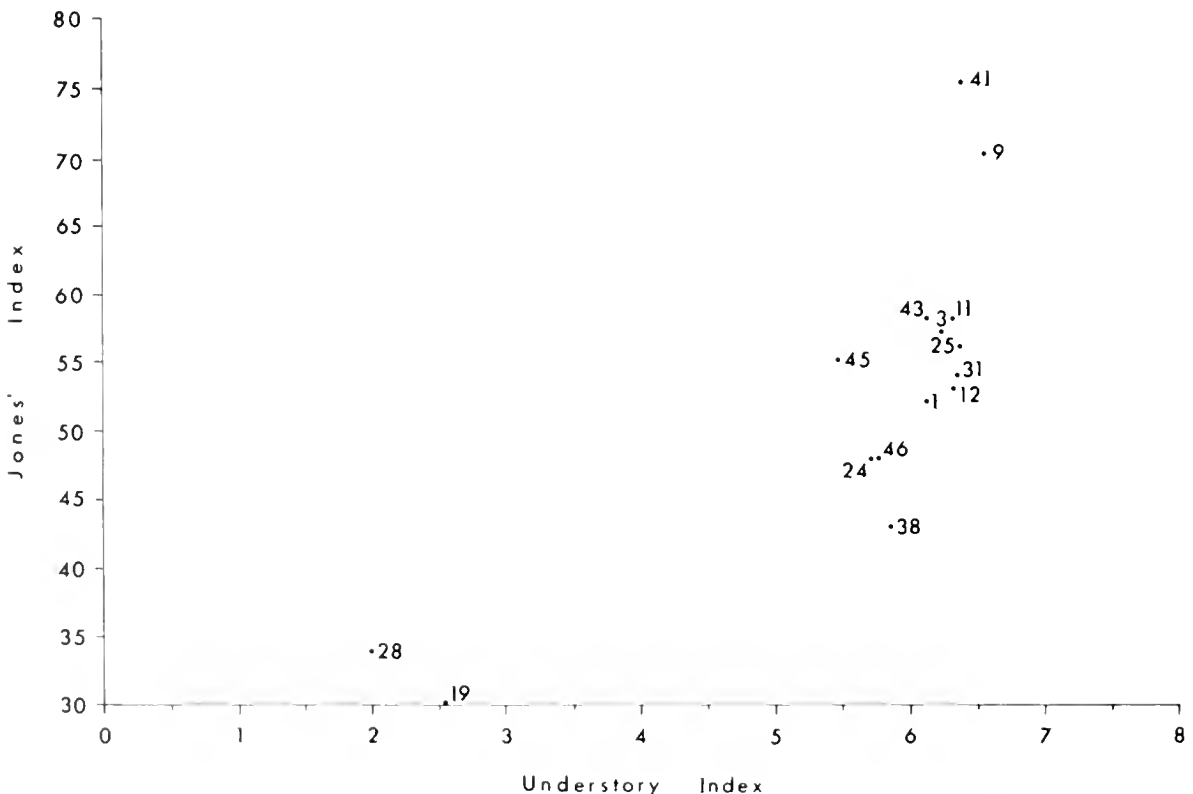


Figure 5. Correspondence between the Jones's Index and the Understory Index based on 15 stands, 11 of which were not used in the original selection of indicators.

height gradient under test, since it is difficult to demonstrate significant trends when the range of variation involved is small (range for the 11 intermediate stands equals 16 units on the Jones index). Adding the two extreme stands from each end of the height gradient represented in Fig. 4 is actually less "loaded" than might appear at first glance. Indicators were selected on the basis of stand groups, not individual stands. Hence the contribution of the tallest and the shortest stands was no more or less than that of other stands in the two groups. Utilization of the tallest and the shortest stands in the new test of utility of the indicator approach thus seems no more objectionable than would the use of an equal number of randomly selected stands from the two stand groups.

The results of the foregoing test of correlation between the Jones and understory indices give an r -value of 0.79 (highly significant). Thus the understory index for these stands accounts for roughly 62 percent of the variation in the Jones index for the same stands. This is an even stronger correlation than was obtained in the original test of the understory index (Fig. 4, r -value of 0.70), in which almost 75 percent of the stands had been used in the initial selection of indicators.

These results indicate that one can expect the understory index as here calculated to consistently predict 50 percent or more of the variation in site potential for aspen growth in Utah. Furthermore, there is reason to believe that the index can be refined to permit even better predictions. The aspen stands on which the present study is based were not initially sampled for the purpose of clarifying relations between tree height and understory vegetation. Also the study extended into at least two somewhat distinct floristic zones (the Wasatch Mountains and the southern plateaus). Accordingly, many species of potential worth as indicators were rejected as being statistically nonsignificant because they occurred in only a few of the stands sampled. By selecting numerous stands of markedly different site potential within a given floristic zone, one should be able to increase the number and reliability of indicators and thus produce a more precise index. Perfection of a technique for stratifying stands according to the degree of grazing disturbance should also permit more accurate estimates (Harper and Hutchins, 1965).

Other attempts at predicting site-quality for aspen from understory vegetation have been made by Kittredge (1938) and Graham, Harrison, and Westell (1963). Both studies consider aspen forests of the Great Lakes area. Kittredge's "natural community plant-indicator" index was

relatively efficient as a predictor of site-quality for aspen ($r = 0.76$), but its use required a highly technical knowledge of the ecology of all the major forest types of northern Minnesota and Wisconsin. Graham, Harrison, and Westell (1963) report that in Michigan sweet fern (*Comptonia peregrina*) is common on sites of low quality for aspen, while height growth of bracken fern (*Pteridium aquilinum*) is positively correlated with increasing site-quality. Nevertheless, they conclude that prediction of site-quality from individual understory species is too imprecise to be useful. Kittredge (1938, p. 238) came to a somewhat similar conclusion for individual species, saying, "On the whole, the conclusion seems justified that individual species do not characterize the site index of aspen specifically enough to be used for prediction with any degree of confidence" and that "indicator value of individual species is distinctly less than that of groups of species." Data from the current study seem fully compatible with this view.

Jones (1967a), working in Colorado, Wyoming, and New Mexico, has attempted to predict site-quality for aspen using temperature and moisture. His results show that the multiple regression of average height of aspen at age 80 on these two ordinates accounted for only slightly more than 30 percent of the total variation in the site index. Working in the nonmountainous terrain of northern Minnesota, Kittredge (1938) was able to account for over 60 percent of the total variation in site index using soil-profile groups as the independent variable.

It seems apparent that methods utilizing environmental parameters as predictors of site-quality are not likely to be any more efficient than indices based on understory vegetation. In fact, the environmental data from this study (Table 9) and those from Jones (1967a) would seem to warn that predictive indices based on environmental parameters will be very difficult to perfect in topographically complex areas such as characterize aspen forests in the Mountain West. Certainly indices based on environment will be more time consuming and expensive than indices based on understory vegetation. Understory indices tell one nothing, however, about causes of variation in site-quality. For that reason, there must be continuing attempts to identify potent environmental predictors of site-quality.

As Jones (1967a) and numerous others (see Baker, 1921; Pauley, 1949; Cottam, 1954; Marr, 1961; Egeberg, 1963; Garret, 1964; and Strain, 1964) point out, marked genetic variation occurs among aspen populations throughout North America. Such variation coupled with the clonal

habit is likely to place a rather low upper limit on the amount of variation in height growth that one can account for with any kind of predictive technique. In Utah, it is not uncommon to find large height differences between contiguous aspen clones of identical age in what appears to be an essentially uniform environment. Obviously such phenomena could inject considerable variation into analyses in which understory or environmental indices are correlated with site potential for trees. Thus, in the absence of control of tree genetics, one could never expect perfect correlations between predictive indices and tree height.

As Daubenmire (1952, p. 305, 323) has pointed out, frequency values for understory species are more likely to be altered by disturbing influences such as grazing, logging, or fire than is presence. Thus he uses presence in preference to frequency data in identification of habitat-types (or site-quality classes) which are intended to reflect basically different abiotic environments. In theory, species frequency is so sensitive to disturbing influences that its use could confuse rather than clarify understanding of the abiotic system. Results of this study indicate, however, that frequency data carry more information content concerning site-quality (as indicated by the coefficient of determination) than does presence alone.

Data in Table 10 reveal an interesting characteristic of the two groups of indicators employed in calculation of the understory index. None of the indicators of good sites are significantly negatively associated (only 1 of 15 possible comparisons is negative). On the other hand, 17 percent of the possible comparisons among indicators of poor sites are significantly negative. Of the 6 possible comparisons, 3 bear a minus sign. These data seem to suggest that environmental conditions correlated with good height growth of aspen are relatively uniform but that dissimilar kinds of environments can cause poor growth of aspen. How else can one account

for species being significantly correlated with sites of poor growth for aspen, while being significantly disassociated from each other? This explanation seems easily defensible on theoretical grounds.

A puzzling aspect of the interrelationships among the indicator species reported in Table 10 is the fact that two indicators of good sites (i.e., *Lathyrus lanszwertii* and *Poa pratensis*) are significantly positive in their association (Fig. 4) with *Polygonum douglasii*, an indicator of poor sites. One is tempted to reject all three as indicators under such circumstances, but the fact that both *L. lanszwertii* and *Poa pratensis* are significantly positive in their association with four of the other five indicators of good sites indicates that there is no *a priori* reason for doing so. However, the indicator value of these species should be viewed with caution until such time as their status is clarified by independent data.

Both *Poa curta* and *Polygonum douglasii* are known to be strong increasers on overgrazed aspen ranges of northern Utah (Hutchins, 1965). Hutchins also shows that *L. lanszwertii* declines slowly with moderate grazing, but more rapidly as grazing pressure becomes more abusive. The anomalous response described for these species in the preceding paragraph may be caused by differential grazing pressure among the aspen forests sampled. One could postulate a system in which *Polygonum douglasii* is largely confined to sites of low quality when grazing pressure is minimal. With abusive grazing, the species may become abundant on sites of better quality. It is possible that *Poa pratensis*, another increaser with grazing, increases on both good and poor sites under grazing but is best adapted to good sites. *L. lanszwertii*, being moderately resistant to grazing, could associate with *Poa pratensis* and *Polygonum douglasii* on good and poor sites alike but be most abundant on sites of good quality. Clearly, a stratification of stands according to grazing intensity would help clarify these possibilities.

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Science Bulletin**

THE BORAGINACEAE OF UTAH

by

Larry C. Higgins



BIOLOGICAL SERIES — VOLUME XVI, NUMBER 3

JULY 1972

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Frontispiece — *Entrichium nanum* (Vill.) Schrad var. *elongatum* (Rydb.) Cronq.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
TAXONOMY	1
<i>Boraginaceae</i>	1
<i>Amsinckia</i>	2
<i>Achusa</i>	4
<i>Asperugo</i>	5
<i>Borago</i>	5
<i>Coldenia</i>	6
<i>Cryptantha</i>	8
<i>Echinum</i>	54
<i>Eritrichium</i>	54
<i>Hickelia</i>	55
<i>Heliotropium</i>	58
<i>Lappula</i>	60
<i>Lithospermum</i>	62
<i>Mertensia</i>	66
<i>Myosotis</i>	75
<i>Pectocarya</i>	75
<i>Plagiobothrys</i>	77
ACKNOWLEDGMENTS	81
LITERATURE CITED	81

THE BORAGINACEAE OF UTAH

by

LARRY C. HIGGINS¹

ABSTRACT

This paper presents a revision of the family Boraginaceae for the state of Utah. Ninety-three species in seventeen genera are recognized. The treatment includes keys, synonymy, descriptions, and citations of representative specimens found

in the various herbaria in the state of Utah. The new combination *Lappula occidentalis* (Wats.) Greene var. *cupulata* (Gray) Higgins is presented.

INTRODUCTION

For the last six years I have been engaged in research leading to a revision of the Utah Boraginaceae. This family of flowering plants has long been a stumbling block for beginning students in plant taxonomy and anyone interested in plant identification. For many years the literature encompassing the Utah borages has been

inadequate or nonexistent. Investigators have had to resort to many different publications to possibly identify the plants at hand. At any rate, no single work has been available which could be used to identify the native borages of Utah. This work is an attempt to provide keys and descriptions for all the Boraginaceae found in Utah.

TAXONOMY

Boraginaceae Lindl.

Boraginaceae Lindl., Nat. Syst., ed. 2:274. 1836.

Plants herbaceous, shrubby or sometimes tropical trees, usually bristly; leaves simple, alternate, or sometimes opposite or whorled, entire and pubescent, hispid or setose; flowers perfect, regular, solitary or cymose; cymes glomerate-racemose or spicate, frequently unilateral and coiled (scorpioid), usually with bracts between, to one side of, or opposite the flowers; calyx usually 5-lobed or 5-parted, usually persistent, the lobes valvate; corolla 5-lobed, sometimes crested or appendaged in the throat; stamens 5, borne on the corolla-tube alternate with the lobes; ovary superior, bicarpellate, usually 4-ovulate, entire or lobed, becoming tough or bony at maturity; fruit commonly breaking up into 4 single-seeded lobes (nutlets); style simple or 2-cleft, seated in the pericarp at the apex of the fruit or borne between the fruit-lobes (nutlets) on the receptacle, or on an upward

prolongation thereof (gynobase); endosperm absent or scarce; embryo straight or curved.

The classification of this family is based primarily upon the structure of the fruit. In many cases it is difficult to recognize the genus and almost impossible to obtain a precise identification of the species if the specimens lack mature fruiting structures.

The Boraginaceae are of little or no economic value, but the family has numerous species that are cultivated as ornamentals, principally in the genera *Heliotropium* (heliotrope), *Anchusa*, *Echium*, and *Myosotis* (forget me not).

1. Style 2-cleft; stigmas 2, distinct; flowers solitary or clustered in the stem forks 5. *Coldenia*
1. Style simple, stigmas united (2).
2. Style arising from the pericarp at the apex of the fruit, falling away with the nutlets; stigma annular-peltate, surmounted by a conical or cylindrical, simple or lobed appendage 11. *Heliotropium*
2. Style borne between the lobes of the fruit (nutlets),

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- and attached to the receptacle or gynobase; stigma capitate, unappendaged (3).
3. Nutlets with uncinat, glochidiate or barbed prickles on the back, margins or the apex (4).
 3. Nutlets without hooked or barbed prickles (7).
 4. Nutlets subglobose, with dorsal surface rather uniformly covered with barbed prickles, no definite margins present 7. *Cynoglossum*
 4. Nutlets with a definite margin, the prickles confined to this (back may be muricate or tuberculate) (5).
 5. Nutlets stellately spreading, attached at the apical (radicle) end, armed with hooked appendages. Small slender annuals. 16. *Pectocarya*
 5. Nutlets erect, incurved or weakly divergent, attached at or below the middle, i.e., toward the cotyledon end (6).
 6. Plants annual; pedicels erect or nearly so; styles surpassing the nutlets; subulate gynobase about as long as the nutlets 12. *Lappula*
 6. Plants perennial or biennial; pedicels reflexed in fruit; styles usually shorter than the nutlets; pyramidal gynobase about half as long as the nutlets 10. *Hackelia*
 7. Corolla irregular, the upper lobes usually longer than the lower ones; stamens not all equal in length 8. *Echium*
 7. Corolla regular or nearly so (8).
 8. Calyx in fruit much enlarged, becoming conspicuously veiny, folded and flattened; stems procumbent, angled, with stiff retrorse bristles on the angles 3. *Asperugo*
 8. Calyx in fruit little if any enlarged, not becoming veiny, folded and flattened; stems various but not as above (9).
 9. Nutlet attachment surrounded by a swollen ring, leaving a distinct pit on the gynobase; plants of fields and waste places (10).
 9. Nutlet attachment not surrounded by a rim nor leaving a pit (11).
 10. Stamens appendaged dorsally, closely crowded around the style; corolla rotate 4. *Borago*
 10. Stamens unappendaged, included within the tubular corolla 2. *Anchusa*
 11. Corolla normally blue (aberrant white-flowered plants occasionally are found), or reddish in the bud stage (12).
 11. Corolla white, greenish-white, yellow or orange (14).
 12. Nutlets with an oblique dorsal face encircled by an upturned flange or rim, this often irregularly toothed; depressed-pulvinate plants seldom over 7 cm tall, of alpine areas in Utah 9. *Eritrichium*
 12. Dorsal face of nutlet (if present) not encircled by an upturned flange or rim; plants not depressed-pulvinate, usually over 7 cm tall, most species growing below alpine areas in Utah (13).
 13. Corolla lobes convolute in the bud; nutlets basally attached to a flat gynobase; corolla salverform 15. *Myosotis*
 13. Corolla lobes imbricate in the bud; nutlets obliquely attached to a convex gynobase; corolla with a tube and usually a campanulate throat, not salverform 14. *Mertensia*
 14. Nutlets attached above the base along a usually open and generally basally forked ventral groove or slit, or by a triangular opening in the pericarp 6. *Cryptantha*
 14. Nutlets lacking a distinct ventral groove or opening in the pericarp, this usually replaced by an elevated ventral keel (15).
 15. Plants perennial; nutlets attached by a broad, rounded, quite basal noncaruncular attachment, nutlets ovoid, smooth and shiny; corolla usually yellow or orange 13. *Lithospermum*
 15. Plants annual; nutlets attached by a caruncular scar borne upon or at the basal end of the ventral keel, the attachment usually lateral or suprabasal; nutlets usually rough (16).
 16. Corolla white; cotyledons entire .. 17. *Plagiobothrys*
 16. Corolla orange or yellow, the tube definitely longer than the calyx; cotyledons 2-lobed 1. *Amsinckia*

1. *Amsinckia* Lehm.

Amsinckia Lehm., Delect. Sem. Hort. Hamburg 7. 1831; Johnston, Contr. Gray Herb. 70:44. 1924.

Annual, pungent-bristly, herbaceous plants; stems erect or with spreading branches, leafy; leaves alternate, linear to ovate, usually veinless; racemes usually bractless; calyx cut to base into erect lanceolate or oblong lobes; corolla tubular or salverform, heterostyled, yellow or orange, tube cylindrical, glabrous, unappendaged; lobes spreading, rounded, imbricate; stamens included, affixed in the tube, filaments very short, anthers oblong; obtuse style filiform, included; stigma capitate, emarginate; ovules 4; cotyledons 2-parted; nutlets 4, erect, angulate-ovoid, smooth or rough, unmarginated, strongly keeled ventrally; gynobase pyramidal, frustate, about half the height of the nutlet.

A genus of considerable difficulty which is found mainly in western North America.

Type species: *Amsinckia lycopsoides* Lehm.

1. Corolla-tube 20-nerved below attachment of stamens; calyx-lobes unequal in width and reduced in numbers (2, 3, or 4) by fusion; nutlets tessellate 3. *A. tessellata*
1. Corolla-tube 10-nerved below insertion of stamens; calyx-lobes 5, distinct (2).
2. Corolla orange-yellow, 7-20 mm long, well exerted beyond the calyx; plants usually green; stems hirsute-bristly, but with little or no fine-appressed hairs 1. *A. intermedia*
2. Corolla pale-yellow, 4-7 mm long, little or not at all exerted beyond the calyx-lobes; leaves pubescent with appressed or ascending hairs .. 2. *A. retrorsa*

1. *Amsinckia intermedia* Fisch. & Mey. Ind. Sem. Hort. Petrop. 2:2 and 26. 1836.
Amsinckia campestris Greene, Man. Bay Reg. 263. 1894.
Amsinckia velens Macbride, Contr. Gray Herb. No. 49:14. 1917.
Amsinckia intactilis Macbride, op. cit. 13.
Amsinckia arvensis Suksd., Werdenda 1:32. 1927.

Stems simple or much branched, erect to widely spreading, 3-9 dm tall, sparsely bristly otherwise usually glabrous except for a tomentose pubescence near the base of the spikes; basal and lower cauline leaves linear or linear-lanceolate, the upper lanceolate to nearly ovate, usually clasping at base and acute at apex, thinly hirsute on both sides with spreading, often pustulate hairs; spikes short or usually elongating in fruit, usually leafy-bracted at base; calyx-lobes linear attenuate, about half as long as the corolla, rufous-hispid on the back, densely white-hirsute on the margins; corolla orange-yellow, 8-10 mm long, the limb 3-6 mm wide; nutlets 2.5-3 mm long, incurved, grayish, narrowly keeled on the back and sharply rugose with the surface between papillate or muriculate. A common field and roadside weed; Washington to Idaho, and south to Arizona and northern Baja California. Type locality: near Bodega Bay, California. March-June. Fig. 1.

A. intermedia is a highly variable species of wide geographical range. Suksdorf (Werdenda 1:48-113. 1931) in a study of the genus proposed over one hundred new species that fall within this species. In Utah *A. intermedia* is located almost entirely in Washington County, with a few scattered records in the western tier of counties.

Millard Co., Wah Wah Mountains, Cottam 5659 (UT); Washington Co., St. George, Law s.n. (UT); Terry's Ranch, J.B. Karen 18 (BRY); Beaverdam Mountains, L.C. Higgins 365, 402, 1222 (BRY); Dixie State Park, L.C. Higgins 869 (BRY).

2. *Amsinckia retrorsa* Suksd., Deutsch. Bot. Monatss. 18:134. 1900.
Amsinckia parviflora Heller, Muhlenbergia 2:313. 1907 uot Bernh. 1833.
Amsinckia rugosa Rydb., Fl. Rocky Mts. 729. 1066. 1917.
Amsinckia helleri Brand, Rep. Spec. Nov. 25:212. 1928.

Stems strictly erect, 3-8 dm tall, usually simple below the inflorescence, bristly-hirsute and often more or less cinereous with fine appressed hairs; leaves linear or the upper linear-lanceolate, hirsute on both sides with ascending or

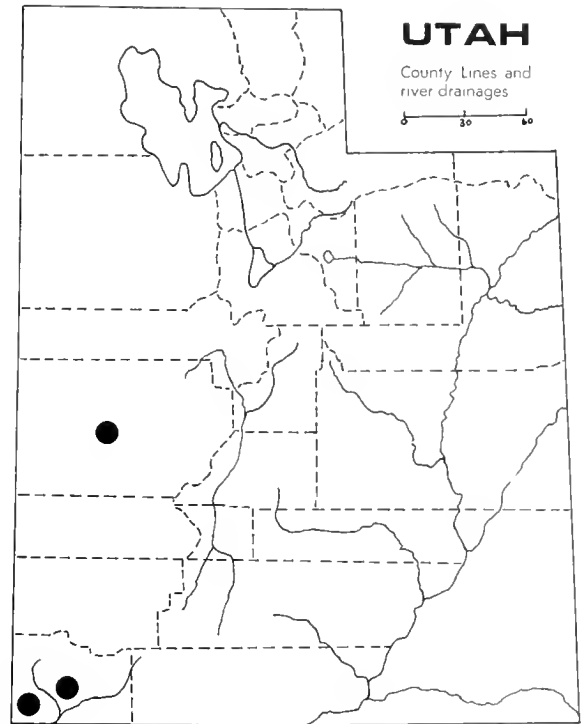


Fig. 1. *Amsinckia intermedia*

appressed hairs; inflorescence of 1 or few, strict, erect or ascending racemes, bractless; calyx-lobes 5, distinct, 7-13 mm long, linear or linear-lanceolate; corolla light-yellow, 5-7 mm long, the tube included or only slightly exerted beyond the calyx-lobes; style 2.5-3 mm long; nutlets 2-3 mm long, broadly ovoid, densely tuberculate all over, with scattered larger tubercles intermixed, the latter on the central and lateral ridges when these are present. Moist slopes and fields or sometimes dry ground. Washington to Idaho and south to Utah and southern California. Type locality: near Bingen, Klickitat County, Washington. April-August. Fig. 2.

Cache Co., 2 miles southwest of Hyrum, T. Jensen 589 (UTC); Pine Canyon, Wellsville Range, B. Maguire 3111 (UTC); Foot of Sardine Canyon, B. Maguire 13788 (UTC); South of Hardware Ranch and Randolph Road Jet, W.P. Cottam 16001B (UT); Davis Co., Centerville, S. Flowers 1192 (UT); Farmington, B. Maguire 12990 (UTC); Salt Lake Co., Salt Lake City, I.E. Diehl, s.n. (BRY); Salt Lake City, K. Brizzee 7780 (UT); Salt Lake City, A.O. Garrett 3640C (UT); City Creek Canyon, K. Brizzee 7845 (UT); Summit Co., Canyon near Gorgoza, A.O. Garrett 8646 (UT); Tooele Co., Stansbury Range, South Willow Creek, B. Maguire 21807 (UTC); Tooele, just northwest of city limits, L.C. Higgins 4092 (BRY); Weber Co., Huntsville, C.P. Smith 1944 (UTC).

3. *Amsinckia tessellata* A. Gray, Proc. Amer. Acad. 10:54. 1874.

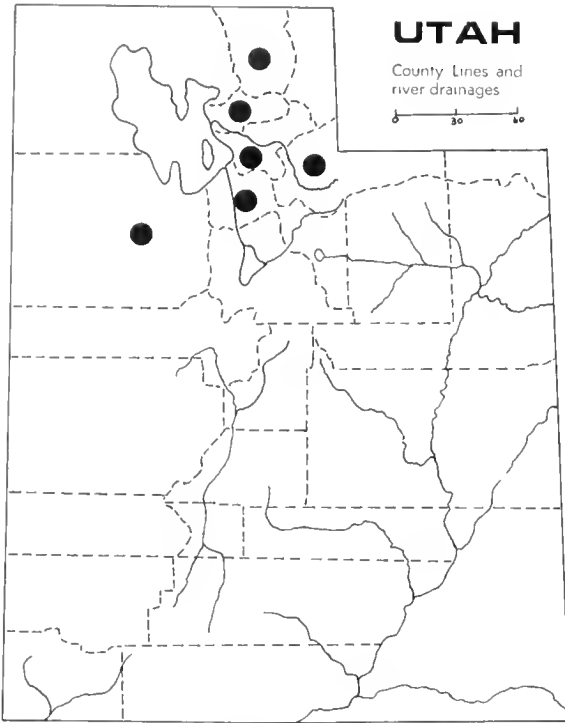


Fig. 2. *Amsinckia retrorsa*

Amsinckia collina Greene, Man. Bay Reg. 263. 1894.

Amsinckia pustulata Heller, *Muhlenbergia* 2:243. 1906.

Amsinckia conica Suksd., *Werdenda* 1:104. 1931. (In the publication fifteen other species referable to *tessellata* were described.)

Stems stout, branched throughout or sometimes simple below, 3-6 dm high, hispid with spreading bristles; leaves linear-lanceolate, 2-7 cm long, rather thinly hispid, the hairs pustulate at base, sessile except the narrowly oblanceolate basal ones; spikes elongating with age, often 5-12 mm long; calyx lobes 3 or 4, when 4 one broader and notched or 2-lobed at apex, when 3 a little broader and notched at apex, hispid and on the margins densely white hirsute, 8-13 mm long; corolla orange, tube 5-10 mm long, limb 2.5-5 mm wide; nutlets 3-3.5 mm long, ovoid, the back low usually with a median line, densely tessellate or papillate, and often transversely rugose. Dry, usually sandy or rocky soils. Eastern Washington to Utah, Arizona and northern Baja California. Type locality: near Mount Diablo, California. March-June. Fig. 3.

Davis Co., near Centerville, S. Flowers s.n. (UT); Washington Co., St. George, F.W. Gould 1479 (BRY); Beaverdam Wash, L.K. Shimway 23 (BRY); Beaver-

dam Wash, W.P. Cottam 5093 (UT); St. George, M.E. Jones 1640 (UT); Beaverdam Slope, Fisk 3 (UT); West slope of the Beaverdam Mountains, D. Nish 69 (UTC); 4 miles northwest of Welcome Springs, B. Maguire 20495 (UTC); 1 mile east of Hurricane, B. Maguire & Blood 1537 (UTC).

2. *Anchusa* L.

Anchusa L., Sp. Pl. 133. 1753.

Annual, biennial or perennial herbs with blue or purple flowers in paniced, scorpioid racemes; calyx divided into narrow lobes; corolla trumpet-shaped, the tube straight, the throat closed by scales, the limb with widely spreading lobes; stamens included, style slender, ovary 4-parted, nutlets 4, their attachment surrounded by an annular ring leaving a pit on the low gynobase.

1. *Anchusa officinalis* L., Sp. Pl. 133. 1753.

Plants perennial, from a taproot; stems erect, branched from near the base, 30-100 cm high; coarsely hirsute, the hairs often pustulate at base; basal leaves 8-20 cm long, oblanceolate, stem leaves lanceolate; calyx 5-8 mm long, the lobes lanceolate to narrowly triangular, about as long as the tube; corolla about 10 mm long, dark blue; nutlets 2-3 mm long, rugose or granulate; inserted by their bases on a flat gynobase. Roadsides and waste places. Native to Eurasia

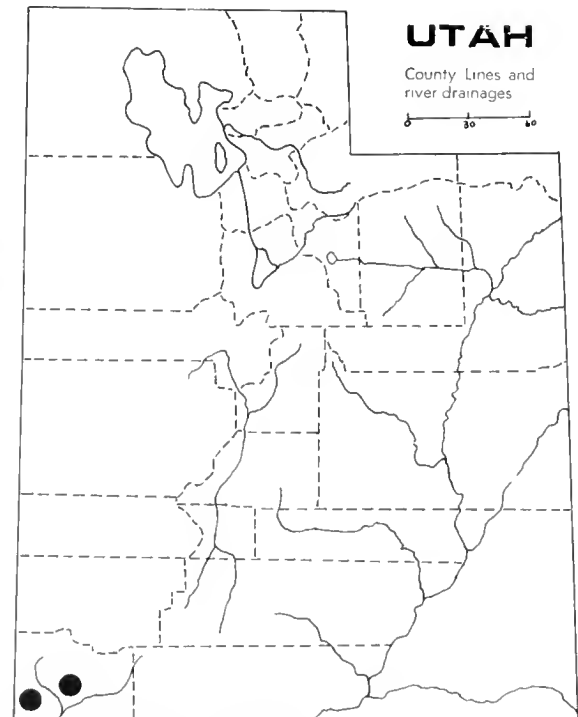


Fig. 3. *Amsinckia tessellata*

and introduced into the eastern United States as far west as Utah. June-August. Fig. 4.

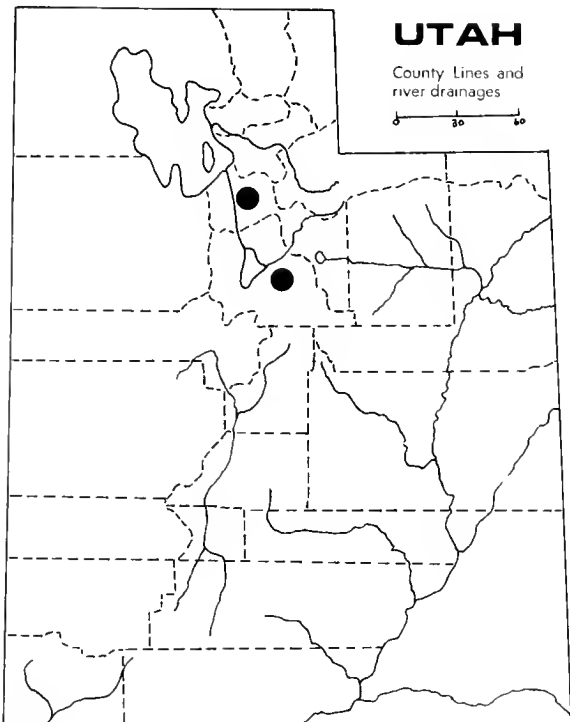


Fig. 4. *Aechusa officinalis*

Salt Lake Co., Salt Lake City, L. Arnow 327 (UT); Utah Co., Rock Canyon, C. Sanders s.n. (UT); Rock Canyon, Cottam s.n. (UT); Rock Canyon, A.O. Garrett 2783 (UT); BYU campus, K. Shaw 29 (BRY); Rock Canyon, P.A. Replogle 85 (BRY); Rock Canyon, L. Hartman 126 (BRY); Rock Canyon, B.F. Harrison 8380 (BRY); Provo, L. Woodbury 33 (BRY); Hobbie Creek, L.C. Higgins 3512 (BRY, WTSU).

3. *Asperugo* L.

Asperugo L., Sp. Pl. 138. 1753.

Rough-hispid, annual, procumbent plants, with stiff bristly hairs; leaves alternate, or the upper sometimes opposite, entire; calyx campanulate, unequally 5-cleft, much enlarged and reticulate-veiny in fruit, lobes incised-dentate, the teeth often appearing as extra lobes in the sinuses; corolla tubular-campanulate, 5-lobed, 1 to 3 together on short, recurved pedicels in the upper leaf axis; stamens 5, inserted on the corolla tube, included; filaments very short; ovary 4-lobed; style short; stigma capitate; nutlets 4, ovoid, erect, granular-tuberculate, attached laterally above the middle to the elongate-conic receptacle, the scar not leaving a pit.

1. *Asperugo procumbens* L., Sp. Pl. 138. 1753.

Stems 2-6 dm long; diffusely branched, slender and procumbent or ascending, retrorsely short-hispid; leaves 1-4 cm long, obovate to oblanceolate, scabrous, obtuse to acutish at apex; fruiting calyx 8-15 mm wide; corolla small, 2-3 mm long, blue, purple or purplish-red; nutlets obliquely ovoid, about 4 mm long, granulate-tuberculate. Waste places. Introduced from Europe in various parts of Canada and the United States. May-August. Fig. 5.

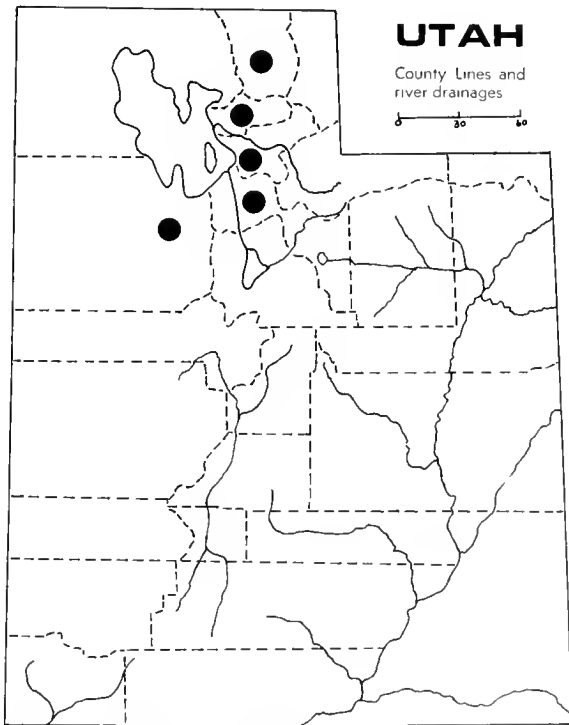


Fig. 5. *Asperugo procumbens*

Cache Co., Logan, in garden, N.H. Holmgren 39 (UTC); USU Campus, B. Maguire 3697 (UTC); 1 mile below Dry Canyon, B. Maguire 13787 (UTC); 1 mile west of Benson, B. Maguire 2417 (UTC); Green Canyon, Melvin Burke 3696 (UTC); Davis Co., Barton Creek, mouth of Holbrook Canyon, B. Anderson 51 (UTC); Bountiful, S. Flowers s.n. (UT); Salt Lake Co., Salt Lake City, Maguire & Blood 1538 (UTC); Salt Lake City, A. Bleak 20 (UT); Red Butte Canyon, G. Swanson 103 (UT); Salt Lake City, A.O. Garrett 8697 (UT); Salt Lake City, W.J. Stubbs s.n. (BRY); Tooele Co., Tooele, just northwest of the city limits, L.C. Higgins 4091 (BRY,WTSU); Weber Co., Weber State College Campus, A. Collotzi 76 (UTC); Foothills east of Ogden, E.L. Miner s.n. (UT).

4. *Borago* (Tourn.) L.

Borago (Tourn.) L., Sp. Pl. 137. 1753.

Hirsute or hispid annual or biennial herbs with alternate, entire leaves and blue flowers in

terminal leafy racemes; calyx deeply 5-cleft or 5-parted; corolla rotate, the tube very short, throat closed by scales, limb 5-lobed, the lobes imbricated, acute; stamens 5, inserted on the corolla tube; filaments dilated below, narrowed above to a slender appendage; anthers linear, erect, and connivent with a beak-like cone; ovary 4-divided; style filiform; nutlets 4, ovoid, erect, attached by their bases to the flat receptacle; scar of attachment large, concave.

1. *Borago officinalis* L., Sp. Pl. 137. 1753.

Stems erect, 5-8 dm tall, with ascending or spreading branches; leaves oblong to obovate, 5-11 cm long, rounded to acute at apex, the upper ones clasping, lower narrowed to a winged petiole; pedicels spreading or recurving, 2-5 cm long; calyx-lobes linear-lanceolate, 7-10 mm long; corolla 15-20 mm broad, bright blue; anther-beak dark purple, about 6-7 mm long; nutlets 4 mm long. An escape from gardens and sparingly naturalized in the western United States, a native of Europe. June-August. Fig. 6.

Cache Co., Logan J. Thieret 209 (UTC).

5. *Coldenia* L.

Coldenia L., Sp. Pl. 1:125. 1753, and Gen. Pl. 61. 1754.

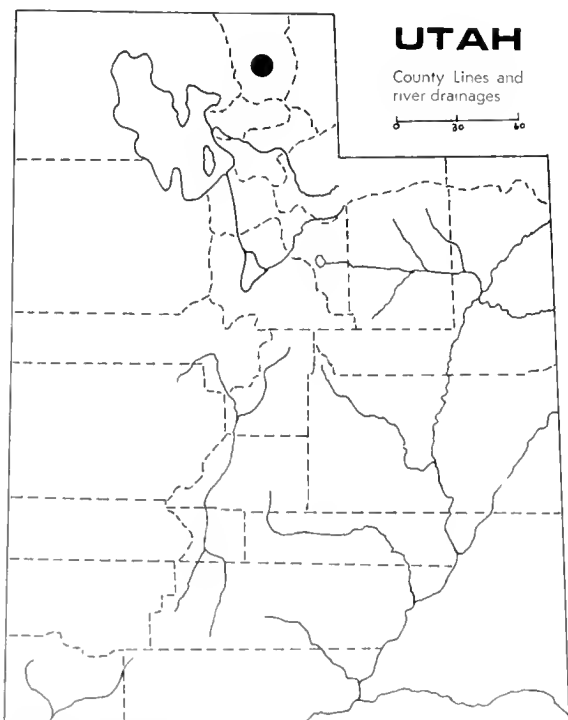


Fig. 6. *Borago officinalis*

Herbaceous or suffruticose plants with slender, forking, usually prostrate or widely spreading stems; leaves small, entire, usually strongly veined, subsessile or petiolate; flowers small, generally white, generally extra-axillary, along leafy twigs or at the forks of the branches, sometimes glomerate; commonly opening in late afternoon; corolla with a short, cylindrical or ampliate tube and spreading lobes, throat naked or sometimes appendaged; stamens 4-5, included, their filaments adnate to the corolla-tube; style terminal on the ovary, short to long, bilobed or biparted; stigmas 2, not much differentiated from the style-branch; ovary 2-celled or sometimes 4-celled by the septum-like placenta, entire or 4-lobed; fruit dry, pyramidal or hemispheric, divided into usually 4 single-seeded nutlets; nutlets more or less broadly united ventrally or joined to a central prolongation of the receptacle.

Except for a single old world species, entirely confined to arid regions of America. Type species: *Coldenia procumbens* L.

1. Fruit nearly globose, unlobed, breaking apart at maturity into quarter sections, each quarter forming a nutlet; leaves ovate to elliptic, white-tomentose, obscurely veined 1. *C. canescens*
1. Fruit deeply 4-lobed, the lobes joined only by their inner angle, each lobe forming a nutlet, leaves not tomentose (2).
2. Plants perennial; leaves not evidently nerved, lanceolate to linear, usually very pungently setose; base of petiole expanded, indurate, usually villous; flowers solitary in the leaf axils; nutlets finely warty, ovate 2. *C. hispidissima*
2. Plants annual; leaves with evident impressed nerves, ovate or obovate to nearly orbicular; base of petiole not expanded, or indurate or villous; flowers in dense clusters at the forks of the stem; nutlets smooth or granulate 3. *C. nuttallii*

1. *Coldenia canescens* DC., Prodr. 9:559. 1845. Type from between Santander (i.e., Jimenez) and Victoria, Tamaulipas, Mexico, Berlandier 2256.

Stegnocarpus canescens (DC.) Torr., in Torr. & Gray Pacif. R. R. Reports, ed. 2, Vol. 2:170, tab. 7. 1857.

Stegnocarpus leiocarya Torr., Pacif. R. R. Reports, ed. 1, 320. 1855.

Coldenia canescens var. *subnuda* Johnst., Proc. Calif. Acad. Sci. IV. 12:1137. 1924.

Plant suffruticose, perennial, often forming mats 2-6 dm in diameter; stems several to numerous, mostly prostrate but sometimes ascending, furcately branched; old stems decorticating, rough, dark-colored; leafy stems and

branches pallid, tomentose; leaves numerous, white tomentose; petiole slender, 2-7 mm long, in extreme maturity usually breaking off near the middle leaving a stub attached to the stem; leaf blade ovate to elliptic-lanceolate, obtuse to broadly acute at the ends, 7-10 (15) mm long, 2-7 (9) mm wide, thickish, the margins somewhat revolute tomentose; flowers usually solitary in the axils of the leaves and along the main stem and branches; calyx sessile, persistent, at anthesis 3-4 mm long, lobes about as long as the corolla tube, unequal, united above the base; lobes of the fruiting calyx lanceolate, usually long-attenuate, 4-7 mm long; corolla 5-6 (8) mm in total length, pink, rose or rarely white, the lobes broad and rounded, 1.8-3 (4.5) mm wide, 1.5-2 (3.5) mm long, usually villous in the buds, margins frequently erose; filaments all differing slightly in length and height of attachment; ovary 4-ovulate, at anthesis subglobose, about 0.8 mm high, marked with 4 longitudinal grooves; fruit at maturity glabrous or hairy, ovoid-globose, 2.5-3 mm in diameter, 2-2.5 mm high, not lobed; nutlets bony, back convex, densely and minutely tuberculate; style seated in the pericarp at the apex of the fruit, persistent until the fruit breaks up into 4 nutlets 1.5-2.5 mm long. Rocky ridges and benches. Southwestern Utah, east to Texas, and south to Baja California and northern Mexico. In Utah *C. canescens* is limited and very rare in Washington County. April-June. Fig. 7.

Washington Co., West slope of the Beaverdam Mountains, D. Nish 43 (UTC).

2. *Coldenia hispidissima* (Torr. & Gray) Gray, Proc. Amer. Acad. 5:340. 1862; Synop. Fl. 2:pt. 1, 182. 1878.

Eddya hispidissima Torr. & Gray, Pacif. R. R. Reports, ed. 2, 2:170, Pl. 9. 1857.

Ehretia hispida Torr., Pacif. R. R. Reports, ed. 1, 320, 1855; without description. Type is *C. Wright* 485.

Plants prostrate, forming mats 2-6 dm in diameter; stems several to numerous, dicotomously branched, spreading from a woody taproot; younger branchlets villulose-hispidulous; leaves clustered, borne mostly on very short branchlets along the main stem; petioles 1-2 mm long, broadest (1-1.5) mm at the base, becoming indurate, usually pallid, margin hispid-ciliate and the back usually glabrous or nearly so; leaf blades usually linear revolute (rarely ovate or elliptic), 4-10 mm long, 0.6-1 mm wide, usually narrower than the indurate petiole-base; flowers borne among the leaves; calyx sessile, broadly

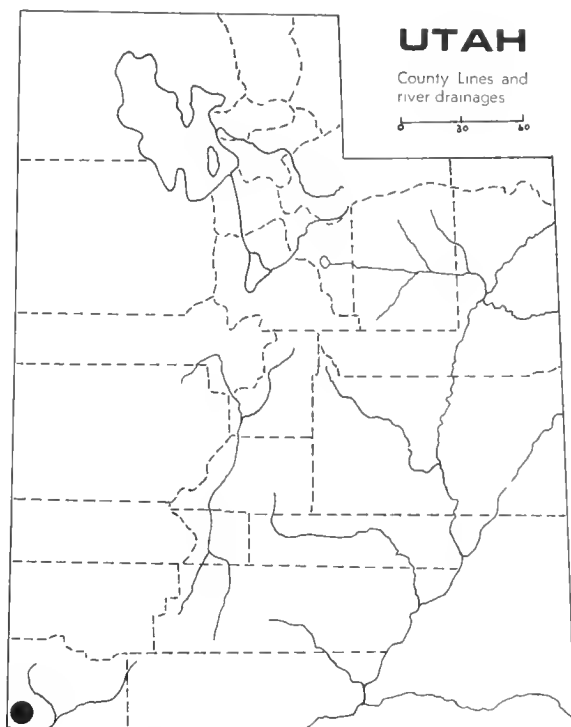


Fig. 7. *Coldenia canescens*

and permanently attached in the leaf axil, at anthesis about 3 mm long, lanceolate, united at the base, villulose-ciliate below the middle, frequently terminated with a stiff bristle; corolla usually pink, about 7.5 mm long; corolla lobes rounded, spreading, about 2 mm long and 3 mm broad; stamens 5, unequal in length and position within the corolla tube; style 1.5-2.2 mm long, somewhat flattened, apex bilobed; nutlets ovoid, usually only 1 or 2 maturing, 1.1-1.4 mm long, 0.8-1 mm broad, papillate, back convex, ventral rounded or somewhat flattened; scar open, 1.5-2 mm wide at base, nearly as long as the nutlet, surrounded by a narrow band of smooth non-papillate pericarp, traversed down the center by a lineate ridge. Nevada, southern Utah, northern Arizona, and east to Texas and south to northern Mexico. Usually growing on sand dunes and dry slopes. April-September. Fig. 8.

Emery Co., San Raphael Desert, Bryan & Redd 12-8 (UTC); 6 miles north of Hanksville, B. Maguire 19386 (UTC); Garfield Co., Clay Point, J.C. Pederson 49 (BRY); 2 miles downstream from Hite, B.F. Harrison 11737 (BRY); Hite, W.P. Cottam 14769 (UT); Grand Co., Castle Valley, S.L. Welsh & D. Atwood 9954 (BRY); 1 mile north of Moab, B. Maguire 5722 (UTC); 6 miles up river from Moab, Bryan & Moab School 6-8 (UTC); Kane Co., Bullfrog Canyon, D.W. Lindsay 93 (UT); San Juan Co., West of Bluff, W.P. Cottam 2560 (BRY); along the San Juan River, Rydberg & Garrett 9942 (UT); Middle Blue Notch Canyon, L. Wilson 273 (UTC); 9 miles southwest of Bluff, B.

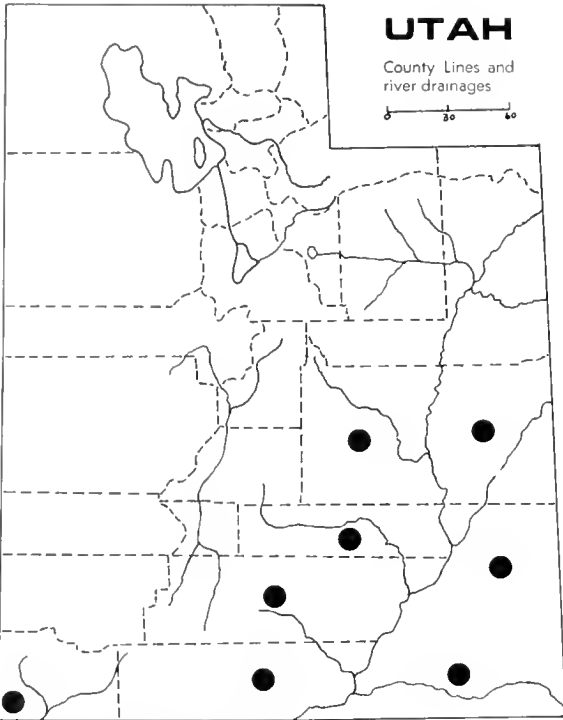


Fig. 8. *Coldenia hispidissima*

Maguire 5719 (UTC); 35 miles southwest of Bluff, B. Maguire 5722 (UTC); Washington Co., Beaverdam Mountains, L.C. Higgins 838 (BRY); Wayne Co., Hanksville, R.V. Hardy 41 (BRY); 5 miles north of Hanksville, S.L. Welsh & G. Moore 3611 (BRY); desert between Hanksville and mountains, W.P. Cottam 5126 (BRY).

3. *Coldenia nuttallii* Hooker, Kew Journ. Bot. 3:296. 1851. Type: "Rocky Mountains," collected by Nuttall.

Tiquilia parviflora Nutt. ex Hook., loc. cit. as a synonym.

Tiquila brevifolia Nutt. ex Torr., Bot. Mex. Bound. 136. 1859.

Prostrate annual with slender, somewhat brittle, dicotomously branched stems forming mats 1-3.5 dm broad, finely strigose; leaves ovate, to nearly suborbicular, 4-8 mm long, narrowly revolute, and often hispid on the margins, with 2-3 pairs of distinct veins on the back, thinly strigose on the upper surface with somewhat stiff hairs, hirsute on the lower surface; petioles slender, usually as long or longer than the blade; flowers in compact clusters in the forks and at the ends of the branches; calyx lobes linear-subulate, 4-5 mm long, villous or setulose on the back, sparsely but conspicuously hispid on the margins; corolla pink or nearly white, little exceeding the calyx, the limb 2-2.5 mm broad, the tube with 5 triangular scales near the base; nutlets oblong-

ovoid, smooth and shining. Sandy or alkaline soil, on plains and hillsides. Washington, east through Idaho to Wyoming and south to Utah, Arizona, and southern California, May-August. Fig. 9.

Beaver Co., Pine Valley, W.P. Cottam 5701 (UT); Box Elder Co., Copper Mountain, W.P. Cottam 4551 (BRY, UT); Iron Co., Hamblin Valley, W.P. Cottam 3335 (BRY, UT); sand dune areas, W.D. Stanton s.n. (UT); Millard Co., desert area, W.P. Cottam 5701 (UT); 6 miles north of Gandy, Maguire & Richards 2752 (UTC); 2 miles south of Desert Range Experiment Station Headquarters, B. Maguire 20913 (UTC); 3 miles south of Garrison, B. Maguire 20854 (UTC); Uintah Co. Willow Creek, 16 miles south of Ouray, R.C. Rollins 1724 (UTC); Washington Co., Beaverdam Mountains, L.C. Higgins 649 (BRY).

6. *Cryptantha* Lehm.

Cryptantha Lehm., Del. Sem. Hort. Hamburg 4. 1833, and Fisch. & Mey., Ind. Sem. Hort. Petrop. 2:35. 1836; Johnston, Contr. Gray Herb. 74:1-114. 1925, and Contr. Gray Herb. 78:30. 1927.

Krynitzkia Fisch. & Mey., Ind. Sem. Hort. Petrop. 7:52. 1841.

Annual or perennial, herbaceous or fruticose plants, usually with coarse stiff pubescence; leaves opposite at base, or alternate throughout, firm, veinless; flowers white or rare-

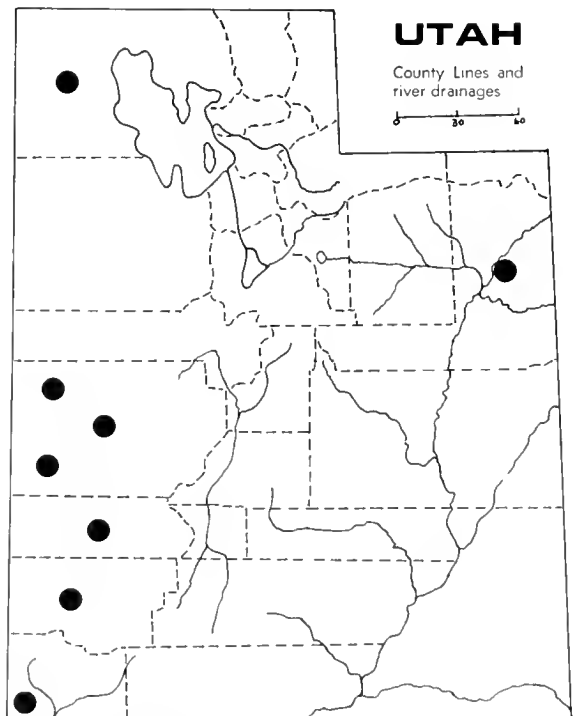


Fig. 9. *Coldenia nuttallii*

ly yellow, in bractless or bracted spikes or racemes; calyx divided to the base, the lobes erect or connivent, linear or oblong; mature calyx investing the nutlets and falling away entire, or the calyx persistent and the nutlets falling away separately; corolla with a short to somewhat elongate cylindrical tube with or without scales at the base of the tube, the throat with intruded appendages; corolla lobes imbricate, rounded, spreading; style slender, short or long, included; stigma capitate; ovules 2-4; nutlets 1-4, erect, ovate to triangular, roughened or smooth, winged, margined or marginless, affixed laterally through a medial ventral and commonly basally forked groove to a usually columnar, subulate or pyriform gynobase.

This is one of the most perplexing genera in the entire family. It is exclusively American, mostly in the western United States, but common in the deserts of South America as well. Several species are reported to have some value as a forage for sheep.

Type species: *Cryptantha glomerata* Lehm.

1. Plants annual; stems slender; Subgenus *Krynitzkia* (2).
1. Plants biennial or perennial; stems coarse; Subgenus *Oreocarya* (31).
2. Nutlets with the margins decidedly winged or knifelike (3).
2. Nutlets with the margins rounded or angled, never with a marginal wing or knifelike edge (6).
3. Pedicels usually evident, slender, 1-4 mm long; nutlets heteromorphous. 18. *C. racemosa*
3. Pedicels obscure or none, less than 1 mm long (4).
4. Nutlets heteromorphous, the odd nutlet abaxial 12. *C. inaequata*
4. Nutlets homomorphous or if slightly heteromorphous the odd nutlet axial (5).
5. Nutlets solitary or rarely 2; calyx obliquely conical at base; corolla conspicuous 22. *C. Utahensis*
5. Nutlets 4; calyx symmetrical; corolla inconspicuous. 17. *C. pterocarya*
6. Nutlets all smooth (7).
6. Nutlets all rough or at least some of them so (14).
7. Hairs on the calyx unciniate or decidedly arcuate. 10. *C. flaccida*
7. Hairs on the calyx straight (8).
8. Nutlets with an eccentric groove; flowers in biserial naked spikes 1. *C. affinis*
8. Nutlets with a centrally placed groove (9).
9. Nutlets broadly ovate (10).
9. Nutlets oblong-ovate to lanceolate (12).
10. Spikes usually geminate; inflorescence projected above the leafy mass of the plant, well defined 21. *C. torreyana*
10. Spikes usually solitary, not sharply differentiated from the leafy peduncular stems (11).
11. Nutlets homomorphous 2. *C. ambigua*
11. Nutlets slightly heteromorphous 16. *C. pattersonii*
12. Style reaching $\frac{1}{4}$ to $\frac{3}{4}$ the height of the nutlets; calyx densely appressed hispid-villous, commonly lacking conspicuous spreading bristles. 11. *C. gracilis*
12. Style almost reaching the nutlet-tips or surpassing them (13).
13. Margin of nutlets acute, at least above the middle. 23. *C. watsoni*
13. Margin of nutlets rounded or obtuse 9. *C. fendleri*
14. Nutlets decidedly heteromorphous (15).
14. Nutlets homomorphous (22).
15. Mature calyces strongly appressed to the flattened rachis, decidedly gibbous on the axial side, persistent 8. *C. dumetorum*
15. Mature calyces somewhat spreading, not at all gibbous (16).
16. Odd nutlet abaxial, surpassed by style (17).
16. Odd nutlet axial; style surpassed or occasionally reaching to the nutlet-tips (20).
17. Spikes bracteate throughout; calyx persistent 14. *C. micrantha*
17. Spikes naked or nearly so; calyx deciduous (18).
18. Pedicels slender, 1-4 mm long 18. *C. racemosa*
18. Pedicels stout and obscure, less than 1 mm long (19).
19. Nutlets 1.3-1.7 mm long; calyx 2-3 mm long 12. *C. inaequata*
19. Nutlets about 1 mm long; calyx 3-4 mm long 3. *C. angustifolia*
20. Odd nutlet spinular-muricate; calyx-lobes conspicuously thickened 6. *C. crassisejala*
20. Odd nutlet more or less granulate; calyx lobes moderately thickened (21).
21. Nutlets ovate, smoothish or sparsely tuberculate, odd one about 1.9 mm long 16. *C. pattersonii*
21. Nutlets lanceolate or narrowly ovate, coarsely tuberculate, odd one 2-2.6 mm long ... 13. *C. kelseyana*
22. Calyx circumscissile 5. *C. circumscissa*
22. Calyx not circumscissile (23).
23. Style surpassing the nutlets 14. *C. micrantha*
23. Style not surpassing the nutlets or about reaching to the tips of the nutlets (24).
24. Corolla conspicuous, 2-5 mm broad (25).
24. Corolla inconspicuous, 0.5-2 mm broad (26).
25. Abaxial nutlet developing; gynobase reaching $\frac{1}{2}$ to $\frac{2}{3}$ the height of the nutlet 7. *C. decipiens*
25. Axial nutlet developing; gynobase about $\frac{1}{3}$ height of nutlet 22. *C. utahensis*
26. Ovules 2; outlet and calyx bent 19. *C. recurvata*
26. Ovules 4; nutlets and calyx straight (27).
27. Nutlets usually solitary, abaxial; gynobase reaching $\frac{1}{3}$ to $\frac{1}{2}$ the height of the nutlet 7. *C. decipiens*

27. Nutlets usually 4 (28).
28. Nutlets decidedly ovate, with low rounded tuberculations 2. *C. ambigua*
28. Nutlets more or less lanceolate (29).
29. Stems spreading-hirsute 4. *C. barbiger*
29. Stems strigose (30).
30. Nutlets verrucose or verrucose-muricate.....
..... 15. *C. nevadensis*
30. Nutlets spinular-muricate 20. *C. scoparia*
31. Corolla tube elongate, distinctly surpassing the calyx; flowers usually heterostyled (32).
31. Corolla tube short, scarcely if at all surpassing the calyx; flowers not heterostyled (46).
32. Nutlets smooth and shining (33).
32. Nutlets more or less roughened (38).
33. Corolla yellow (34).
33. Corolla white (35).
34. Inflorescence an elongate, cylindrical thyrses; nutlets lanceolate with acute margins, usually only 1 developing 33. *C. flava*
34. Inflorescence consisting of a large terminal cluster with 1 or more remote, at maturity frequently stalked much smaller lateral clusters; nutlets broadly ovate, with winged margins, all 4 usually maturing 31. *C. confertiflora*
35. Inflorescence capitate, 0.1-0.4 dm long; corolla limb 6-8 mm broad, the tube little surpassing the calyx; nutlets lanceolate 29. *C. capitata*
35. Inflorescence elongate, 0.4-4.4 dm long; corolla limb 8-17 mm broad, the tube distinctly surpassing the calyx except in *C. barnebyi*; nutlets ovate (36).
36. Ventral surface of the leaves glabrous
..... 48. *C. semiglabra*
36. Ventral surface of the leaves strigose or setose-hispid (37).
37. Corolla limb 13-17 mm broad, crests at base of tube absent; nutlets 3-3.5 mm long; native to San Raphael Swell 39. *C. johnstonii*
37. Corolla limb 8-11 mm broad, crests at base of tube conspicuous; nutlets 3.5-4.5 mm long
..... 26. *C. barnebyi*
38. Nutlets uniformly muricate or papillose, or occasionally in *C. jonesiana* also with some inconspicuous ridges (39).
38. Nutlets more or less rugose or tuberculate, or sometimes with a few inconspicuous murications (40).
39. Leaves oblanceolate, strigose with pustulate hairs small or lacking; corolla 7-10 mm long, fornicies elongate 35. *C. fulvocanescens*
39. Leaves spatulate, hispid with pustulate bristles; corolla 10-15 mm long, fornicies low and broad
..... 40. *C. jonesiana*
40. Ventral or inner surface of the nutlets smooth or nearly so 46. *C. rollinsii*
40. Ventral surface of the nutlets distinctly roughened (41).
41. Leaves conspicuously pustulate ventrally; corolla tube 12-16 mm long; calyx segments 7-10 mm long in anthesis 41. *C. longiflora*
41. Leaves sparsely if at all pustulate ventrally; corolla tube 5.5-12 mm long; calyx segments 3.5-7 mm long in anthesis (42).
42. Inflorescence 0.1-0.4 dm long; corolla tube 10-12 mm long; margin of nutlets not in contact; plants less than 1.5 dm tall 45. *C. paradoxa*
42. Inflorescence 0.5-3 dm long; corolla tube 5-10 mm long; margin of nutlets in contact or nearly so; plants usually over 1.5 dm tall (43).
43. Scar of nutlets surrounded by an elevated margin but tightly closed; style 1-2 mm long; calyx 3.5-4 mm long in anthesis 25. *C. bakeri*
43. Scar of nutlets conspicuously open; style 3-8 mm long; calyx 4.5-7 mm long in anthesis (44).
44. Scar of nutlets conspicuously open and surrounded by a definite elevated margin 34. *C. flavoculata*
44. Scar of nutlets slightly open and with only an inconspicuous elevated margin if any (45).
45. Leaves linear-spatulate; nutlets sharply and deeply rugose; corolla tube 5.5-7 mm long; fornicies low and broad 52. *C. tennis*
45. Leaves obovate or broadly oblanceolate; nutlets with rounded ridges and tubercles; corolla tube 7-10 mm long, fornicies long papillose
..... 54. *C. uetherillii*
46. Nutlets smooth on their dorsal surface, not rugose, muricate or tuberculate (47).
46. Nutlets more or less roughened, muricate, rugose or tuberculate at least on the dorsal surface (48).
47. Fruit depressed globular, nutlets not in contact by their margins; style exceeding mature fruit 1-3 mm; corolla tube 2.5-3 mm long 38. *C. jamesii*
47. Fruit conical, ovoid or lanceolate, nutlets in contact by their margins or nearly so; style exceeding mature fruit 5-6 mm; corolla tube 5-7 mm long.....
..... 26. *C. barnebyi*
48. Ventral surface of nutlets smooth or nearly so (49).
48. Ventral surface of nutlets rugose or variously wrinkled (52).
49. Nutlets bordered by a conspicuous wing; robust plants 5-10 dm tall, with long ebracteate spikes
..... 50. *C. setosissima*
49. Nutlets never conspicuously winged, sometimes with an acute margin; plants usually lower and caespitose (50).
50. Corolla tube 7-9 mm long; calyx 6-9 mm long in anthesis 46. *C. rollinsii*
50. Corolla tube 2-6 mm long; calyx 2.5-6 mm long in anthesis (51).
51. Nutlets scarcely or not at all muricate between the rugae; strictly erect, conspicuously hispid perennials from northeastern Utah 51. *C. stricta*
51. Nutlets distinctly muricate or tuberculate between the rugae and near the margins; western Utah.....
..... 47. *C. rugulosa*
52. Nutlets conspicuously muricate, or in *C. humilis* also with a few irregular ridges (53).
52. Nutlets not exclusively muricate, but rugose or tuberculate (55).

- 53. Pubescence of the leaves silky-strigose or strigillose but not subtomentose or tomentose 27. *C. breviflora*
- 53. Leaves distinctly subtomentose or tomentose, also setose in *C. humilis* (54).
- 54. Plants 0.3-1 dm tall; leaves 0.5-2.5 cm long; calyx 2-2.5 mm long in anthesis; corolla tube 1.8-2.2 mm long; Millard County, Utah 30. *C. compacta*
- 54. Plants 0.4-2.5 dm tall; leaves 2.5 cm long or longer; calyx 3-5 mm long in anthesis; corolla tube 3-5 mm long; plants widespread 37. *C. humilis*
- 55. Scar of nutlets open some distance above the base (56).
- 55. Scar of nutlets closed or nearly so, without a conspicuous triangular opening toward the base (63).
- 56. Scar somewhat constricted some distance below the middle of the open portion (57).
- 56. Scar triangular and not constricted below the middle (58).
- 57. Elevated margin of the scar definitely limited; pustules present on both leaf surfaces 42. *C. mensana*
- 57. Elevated margin indefinitely limited; pustules present only on dorsal surface of the leaves 44. *C. osterhoutii*
- 58. Some tendency to an elevated margin evident around the scar (59).
- 58. No tendency to an elevated margin around the scar (60).
- 59. Cymules elongating and so the inflorescence broad; biennial or short-lived perennials; nutlets usually with an evident dorsal ridge 53. *C. virginensis*
- 59. Cymules shorter and the inflorescence narrow; long-lived caespitose perennials; nutlets with only a slight dorsal ridge if any 24. *C. abata*
- 60. Style not exceeding the mature nutlets by more than 0.5 mm; plants usually less than 1.3 dm tall (61).
- 60. Style exceeding the mature nutlets 1.6 mm or more; plants usually taller than 1.3 dm 37. *C. humilis*
- 61. Corolla tube 2-2.6 mm long; nutlets 2.3-3 mm long. 43. *C. ochroleuca*
- 61. Corolla tube 3-4 mm long; nutlets 3-3.5 mm long (62).
- 62. Ventral surface of nutlets deeply rugose and tuberculate 24. *C. abata*
- 62. Ventral surface of nutlets indefinitely muricate; near the Utah border in Summit and Daggett counties 28. *C. caespitosa*
- 63. Upper surface of the leaves uniformly appressed strigose and without pustulate hairs (64).
- 63. Upper surface of the leaves with two distinct kinds of hairs; pustulate at base (66).
- 64. Nutlets sharply rugose and tuberculate, scar closed, and surrounded by an elevated margin 25. *C. bakeri*
- 64. Nutlets not so sharply rugose or tuberculate; scar not surrounded by an elevated margin (65).

- 65. Corolla tube 2-2.5 mm long; style exceeding nutlets by 1 mm or less; endemic to Garfield County 43. *C. ochroleuca*
- 65. Corolla tube 3.5 mm long or longer; style exceeding nutlets by more than 1 mm; northeastern Utah 49. *C. sericea*
- 66. Mature calyx exceeding the nutlets by 2-4 mm; inflorescence broad-topped; Grand County 32. *C. elata*
- 66. Mature calyx exceeding the nutlets by 4-8 mm (67).
- 67. Nutlets tuberculate, scarcely if at all rugose; mostly in the Uintah Basin 36. *C. grahamii*
- 67. Nutlets more or less rugose; widespread but mostly in the western tier of counties 37. *C. humilis*

- 1. *Cryptantha affinis* (Gray) Greene, Pittonia 1:119. 1887.
Krynitzkia affinis A. Gray, Proc. Amer. Acad. 20:270. 1885. Type: east side of Cascades. 1860. Lyall s.n.
Cryptantha geminata Greene, Pittonia 1:119. 1887.
Cryptantha confusa Rydb. Bull. Torr. Bot. Club 46:679. 1909.
Cryptantha eastwoodiae St. John, Fl. S.E. Washington 342. 1937.

Usually sparsely branched herb 1-2 (4) dm tall; branches commonly few and ascending but plant occasionally much branched from the base, hispid or short-hirsute throughout; leaves narrowly to broadly oblanceolate, 1-4 (5) cm long, 2.5-6 (8) mm broad, few, short-hirsute, usually minutely pustulate, obtuse or rounded at tip, lowest pair clearly opposite; spikes geminate or solitary, usually 2 to 8 becoming 15 mm long, slender, remotely flowered, commonly with a very few large leafy bracts below; corolla inconspicuous, 1-2 mm long, limb about 1.5 mm broad; fruiting calyx 2.5-4 mm long, usually about as broad as long, laterally compressed, ascending; pedicels 0.5-1 mm long; mature calyxlobes lanceolate, somewhat connivent, not greatly surpassing the nutlets, midrib weakly thickened on the abaxial lobe, sparsely hirsute, margins appressed hispid; nutlets 4, homomorphous, smooth or very finely granulate, shiny, brownish to greenish, frequently mottled, 1.8-2.5 mm long, ovate, obliquely compressed, back low-convex, margins rounded; groove evidently excentric, closed, simple or shortly and unequally forked at the base; gynobase short, stout, about 1/2 height of nutlets; style evidently surpassed by nutlets or rarely equalling them. Usually in sandy to rocky soils. Washington and western Montana, south to Wyoming, Utah, and southern California. June-September. Fig. 10.

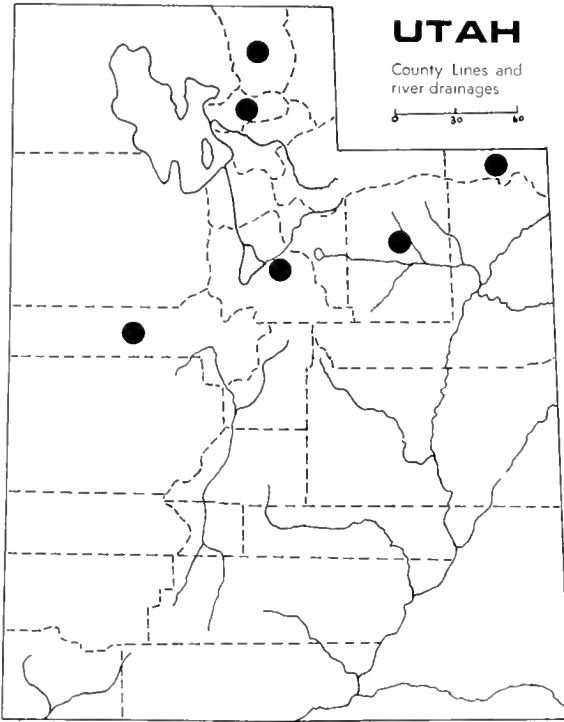


Fig. 10. *Cryptantha affinis*

The most obvious characteristics of this species are the obliquely compressed nutlets which result in the excentric position of the groove.

Cache Co., 10 miles up Smithfield Canyon, Hobson & Piranian 13775 (UTC); Intervale, Spring Hollow, B. Maguire 13839 (UTC); White Pine Lake, B. Maguire 16256 (UTC); Logan Canyon, Spring Hollow, B. Maguire 13778 (UTC); Daggett Co., Flaming Gorge, L. Williams 473 (UTC); Duchesne Co., 10 miles north of Altonah, J. Brotherson 646 (BRY); Juab Co., Granite Canyon, Deep Creek Mountains, Maguire & Becraft 2765 (UTC); Utah Co., Spring Dell, Provo Canyon, A.O. Garrett 2778 (UT); Weber Co., Summit of Little Bear River Canyon, B. Maguire 12976 (UTC).

2. *Cryptantha ambigua* (Gray) Greene, Pittonia 1:113. 1887.

Eritrichium muriculatum var. *ambiguum*

Gray, Synop. Fl. No. Am. 2:194. 1878.

Type: probably in the Walla Walla region of southeastern Washington, collected by the Wilkes expedition.

Krynitzkia ambigua Gray, Proc. Am. Acad. 20:273. 1885.

Cryptantha polycarpa Greene, Pittonia 1:114. 1887.

Cryptantha multicaulis A. Nels. Bot. Gaz. 30:194. 1900.

Cryptantha ambigua var. *robustior* Brand, Pflanzenreich 4, 252:69. 1931.

Stems usually loosely branched from the base, ascending, 1-2.5 dm tall, hirsute and somewhat strigose; leaves linear to narrowly lanceolate, 2-3 (5) cm long, 1-4 (5) mm broad, obtuse to acutish, usually somewhat appressed hispid-hirsute, the hairs commonly pustulate at base; spikes often solitary, 5-15 cm long, bractless, or with the lowermost flowers bracteate, commonly not projecting clear of the leafy mass of the plant and not clearly differentiated from the leafy branches; corolla 1-2 mm broad, inconspicuous; fruiting calyces ovate-oblong, 4-7 mm long, crowded or distant, the tube rounded-obconic at base, lobes linear or linear-lanceolate, more or less connivent, midrib thickened, tawny-hirsute, margins strigose-hirsute; pedicels 0.5-0.9 mm long; nutlets 4, broadly ovoid, 1.6-2 mm long, granulate and coarsely tuberculate or rarely tending to be smooth toward the base, back low-convex, sides obtuse and rounded, groove closed or somewhat open at the always broadly forked base; gynobase narrow, 1-1.2 mm long, 2/3 height of nutlets; style reaching 4/5 to 5/5 height of nutlets. Dry slopes and ridges, open pine forests and sagebrush flats. Southern Washington to southern Montana and then south to northern Colorado, western Nevada, and north-eastern California. June-August. Fig. 11.

C. ambigua is nearly always distinguishable by its habit of growth, but in a few cases is dif-

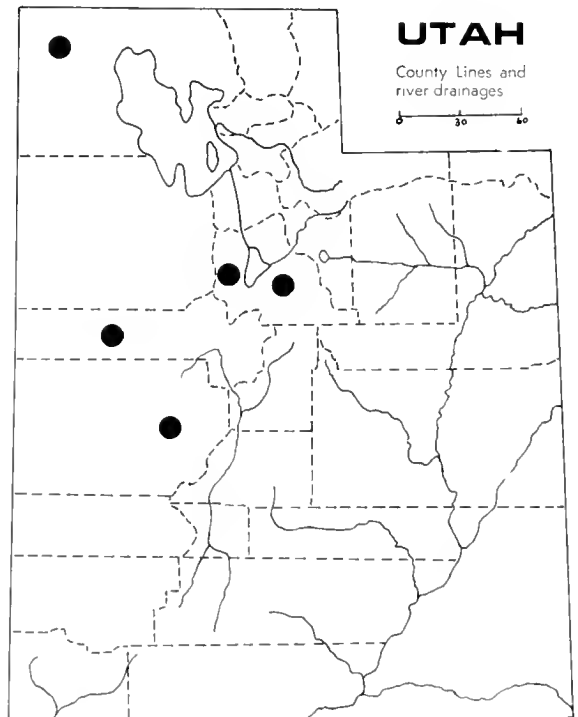


Fig. 11. *Cryptantha ambigua*

ficult to distinguish from *C. kelseyana* and *C. pattersonii*.

Beaver Co., 11.5 miles east of Milford at the Granite Mountain Pass, B. Maguire 20995 (UTC); Box Elder Co., Raft River Mountains, G.M. Alder 132 (UT); Juab Co., Deep Creek Range, Granite Creek, Maguire & Holmgren 21904 (UTC); Utah Co., Thistle, M.E. Jones 5370 (UC).

3. *Cryptantha angustifolia* (Torr.) Greene, Pittonia 1:112. 1887.

Eritrichium angustifolium Torr. Pacif. R. R. Reports 5:363. 1858. Type: Yuma, Arizona, Thomas s.n.

Krynitzkia angustifolia A. Gray, Proc. Amer. Acad. 20: 272. 1855.

Stems diffusely branched from the base, 0.5-3 dm tall; canescent, villous-hirsute, with light ashy gray hairs, the lowest branches decumbent or ascending; leaves narrowly linear, 1.5-4 cm long, 1-2 mm wide, hispid or strigose, somewhat pustulate; spikes usually geminate, about 5 cm long, rather dense, bractless or with 1-2 bracts near the base; corolla minute, the tube 1-2 mm long, limb 1-2.5 mm broad; fruiting calyces ovate-oblong, 3-4 mm long, stiffly ascending, strongly biseriate, slightly asymmetrical; pedicels less than 0.5 mm long; mature calyx-lobes linear-lanceolate, slightly connivent, hispid on the thickened midrib, short villous on the margins, abaxial lobe longest and most hirsute; nutlets usually 4, heteromorphous, ovate-oblong, brown or plumbeous with pale tuberculations or rarely murications, back convex, face flattish, margins somewhat angular; odd nutlet next to the abaxial calyx-lobe, a little larger and more persistent than the similarly colored and shaped consimilar nutlets which are about 1 mm long; groove slightly open above, broadening at the base; gynobase columnar, equalled by consimilar nutlets but shorter than odd nutlet; style usually surpassing even the odd nutlet. Sandy or gravelly washes, Lower Sonoran Zone. Southern California to Southern Utah and south to Baja California, Sonora, and western Texas. March-June. Fig. 12.

I have not seen any specimens of *C. angustifolia* from Utah, but the species has been collected within a few miles of the Utah border in both Arizona and Nevada. This species would most likely be found in the Beaverdam Wash or the valleys of the Virgin River.

4. *Cryptantha barbiger* (Gray) Greene, Pittonia 1:114. 1887.

Eritrichium barbigerum A. Gray, Synop. Fl. No. Amer. 2:194. 1878. Type: Utah

(Parry 171) as designated by I. M. Johnston, Contr. Gray Herb. 74:66. 1925.

Krynitzkia barbiger A. Gray, Proc. Amer. Acad. 20:273. 1855.

Krynitzkia mixta M. E. Jones, Contr. West. Bot. 13:6. 1910.

Stems erect, 1-4 dm high, solitary or several from the base, branches strictly ascending or spreading, very bristly and sparsely if at all strigose except in the inflorescence; leaves oblong to lance-linear, obtuse, 1-5 (7) cm long, 3-7 (13) mm broad, hirsute, more or less pustulate; spikes geminate or rarely solitary or ternate, naked, as much as 15 cm long; corolla inconspicuous, limb 1-2 mm broad; fruiting calyx ascending, 5-10 mm long, narrowly ovoid-oblong to oblong-lanceolate, symmetrical, deciduous; pedicels 0.3-0.7 mm long, villous; mature calyx-lobes lanceolate to linear-lanceolate, connivent above with recurving tips, margin conspicuously long white-villous, midrib thickened and hirsute, abaxial lobe slightly the longest; nutlets 1-4, homomorphous, lance-ovoid, 1.5-2.5 mm long, strongly verrucose, usually brownish, back convex, edges obscurely angled or rounded, groove opened or closed but base gradually dilated to form a triangular areola; gynobase narrow, 2/3 to 3/4 height of nutlets; style reaching to or slightly beyond the nutlet tips. Sandy desert washes or slopes in the Lower Sonoran Zone.

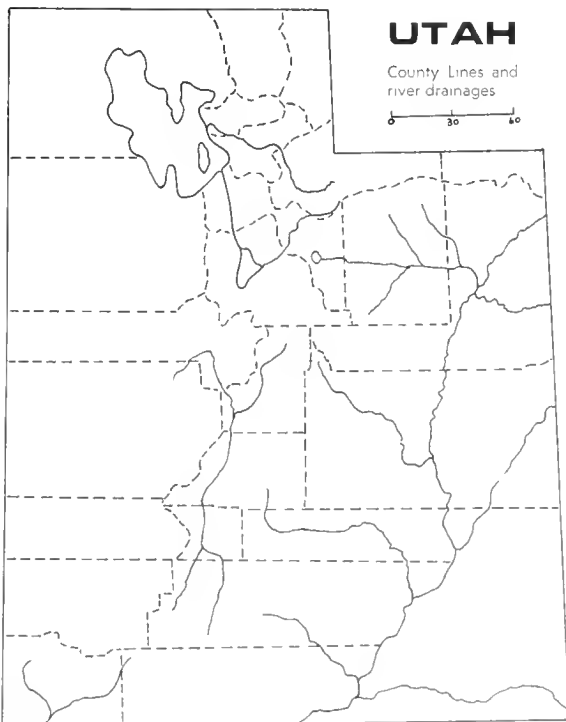


Fig. 12. *Cryptantha angustifolia*

Southern Utah south to southern California, Baja California, Arizona, southern New Mexico, and northern Sonora. February-June. Fig. 13.

San Juan Co., 2 miles west of Bluff, B. Maguire 16279 (UTC); Washington Co., St. George, F. W. Gould 1478 (DIX, UTC); 2 miles west of Rockville, B. Maguire 4978 (UTC); 4 miles northwest of Welcome Springs, B. Maguire 20527 (UTC); 40 miles west of St. George, B. Maguire 20506 (UTC); 10 miles west of Rockville, C.L. Hitchcock 3003 (UTC); St. George, M.E. Jones 1621 (UT); St. George, F.W. Gould 1539 (UT); Black Hill west of St. George, DE. Beck s.n. (DIX); Red hill north of St. George, S. Wilson s.n. (DIX); Beaverdam Mountains at junction of hwy 91 and the Jackson road, L.C. Higgins 447 (BRY); Dixie State Park, L.C. Higgins 930 (BRY); 3 miles south of Touverville, B.R. Stahmann & J.L. Jacobs 21 (BRY); St. George, south slope of Black Hill, F.W. Gould 1478 (BRY); about 5 miles west of hwy 91 along the Jackson road, L.C. Higgins 500 (BRY); St. George, D.H. Galway 8485 (BRY).

5. *Cryptantha circumscissa* (H. & A.) Johnston, Contr. Gray Herb. 68:55. 1923. Type: Snake Fort, Snake River, Idaho.

Lithospermum circumscissum H. & A. Bot. Beechey 370. 1840.

Piptocalyx circumscissus Torr. in S. Wats. Bot. King Expl. 240. 1871.

Eritrichium circumscissum Gray, Proc. Amer. Acad. 10:58. 1874.

Krynitzkia circumscissa Gray, Proc. Amer. Acad. 20:275. 1885.

Wheelerella circumscissa Grant. Bull. Soc. Calif. Acad. Sci. 5:28. 1906.

Cryptantha depressa A. Nels. Bot. Gaz. 34:29. 1902.

Greenocharis circumscissa Rydb. Bull. Torrey Club 36:677. 1909.

Stems few to many from the base, strigose, more or less branched above, often forming a dense hemispherical mass 2-10 cm high, the outer ones often decumbent; leaves oblanceolate, 3-15 mm long, 1-2 mm broad, obtuse, surface siliceous especially toward the pale base, strigose or short-hispid, obscurely pustulate; flowers in the axils of foliaceous bracts in short somewhat indefinite racelike clusters; corolla inconspicuous, 1-2 (3) mm broad; fruiting calyx 2.5-4 mm long, oblong-ovoid, united to near the middle, at maturity the upper half falling away by a circumscission just below the sinuses, basal part persistent, cupulate, appressed-hispid; mature calyx lobes narrowly linear-lanceolate, firm-herbaceous, scarcely ribbed, more or less hispid; pedicels obscure, about 0.5 mm long; nutlets 4, homomorphic, or with the abaxial one slightly longer, smooth or inconspicuously muricate, triangular-ovoid or oblong-lanceolate, 1.2-1.7 mm long, back flattened, especially near the apex.

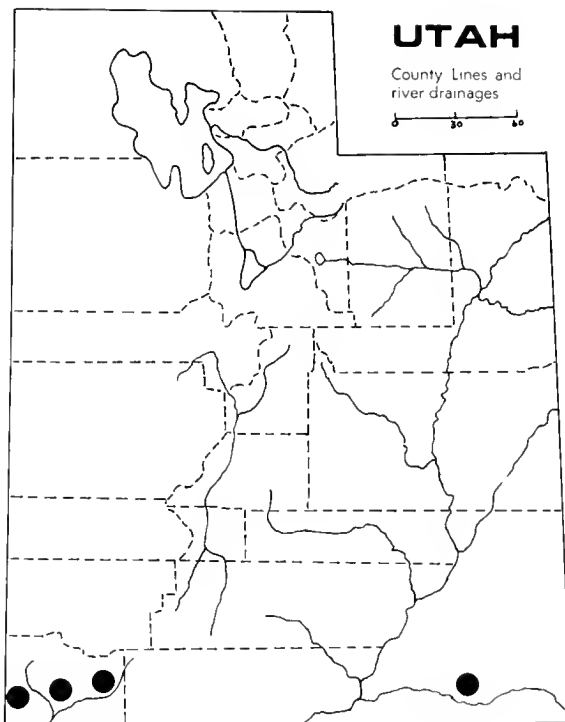


Fig. 13. *Cryptantha barbigeria*

margins angled, groove closed and forked at base, gynobase about 2/3 height of nutlets; style equalling or barely exceeded by nutlets. Sandy to gravelly soils, Sonoran to arid Transition Zone. Southern British Columbia and Idaho, south to Arizona and Baja California. April-August. Fig. 14.

Beaver Co., 8.5 miles east of Milford, B. Maguire 21020 (UTC); Garfield Co., Egnog Spring, Bullfrog Creek west of Henry Mountains, Welsh 3984 (BRY); Iron Co., 16 miles south of Lund, L. Anderson 711 (UTC); Juab Co., 3 miles from Trout Creek, Maguire & Becraft 2769 (UTC); Kane Co., 6 miles south of Grosvenor Arch, J. L. Reveal 809 (UTC); 57 miles east of Kanab, A. Cronquist 10163 (BRY, UTC); ½ mile west of Paria River Bridge along hwy 89, Welsh & Atwood 9747 (BRY); 25 miles southeast of Escalante, Holmgren, Reveal & LaFrance 2068 (BRY); Johnson Canyon northeast of Kanab, D. Atwood 1791A (BRY); Millard Co., 60 miles west of Delta, Maguire & Becraft 2768 (UTC); 20 miles west of Hineckley, B. Maguire 20761 (UTC); Desert Range Exp. Station, M. Barlow 47 (BRY); Desert Range Exp. Station, S. Browster 22 (BRY); San Juan Co., 8 miles east of Hite, A. Cronquist 9041 (UTC); Tooele Co., Little Granite Mountain, S. Flowers 185 (UT); Washington Co., 20 miles southeast of Hurricane, A. Cronquist 10096 (UTC); St. George, M.E. Jones s.n. (UTC); Anderson's Ranch, 32 miles south of Cedar City, B. Maguire 13561 (UTC); west slope of the Beaverdam Mountains, D. Nish 12 (UTC); 11 miles south of Hurricane, F.W. Gould 1685 (UT); St. George, M.E. Jones 1652 (UT); St. George, Red Hill north of town, D. Hall s.n. (BRY, DIX); 1 mile southeast of Ivins Reservoir along hwy 91, L.C. Higgins 4102 (BRY, WTSU); Santa Clara, W.P. Cot-

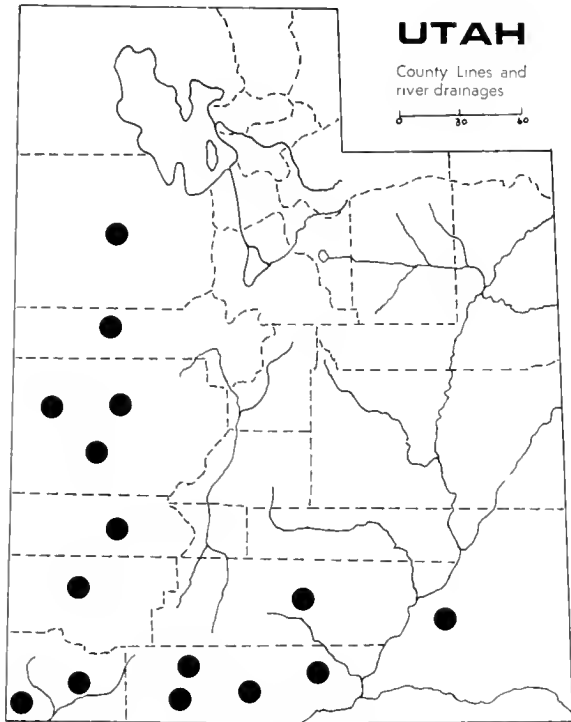


Fig. 14. *Cryptantha circumscissa*

tam 1164 (BRY); St. George, D. Hall 6283 (BRY); Belveau Flats, W.P. Cottam 4674 (BRY); Snows Canyon, D.H. Galway s.n. (BRY); 4 miles east of Harrisburg, Welsh & Moore 6842 (BRY); near Utah-Arizona border west of Colorado City, L.C. Higgins 1380 (BRY).

6. *Cryptantha crassisepala* (Torr. & Gray) Greene var. *elachantha* Johnst. *Wrightia* 2:20. 1959. Type: North end of Quitman Mountains, 8 miles west of Sierra Blanca, Hudspeth County, Texas, R. McVaugh 8040.

Erect or widely spreading herb 5-15 cm high, stems normally numerous, loosely ascending, branched, hirsute to hispid; leaves oblanceolate, 2-3 (6) cm long, 3-4 (6) mm wide, rounded or obtuse, thickish, hirsute, pustulate, the upper scarcely reduced; spikes solitary or rarely geminate, naked or few bracted below, 5-8 (15) cm long, frequently produced from the lowest axils; corolla inconspicuous, 1-1.5 mm wide; fruiting calyces 6-7 (10) mm long, oblong-ovoid, somewhat asymmetrical, becoming distant below; mature calyx lobes linear-lanceolate, connivent above, midrib strongly thickened and indurate, hispid, the margins short hispid; pedicels short, 0.5-1.2 mm long; nutlets 4 (1 or 2 rarely aborted), distinctly heteromorphous; odd nutlet next to the axial calyx lobe, persistent, 2-2.5 (3) mm long, brownish, ovoid, acute, finely granulate and spinular-muricate; consimilar nutlets

readily deciduous, 1.2-1.5 (2) mm long, oblong-ovoid, thickish, coarsely tuberculate, very obscurely if at all granulate, groove usually dilated and commonly excavated to form an areola occupying much of the ventral face of the nutlet; gynobase narrowly oblong, usually about 2/3 height of consimilar nutlets; style equalling or a trifle exceeding the consimilar nutlets, surpassed by odd nutlet. Sandy to gravelly places. Southern Utah and Colorado, southward to Arizona, Texas and northern Mexico. March-July. Fig. 15.

Carbon Co., east of Wellington, W.P. Cottam 2067 (BRY); Emery Co., 20 miles north of Green River, B. Maguire s.n. (UTC); San Raphael Swell, B. Maguire 18297 (UTC); Robbers Roost, W.A. Shands s.n. (UT); Buckhorn Wash, 22 miles southeast of Lawrence, Pyrah, Pitts & Barnett 15 (BRY); 5 miles southwest of Temple Mountain, L.C. Higgins 1327 (BRY); 13 miles east of Buckhorn Wash, Welsh & Atwood 9852 (BRY); Garfield Co., Upper Cottonwood Wash near Cannonville, Reveal, Gentry & Davide 757 (BRY, UTC); 8 miles southeast of Escalante, Holmgren, Reveal & LaFrance 2038 (BRY, UTC); 25 miles south of Hanksville, Welsh, Atwood & Higgins 8961 (BRY, UTC); east side of Mount Ellen, W.P. Cottam 5288 (UT); Sandy Ranch, B.F. Harrison 11476 (BRY); Willow Tank, 45 miles south of Escalante, Beck & Tanner s.n. (BRY); Grand Co., 1/2 mile from Dead Horse Point, A. Carter 1564 (UTC); northwest of Moab, A.H. Holmgren 3309 (UTC); entrance to Arches Natl. Monument, R. Vickery 735 (UT); 7 miles east of Crescent Junction, Floy Canyon, W.A. Shands (UT); Arches Natl. Monument, Pitts, Pyrah & Barnett 64 (BRY); Arches Natl. Monument, B.F. Harrison 11127 (BRY);

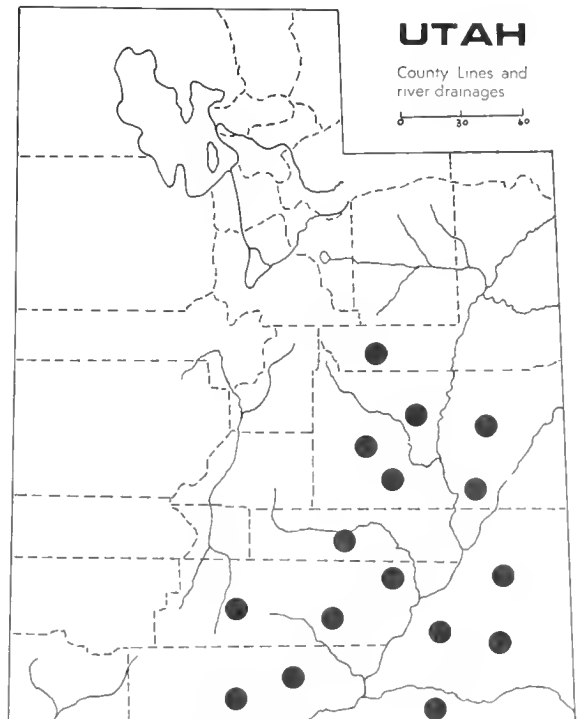


Fig. 15. *Cryptantha crassisepala*

Gunnison Butte, W.P. Cottam 2094 (BRY); 5 miles west of the mouth of Seven Mile Canyon, B.F. Harrison 12026 (BRY); 22 miles south of Crescent Junction, D. Atwood 2428 (BRY); Kane Co., 0.5 miles east of Kodachrome Flat road, J.L. Redd 802 (UTC); 57 miles east of Kanab, A. Cronquist 10157 (UTC); Glen Canyon road across Paria River, J.R. Murdock 324 (BRY); Escalante Desert near Willow Tank, B.F. Harrison 9025 (BRY); 50 Mile Spring south of Escalante, J.R. Murdock 351 (BRY); ½ mile west of Paria River bridge along hwy 89, Welsh & Atwood 9748 (BRY); just east of Kanab, D. Atwood 1797 (BRY); San Juan Co., 17 miles west of Blanding, B. Maguire & Redd 2061 (UTC); 7 miles northwest of Mexican Hat, B. Maguire 16293 (UTC); west of Bluff, S. Flowers s.n. (UT); between Moab and Monticello, W.C. Twiss s.n. (UT); 5.5 miles north of Bluff along hwy 47, C.A. Hanson 80 (BBY); 3 miles west of Bluff, B.F. Harrison 10331 (BRY); vicinity of Dead Horse Point, G.L. Richards s.n. (BRY); Island in the Sky area, G. Moore 233 (BRY); Blanding, Cottam & Hutchings 2504 (BRY); Squaw Canyon, 1 mile west of Cave Spring, Welsh, Moore & Canter 2834 (BRY); Canyonlands Natl. Park, Virginia Park, G. Moore 318 (BRY); 2 miles west of Dugout Bock, Welsh, Atwood & Higgins 8886 (BRY); 7.5 miles west of Bluff, D. Atwood 2470 (BRY); 21 miles southwest of Bluff, D. Atwood 2493 (BRY); 15 miles south of Blanding, D. Atwood 2440 (BRY); Wayne Co., Fremont Canyon west of Fruita, B. Maguire 18116 (UTC).

7. *Cryptantha decipiens* (M. E. Jones) Heller, *Muhlenbergia* 8:48. 1912. Type: Yucca, Arizona.

Krynitzkia decipiens M. E. Jones, *Contr. West. Bot.* 13:6. 1910.

Stems 1-4 dm high, slender, loosely branched, strigose and frequently short-hispid; leaves few, linear, obtuse, 1-3 cm long, 1-3 (4) mm wide, strigose and sometimes hispid, minutely pustulate; spikes slender, geminate or rarely solitary or ternate, bractless, usually becoming loosely flowered, 4-10 cm long; corolla inconspicuous in ours, 0.8-1 mm broad; fruiting calyx ovoid to ovoid-oblong, strictly ascending, asymmetrical, 2.5-7 (9) mm long, deciduous, sessile; mature calyx lobes lance-linear, decidedly connivent above with the tips frequently spreading or even recurving, midrib thickened and usually evidently hirsute, the margins strigose, abaxial lobe evidently the longest and most hirsute; nutlets 1 or rarely 2, next the abaxial calyx lobe, ovoid-lanceolate, 1.5-2.4 mm long, muriculate-granulate to tuberculate, usually brownish, back convex, sides rounded, groove open or closed but always dilated below to form a definite areola; gynobase half to a third as high as nutlet; style much surpassed by nutlet, half to two-thirds the height of nutlet. Sandy to gravelly slopes and ridges, Lower Sonoran Zone. Southwestern Utah, southern Nevada, western Arizona and southern California. March-May. Fig. 16.

Washington Co., 4 miles northwest of Welcome Springs, B. Maguire 20499 (UTC); 1 mile southwest of St. George, south slope of Black Hill, D.H. Galway 8528 (BRY).

8. *Cryptantha dumetorum* Greene, *Pittonia* 1:112. 1887. Type: California, half climbing among bushes at Tehachapi Pass, 1884, Curran.

Krynitzkia dumetorum Greene in Gray, *Proc. Amer. Acad.* 20:272. 1885.

Laxly branched closely strigose herb; stems at first erect but later commonly much elongated and sprawling or climbing among bushes; leaves lanceolate, thickish, 2-4 cm long, 2-4 (8) mm wide, sparsely appressed hirsute-villous, closely pustulate below and finely so above; spikes solitary or geminate, usually remotely flowered, 5-15 cm long, occasionally with foliaceous bracts toward base, rachis brittle and tortuously flattened; corolla inconspicuous, about 1 mm broad; fruiting calyx closely appressed to rachis, 2-3 mm long, very asymmetrical, not deciduous, base very oblique and downwardly gibbous on axial side; mature calyx lobes connivent and reaching about equal height; 3 abaxial lobes lanceolate, somewhat strigose, with the thickened midribs deflexed hirsute; 2 axial lobes partly united, hirsute only on outer margins; nutlets 4, heteromorphous, granulate and muricate, odd

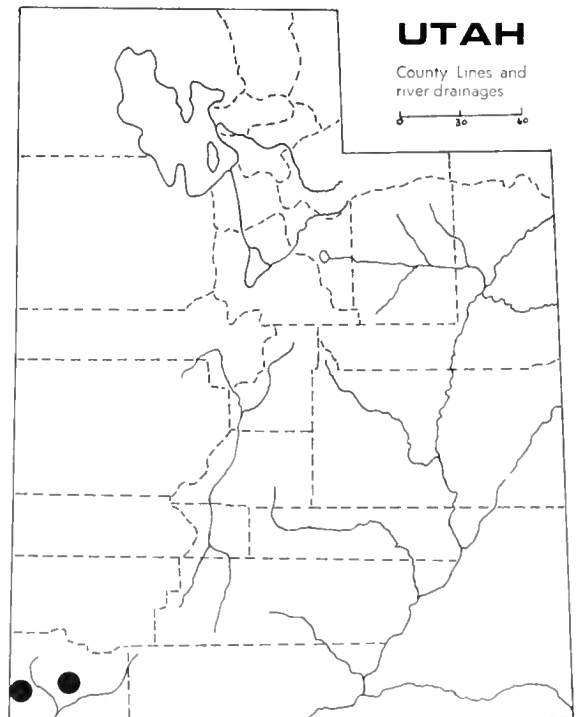


Fig. 16. *Cryptantha decipiens*

nutlet persistent, axil, broadly lanceolate, 2-3 mm long, base much developed and distorting the calyx, groove open and broad, consimilar nutlets 1.5-2 mm long, deciduous, lanceolate, groove closed or very narrow; gynobase narrow, style shortly surpassed by nutlets or reaching to their tips. Sandy to gravelly deserts. Southwestern Utah to southern California. March-May. Fig. 17.

Washington Co., Black sandy soil just west of Ivins Reservoir, L.C. Higgins 4130 (BRY, WTSU).

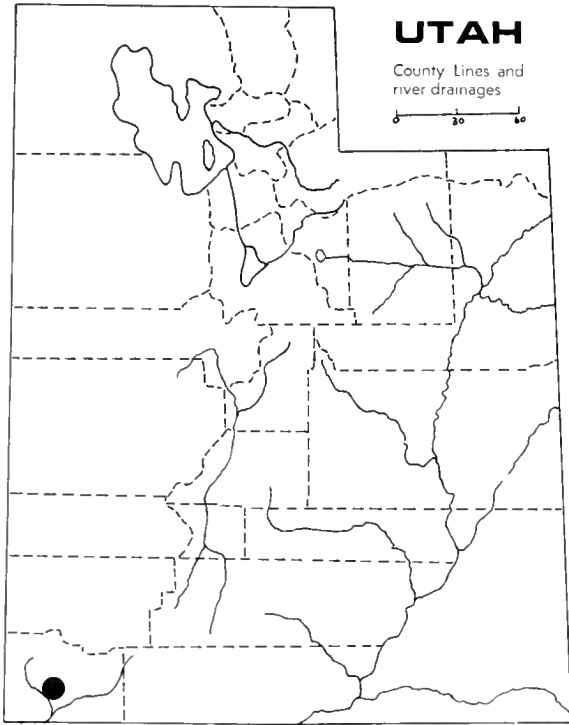


Fig. 17. *Cryptantha dumetorum*

9. *Cryptantha fendleri* (Gray) Greene, Pittonia 1:120. 1887. Type: Probably New Mexico, Fendler s.n. 1847.

Krytitzkia fendleri Gray, Proc. Amer. Acad. 20:268. 1885.

Eritrichium hispidum var. *leiocarpum* Kuntze, Rev. Gen. Pl. 2:437. 1891.

Cryptantha ramulosissima A. Nels. Erythea 7:68. 1899.

Cryptantha wyomingensis Gandoger, Bull. Soc. Bot. France 65:62. 1918.

Stems erect, usually evident throughout and bearing lateral branches mostly above the middle, sometimes rather bushy-branched from near the base, 1-5 dm tall, more or less densely hispid and frequently appressedly so; leaves narrowly oblanceolate to linear, 2-5 cm long, 2-4 mm

broad, appressed-hirsute, often pustulate on the lower surface; spikes solitary or geminate, 2-12 cm long, loosely flowered, bractless or rarely bracted below; corolla inconspicuous, about 1 mm broad; fruiting calyces ovate-oblong, 4-5 (7) mm long, ascending, slightly asymmetrical, obscurely biserial; pedicels about 0.5 mm long; mature calyx lobes linear to lance-linear, usually loosely connivent with the tips somewhat spreading, midrib hirsute, thickened, margins strigose; nutlets 4, homomorphous, or sometimes reduced to 1-3, smooth, somewhat shiny, lanceolate, acuminate, 1.5-2 mm long, convex on dorsal face, sides rounded or somewhat obtuse; groove closed above, but at base opening into a definite deltoid areola; gynobase subulate, twice the length of the style, at least two-thirds height of nutlets; style equalling or barely surpassing the nutlets. Sagebrush plains or Pinyon-Juniper association. Southern Alberta and Saskatchewan to eastern Nebraska, northern New Mexico and Arizona to eastern Oregon and Washington. June-August. Fig. 18.

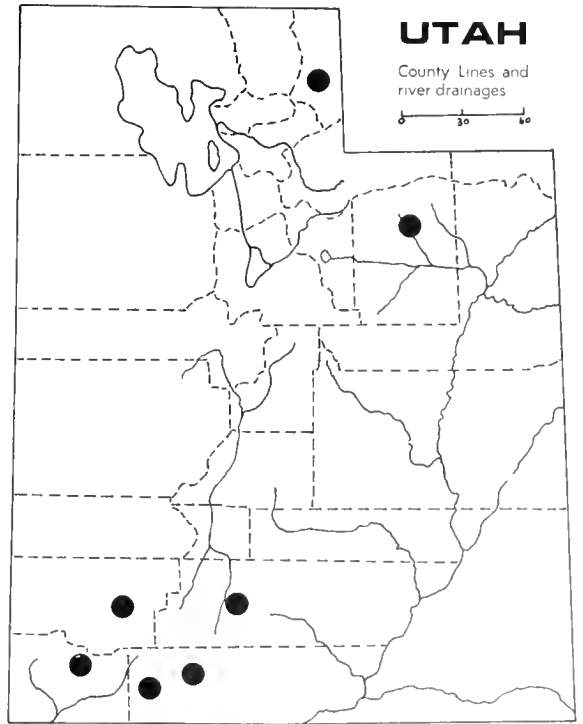


Fig. 18. *Cryptantha fendleri*

Duchesne Co., 5 miles south of Moon Lake, Maguire & Piranian 12524 (UTC); Garfield Co., Juniper-Pinyon belt, Holmgren & Nielsen 7747 (UTC); Iron Co., 5 miles west of Cedar City, B. Maguire 12979 (UTC); Kane Co., 10 miles north of Kanab, B. Maguire 18771 (UTC); 6 miles north of Kanab, Holmgren & Nielsen 7188 (UTC); 3 miles south of Mount Carmel junction, B. Maguire 18894 (UTC); 3 miles south

of Mount Carmel junction, D. Atwood 1382 (BRY); 1 mile west of Mount Carmel junction, L.C. Higgins 3375 (BRY); Orderville, Cottam & Hutchings 2725 (BRY); Rich Co., south end of Bear Lake, B. Maguire 227 (UTC); Washington Co., vicinity of Pine Valley, Maguire & Richards 12978 (UTC).

10. *Cryptantha flaccida* (Dougl.) Greene, Pittonia 1:116. 1887. Type: Probably in eastern Oregon or Washington, collected by Douglas. *Myosotis flaccida* Dougl. in Lehm. Pügel. 2:22. 1830.

Eritrichium oxycaryum Gray, Proc. Amer. Acad. n. 58. 1874.

Krynitzkia oxycarya Gray, Proc. Amer. Acad. 20:269. 1885.

Cryptantha multicaule Howell, Fl. N. W. Amer. 1:487. 1901.

Cryptantha Howellii Nels. Bot. Gaz. 34:30. 1902.

Subsimple or ascendingly branched pallid strigose herb 1.5-4.5 dm high; stems sparsely closely strigose with short pallid encrusted hairs; leaves oblanceo-linear to nearly linear or filiform, 2-6 cm long, 1-2 mm wide, closely strigose, strict or ascending firm, basal portion of lower leaves somewhat persistent; spikes quinate to solitary, naked, usually stiffish, 4-8 (16) cm long; corolla inconspicuous or medium sized, 1-4 mm broad; fruiting calyces oblong-ovate, 2-4 mm long, evidently asymmetrical, usually strict and closely hugging the stem, commonly firm and stiff, sessile or subsessile, base broadly conic; mature calyx lobes lance-linear, connivent above with the tips commonly spreading, margins ciliate or strigose, midrib thickened and armed with pale spreading coarse encrusted arcuate or uncinate bristles, abaxial lobe longest and most hirsute; nutlet 1, lance-ovate, rostrate-acuminate, subterete or only slightly compressed, smooth or very finely granulate; groove closed; style $\frac{1}{2}$ to $\frac{1}{2}$ as high as nutlet. Washington and Idaho to southern California and east to Utah (?). April-June. Fig. 19.

Washington Co., Black Lava Hill west of St. George, C.W. Cottam s.n. (BRY, DIX). This collection fits the description of *C. flaccida* but may be only an immature *C. decipiens*.

11. *Cryptantha gracilis* Osterh. Bull. Torrey Club 30:236. 1903. Type: Glenwood Springs, Colorado, Osterhout s.n.

Cryptantha hillmannii Nels. & Kenn. Proc. Biol. Soc. Wash. 19:157. 1906.

Cryptantha gracilis var. *hillmannii* Munz & Johnston, Bull. Torrey Club 49:39. 1922.

Stems slender, 1-2 dm high, erectly branched, usually solitary, densely spreading short-hirsute; leaves linear or narrowly oblanceolate, the lower 1.5-3 cm long, 1-3 mm broad, the upper usually much reduced, obtuse or rounded, ascendingly short-hirsute, minutely pustulate; spikes solitary or geminate, usually dense, 1-2 dm long, naked; corolla minute, the limb 0.6-1 mm broad; fruiting calyx ovate, divaricate, 2-2.8 mm long, early deciduous, base evidently conical, sessile; mature calyx lobes lanceolate, densely appressed tawny hispid-villous, tips erect, midrib slightly thickened and inconspicuously short-hispid; nutlets 1 or rarely 2-3 and unequally developed, lanceolate, 1.5-2 mm long, 0.8-1 mm

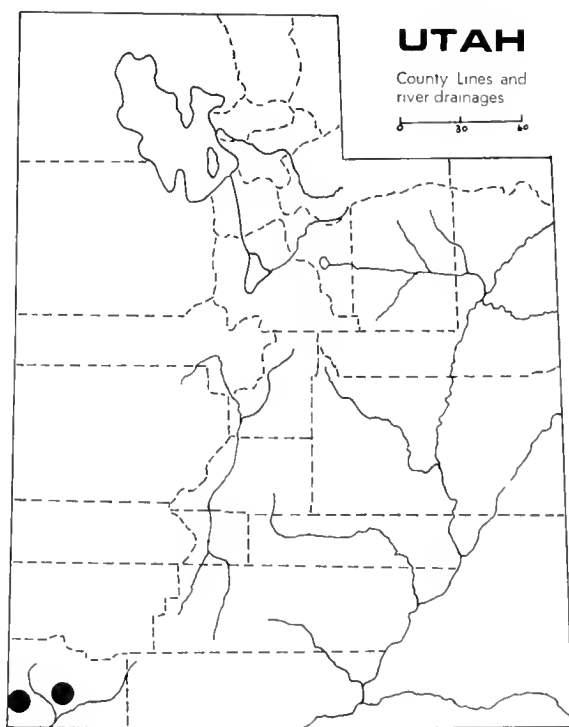


Fig. 19. *Cryptantha flaccida*

broad, smooth and shiny, acute, back nearly flat, sides rounded at least near the apex, groove mostly opened to above the middle and scarcely forked below; style reaching to $\frac{2}{3}$ - $\frac{3}{4}$ height of nutlet. Dry usually brushy slopes and ridges. Southern Idaho and Colorado to northern Arizona and southern California. April-July. Fig. 20.

Beaver Co., Wah Wah Mountains, Pine Canyon Pass, B. Maguire 20960 (UTC); Daggett Co., Green River at Hideout Forest Camp, S. Flowers s.n. (UT); Juab Co., just north of the Sanpete-Juab County line, T.L. Jensen 503 (UTC); Kane Co., 25 airline miles southeast of Escalante, Holmgren, Reveál & LaFrance 2065 (BRY, UTC); Kanab Fairgrounds, McClain s.n. (UTC); Clay-loam ridge, B.F. Harrison 9070A (BRY);

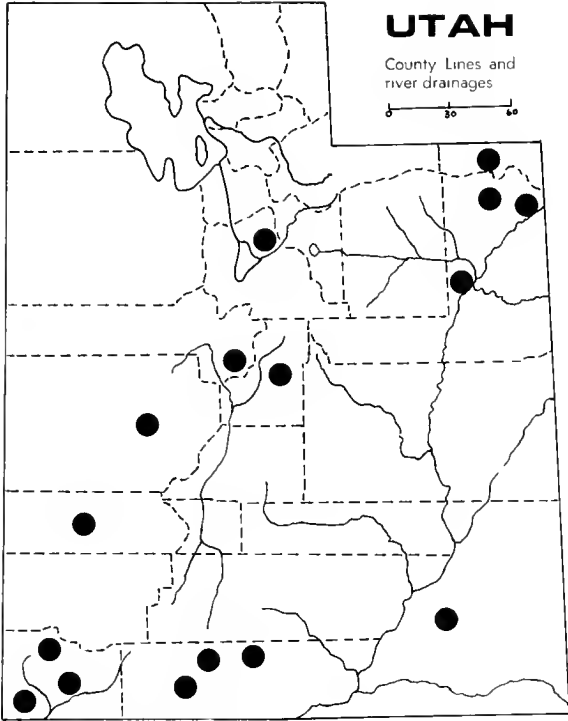


Fig. 20. *Cryptantha gracilis*

northeast slope of Kaiparawits south of Willow Tank, B.F. Harrison 9070 (BRY); Johnson Canyon, northeast of Kanab, D. Atwood 1789D (BRY); Millard Co., 43 miles north of Beaver, Maguire & Holmgren 25076 (UTC); Black Rock Volcano west of Kanosh, C. McMillan 1453 (UT); 10 miles west of Fillmore, W.P. Cottam 9568 (UT); San Juan Co., Fry Canyon Mesa, L. Wilson 23 (UTC); Canyonlands Natl. Park, Squaw Flat Campground, C. Moore 279 (BRY); Sanpete Co., Ephraim Canyon, B. Crane s.n. (UTC); Utah Co., below Timp Cave, s.n. (UT); Uintah Co., Dinosaur Natl. Monument, J. Brotherson 804 (BBY); Hill Creek, 12 miles south of Ouray, J. Brotherson 1063 (BRY); 3.6 miles north of Brush Creek along the Manila hwy, L.C. Higgins 1872 (BRY); 35 miles south of Ouray along the Hill Creek road, L.C. Higgins 1879 (BRY); Washington Co., 10 miles east of Hurricane, W.P. Cottam 8469 (UT); north of Enterprise, D. Hall EN35 (UTC); Black Hill west of St. George, J.W. Harrison s.n. (BRY); north of St. George, D.H. Galway s.n. (BRY); Terry's Ranch on the Beaverdam Wash, E. Matthews 86 (BRY).

12. *Cryptantha inaequata* Johnston, Univ. Calif. Publ. Bot. 7:444. 1922. Type: Among rocks, Pleasant Canyon, Panamint Mountains, Hall & Chandler 6925.

Johnstonella inaequata Brand, Rep. Spec. Nov. 21:250. 1925.

Stems erect or ascending, 3-4 dm high, branched throughout, or sometimes the basal branches elongated and simple or nearly so, hispid and strigose or hirsute toward the base; leaves linear to narrowly-oblongate, 2-4 cm

long, acute, often becoming more or less convolute, more or less hispid, pustulate, especially beneath; spikes geminate or solitary, 4-12 cm long, at times sparsely bracted below; corolla inconspicuous, the tube shorter than the calyx, limb 1-2.5 mm broad; fruiting calyx ovoid-oblong, 2.5-3 mm long, ascending; pedicels less than 0.5 mm long; mature calyx-lobes lanceolate, midrib thickened and hirsute, villous-ciliate on the margins; nutlets 4, heteromorphous, triangular-ovate, dark with small pale tuberculations, margins acute, groove closed above but below gradually enlarging into a shallow triangular areola, odd nutlet about 1.7 mm long, somewhat persistent, slightly lighter than the others, next the abaxial calyx-lobe; consimilar nutlets about 1.3 mm long; gyno-base equalling consimilar nutlets but surpassed by odd nutlet; style much surpassing the nutlets. Among rocks and shrubs. Southwestern Utah to northwestern Arizona and southeastern California. March-May. Fig. 21.

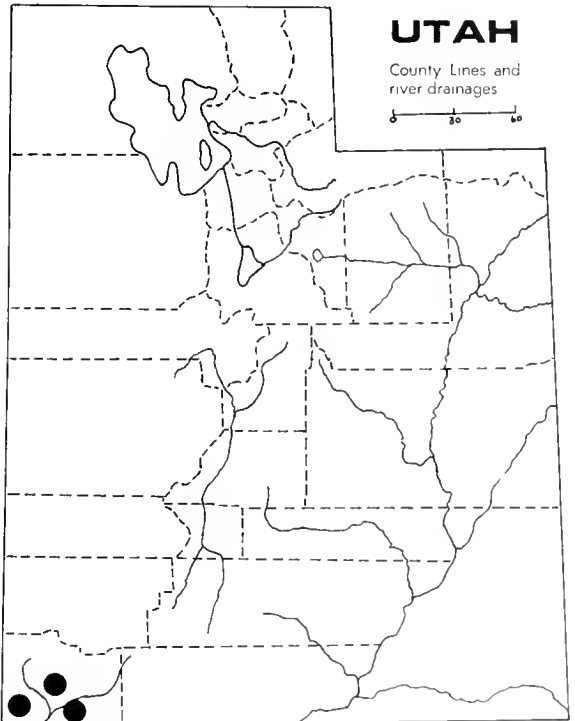


Fig. 21. *Cryptantha inaequata*

Washington Co., Black Lava Hill west of St. George, C.W. Cottam s.n. (DIX); Black Hill, St. George, Field Biology Class s.n. (UT); clay hills northwest of new golf course southwest of St. George, N.D. Atwood 1707 (BRY).

13. *Cryptantha kelseyana* Greene, Pittonia 2:232. 1892. Type: Elliston, Montana, August 1889, Greene s.n.

Spreading or ascending hirsute herb 5-25 cm high; stems 1-several, hirsute and also hispid-strigose; leaves linear or narrowly oblanceolate, 1.5-3 (4) cm long, 2-4 mm wide, rounded or obtuse, thickish, hirsute, pustulate, the upper ones scarcely reduced; spikes usually solitary, 4-9 cm long, naked or with a few bracts near the base; corolla minute, 1-2 mm broad; fruiting calyces 4-6 mm long, ovate-oblong, spreading, loose or dense, somewhat asymmetrical; pedicels short but definite, about 0.8 mm long; mature calyx lobes linear, weakly connivent above, midrib thickened, hirsute to hispid, margins inconspicuously villous-strigose; nutlets 4, heteromorphous; odd nutlet next to the axial calyx-lobe, broadly lance-ovoid, 2-2.6 mm long, smoothish or granulate or muriculate-granulate or rarely somewhat tuberculate, standing off slightly from the gynobase, consimilar nutlets lance or oblong-ovoid, 1.8-2.3 mm long, coarsely tuberculate and usually granulate darker than the odd nutlet, sides rounded, groove narrow or closed, near base abruptly dilated to form a small triangular areola; gynobase subulate, a little longer than the style, $\frac{1}{2}$ to $\frac{2}{3}$ height of consimilar nutlets; style surpassed by odd nutlet and just surpassing or even exceeded by consimilar ones. Sandy plains to rocky hillsides. Saskatchewan and Montana southward through Wyoming to northern Colorado and Utah. May-July. Fig. 22.

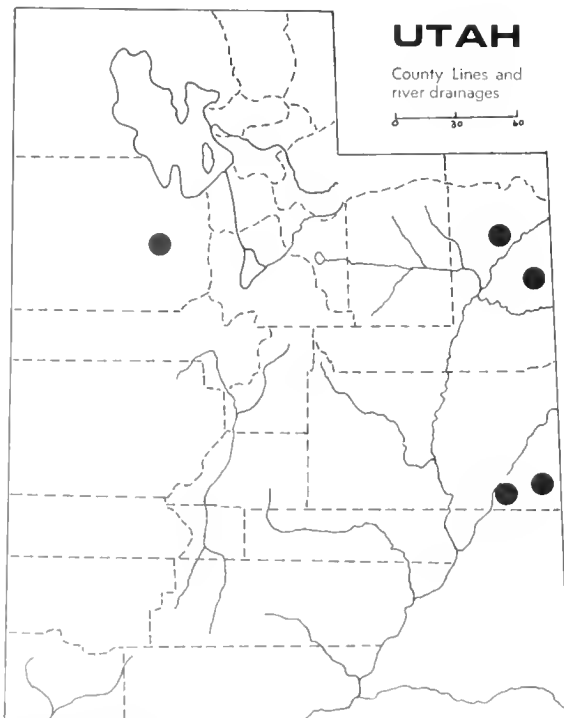


Fig. 22 *Cryptantha kelsoyana*

Grand Co., 13 miles due southwest of Moab, Harrison, Marshal & Nielson 10285 (BRY); Porcupine Ridge, La Sal Mountains, J. Pederson 114 (BRY); Tooele Co., 10 miles southeast of Cline, W.H. Hirst 36 (UTC); Uintah Co., 13 miles west of Vernal, R.S. Ferris 11384 (UTC); 8 miles west of Bitter Creek on Ouray-Bonanza Road, N.D. Atwood 1556A (BRY); 20 miles south of Bonanza, L.C. Higgins 1079 (BRY).

14. *Cryptantha micrantha* (Torr.) Johnston. Contr. Gray Herb. 68:56. 1923. Type: "Sand hills, Fontera, Texas, and in other places along the Rio Grande."

Eritrichium micranthum Torr. Bot. Mex. Bound. 141. 1859.

Krynitzkia micrantha Gray, Proc. Amer. Acad. 20:275. 1885.

Eremocarya micrantha Greene, Pittonia 1:59. 1887.

Eremocarya muricata Rydb. Bull. Torrey Club 36:677. 1909.

Slender, dichotomously branched herb 5-15 cm high, drying brownish; root and lower parts of the stem stained with a purple dye; leaves oblong-oblanceolate, 3-7 mm long, 0.8-1.4 mm wide, whitish-strigose or short hirsute, rounded at apex, uppermost scarcely reduced and extending through the inflorescence; spikes numerous, solitary or geminate, densely flowered and strongly unilateral, leafy-bracted throughout, 1-4 cm long; corolla inconspicuous to medium-sized, limb 0.5-2.5 mm broad; fruiting calyx ovoid-oblong, 1.8-2.5 mm long, slightly asymmetrical, decidedly biseriolate, base broadly conical; pedicels 0.5-0.8 mm long; mature calyx lobes oblong-lanceolate, broad, erect, hirsute, midrib not evidently thickened; nutlets 4, 1-1.3 mm long, smooth or tuberculate, 1 nutlet sometimes a little longer and more persistent than the others, groove extending full length of nutlet, narrow, scarcely broadened at base; gynobase subulate, nearly as long as the calyx, much surpassing the nutlets and bearing at its summit the sessile stigma. Dry sandy soils in the Lower Sonoran Zone. Southeastern Oregon to Utah, southward to Baja California, Arizona, New Mexico, and Texas. March-June. Fig. 23.

Garfield Co., Egnog Spring, Bullfrog Creek, west of Henry Mountains, S.L. Welsh 3983 (BRY); Kane Co., 23 miles south of Alton, A. Cronquist 10192 (BRY, UTC); sand dunes north of Kanab, W.P. Cottam 4304 (BRY); $\frac{1}{2}$ mile west of Paria River bridge along hwy 89, Welsh & Atwood 9746 (BRY); Washington Co., 12 miles northeast of St. George, A. Cronquist 10103 (BRY, UTC); Beaverdam Mountains, D. Nish 64 (UTC); 8 miles southwest of St. George, Holmgren & Thieret 8229 (UTC); $\frac{1}{2}$ mile north of Toquerville, B. Maguire 20475 (UTC); 32 miles south of Cedar City, B. Maguire 13562 (UTC); St. George, M.E. Jones s.n.

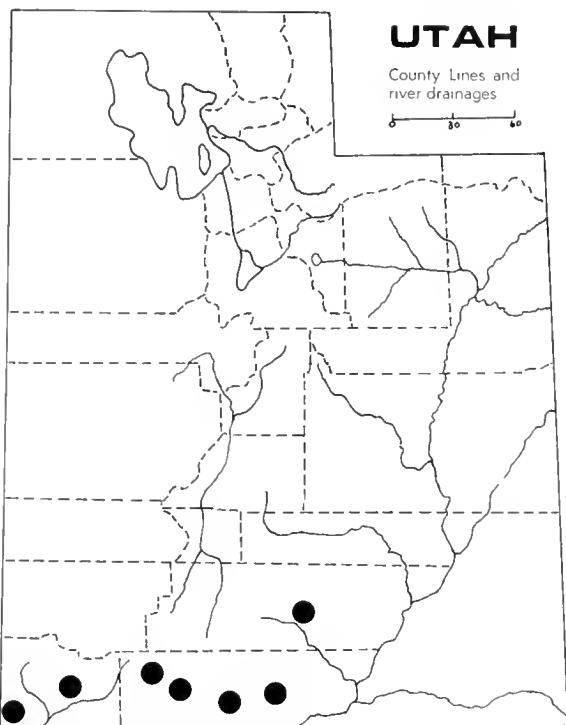


Fig. 23. *Cryptantha micrantha*

(UTC); Diamond Valley, W.P. Cottam 4034B (BRY); St. George, D.H. Galway 6284 (BRY); 5.7 miles south of Gunlock, F.W. Gould 1594 (BRY); Terry's Ranch on the Beaverdam Wash, L.C. Higgins 406 (BRY); Beaverdam Mountains near the Utah-Arizona border, L.C. Higgins 344 (BRY); Dixie State Park, 5 miles northwest of Ivins, L.C. Higgins 857 (BRY); 4 miles east of Harrisburg, south of the Virgin River, Welsh & Moore 684I (BRY); 1 mile southeast of Ivins Reservoir along hwy 91, L.C. Higgins 4103 (BRY); about 4 miles west of Hurricane, L.C. Higgins 4214 (BRY).

15. *Cryptantha nevadensis* Nels. & Kenn. Proc. Biol. Soc. Wash. 19:157. 1906. Type: Reno, Washoe Co., Nevada.

Krynitzkia barbiger var. *inops* Brandg. Zoe 5:228. 1906.

Cryptantha barbiger var. *inops* Macbr. Proc. Amer. Acad. 51:548. 1916.

Cryptantha arenicola Heller, Muhlenbergia 2:242. 1906.

Cryptantha leptophylla Rydb. Bull. Torrey Club 36:678. 1909.

Stems slender, 1-5 dm high, 1 to several, erect or usually flexuose, appressed short-strigose, mostly laxly branched; leaves linear-oblongate to linear, acute or obtuse, 1-4 cm long, 1-5 (7) mm broad, not numerous, appressed short-hispid, more or less pustulate; spikes geminate or ternate, terminal, also scattered along the stem on short, slender, axillary branches, occasionally

bracted toward the base, congested and somewhat glomerate or elongate and becoming 15 cm long; corolla inconspicuous, limb 1-2 mm broad; fruiting calyx oblong-ovoid to lanceolate, 5-12 mm long, ascending, slightly asymmetrical; pedicels about 0.5 mm long; mature calyx-lobes lanceolate or linear, connivent above with the slender tips usually recurving, margins more or less villous and hispid on the somewhat thickened midrib; nutlets 4, homomorphous, verrucose or muriculate toward the tip, lanceolate to lance-ovoid, 2-2.9 mm long, back convex, margins somewhat angled, groove open or closed, dilated below into a small areola; gynobase narrow; style reaching to or almost to the tips of the nutlets. Sandy to gravelly slopes and washes in the Lower Sonoran Zone. Deserts of Utah and Nevada to Arizona and Baja California. March-June. Fig. 24.

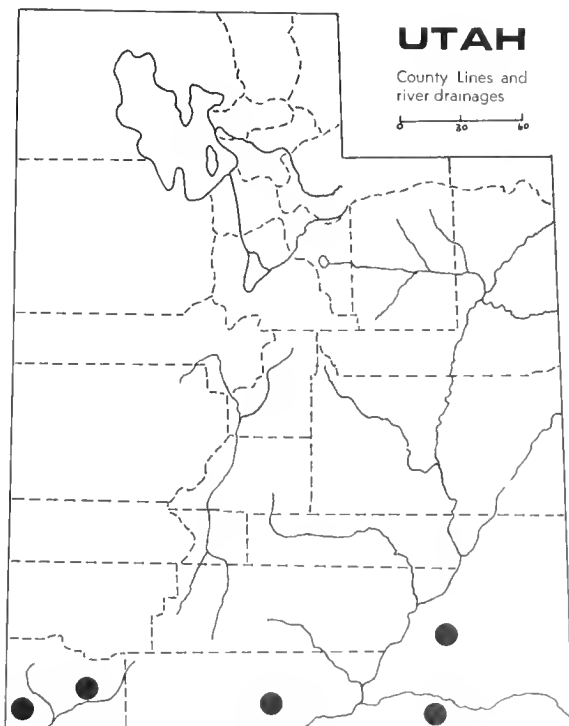


Fig. 24. *Cryptantha nevadensis*

San Juan Co., 10 miles east of Hite, A. Cronquist 9036 (UTC); vicinity of Mexican Hat, B. Maguire 16277 (UTC); Washington Co., west slope of the Beaverdam Mountains, D. Nish 32 (UTC); 2 miles west of Rockville, B. Maguire 4979 (UTC); 1 mile east of Hurricane, Maguire & Blood 1529 (UTC); north of St. George, D.H. Galway s.n. (DIX); Beaverdam Mountains near the Utah-Arizona border along hwy 91, L.C. Higgins 333 (BRY); Black Hill west of St. George, D.H. Galway s.n. (BRY); Terry's Ranch on the Beaverdam Wash, L.C. Higgins 303 (BRY); Dixie State Park, 5 miles northwest of Ivins, L.C. Higgins 852A (BRY).

16. *Cryptantha pattersonii* (Gray) Greene, Pittonia 1:120. 1887. Type: Without locality, 1875 Patterson, but probably came from the Rocky Mountains near Golden, Colorado.

Krynitzkia pattersonii Gray, Proc. Amer. Acad. 20:268. 1885.

Stems usually several, 1-1.5 dm high, loosely branched, hirsute and somewhat strigose; leaves oblanceolate, 1-3 cm long, 2-4 mm broad, rather firm, obtuse, hirsute with somewhat pustulate bases, upper ones little reduced; spikes solitary or geminate, naked, 2-5 (7) cm long; corolla inconspicuous, 1-1.5 mm broad; fruiting calyx oblong-ovoid, 4-5 mm long, spreading, slightly asymmetrical, evidently biseriate, lower-most becoming 2-6 mm distant; pedicels about 0.5 mm long; mature calyx-lobes linear-lanceolate, tips more or less connivent, the midrib hirsute and thickened, margins appressed hispid; nutlets 4, heteromorphous, odd nutlet next to the axial calyx-lobe, slightly the largest, about 1.9 mm long, ovate, acute, smooth or obscurely rugulose or sparsely tuberculate, somewhat persistent, standing off slightly from the gynobase; consimilar nutlets oblong-ovoid, about 1.6 mm long, deciduous, closely appressed to gynobase, smooth, back convex, sides rounded or obtuse, groove opened or closed and abruptly broadened below into a small triangular areola; gynobase narrow, reaching to about $\frac{2}{3}$ height of consimilar nutlets; style exceeded by odd nutlet, equalling or a little shorter than consimilar nutlets. Dry, usually somewhat sandy or gravelly soil, mostly in the mountains. Wyoming, northern Colorado, and northeastern Utah. May-July. Fig. 25.

Duchesne Co., 10 miles north of Altonah, J. Brotherson 651 (BRV).

C. pattersonii is rarely collected. It is also very closely related to *C. kelseyana* and *C. ambigua* and intergrades with both. In habit it is similar to *C. ambigua* and immature specimens are nearly impossible to distinguish.

17. *Cryptantha pterocarya* (Torr.) Greene, Pittonia 1:120. 1887.

Stems erect, branched throughout with ascending branches, 1-5 dm high, short hirsute with either appressed or ascending slender strigose hairs; leaves linear or the reduced uppermost ones lanceolate or oblong, strigose, 1-2.5 (4) cm long, 1-3 (5) mm broad, obtuse, conspicuously pustulate below but usually finely so above; spikes geminate or rarely ternate or solitary, naked or bracted below, 2-6 (12) cm long, becoming loosely flowered, corolla incon-

spicuous, 0.5-1 (2) mm broad; fruiting calyces distinctly accrescent, (2) 3-5 mm long, symmetrical, ascending on short pedicels 0.5-1 mm long; mature calyx-lobes ovate to lanceolate, somewhat connivent, thin, margins more or less tawny, appressed hispid, midrib slightly thickened and sparsely hispid; nutlets 4, homomorphous and all winged, or heteromorphous with axial nutlet wingless; body of nutlet oblong-lanceolate or lanceolate, 2-2.5 (3) mm long, muricate or verrucose, wing-margin of nutlet broad or narrow, entire or crenate or lobed, extending completely around the nutlet or only down the sides, groove open or closed (even in the same plant) and dilated below into an open excavated areola; gynobase slender, about $\frac{2}{3}$ height of nutlets; style subulate, slightly surpassing or somewhat surpassed by the wing-margin of the nutlets but always exceeding the body proper.

1. Nutlets heteromorphous, axial one wingless 17A. var. *pterocarya*
1. Nutlets homomorphous, all winged 17B. var. *cycloptera*

17A. *Cryptantha pterocarya* (Torr.) Greene var. *pterocarya*. Type: Walla Walla, Washington, as designated by I. M. Johnston, Contr. Gray Herb. 74:53. 1925.
Eritrichium pterocaryum Torr. Bot. Mex. Bound. 142. 1859.

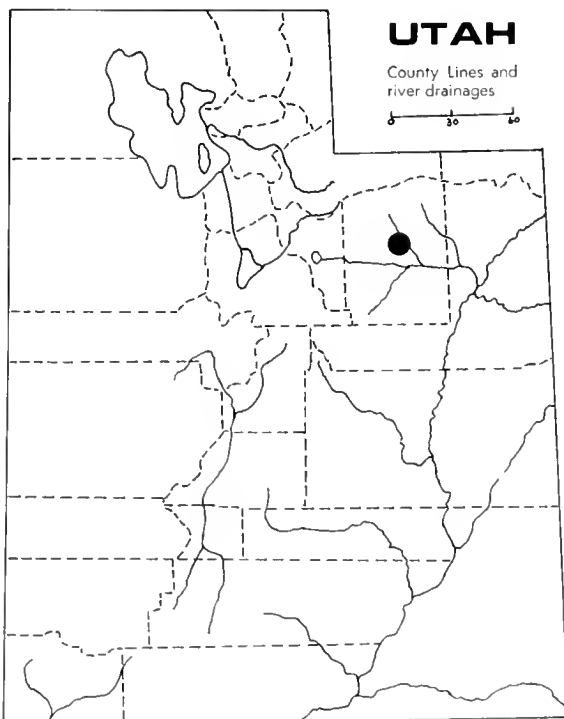


Fig. 25. *Cryptantha pattersonii*

Eritrichium pterocaryum var. *pectinatum*

Gray, Proc. Amer. Acad. 10:61. 1874.

Krynitzkia pterocaryum var. *pectinata*

Gray, op. cit. 20:276. 1885.

Krynitzkia pterocarya Gray, Proc. Amer. Acad. 20:276. 1885.

Nutlets heteromorphous, axial one wingless. Sandy or gravelly places, Upper and Lower Sonoran Zones. Southern Washington, southern Idaho, Utah, Arizona, and northern Sonora. April-June. Fig. 26.

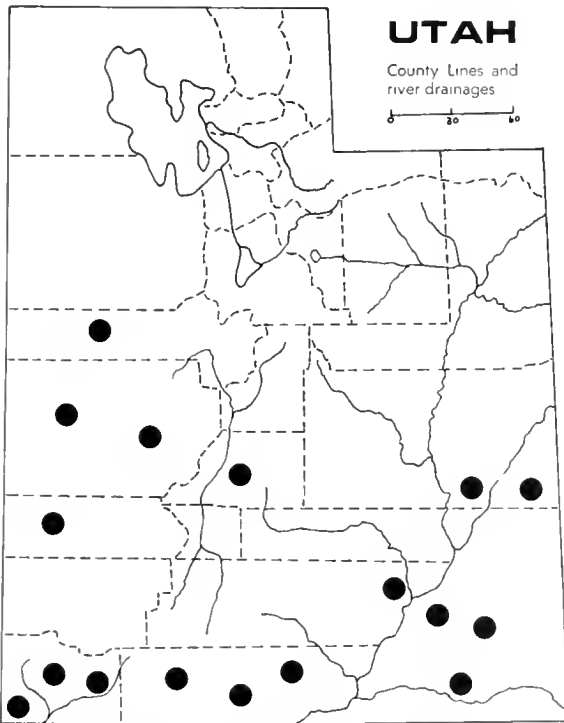


Fig. 26. *Cryptantha pterocarya* var. *pterocarya*

Beaver Co., Warm Point Ridge, Stahmann & Hutchings 67 (UT); Garfield Co., 4 miles northeast of Hite, A. Cronquist 9053 (UTC); Grand Co., west of Moab, E.L. Miner 1 (UT); confluence of Delores & Colorado Rivers, Vickery 287 (UT); Juab Co., 7 miles east of Trout Creek, B. Maguire 2777 (UTC); 39 miles west of junction of Utah hwy 50-6 and Jericho road along the Callao Road, K.D. Kaneko 50 (BRY); Kane Co., 25 airline miles southeast of Escalante, Holmgren Reveal & LaFrance 2064 (UTC); 57 miles east of Kanab, A. Cronquist 10155 (BRY, UTC); 23 miles south of Alton, A. Cronquist 10193 (BRY, UTC); Johnson Canyon, northeast of Kanab, N.D. Atwood 1789A (BRY); Millard Co., Black Rock Volcano west of Kanosh, C. McMillan 1484 (UT); 43 miles north of Beaver, Maguire & Holmgren 25075 (UTC); Desert Range Exper. Station, Maguire & Holmgren 25109 (UTC); White Sage Valley, B.F. Harrison 6377 (BRY); east side of Pine Valley, B.F. Harrison 6393 (BRY); Warm Point Ridge, Stahmann & Hutchings 50 (BRY); San Juan Co., 2 miles west of Bluff, B. Maguire 13525 (UTC); Comb Wash, L. Arnow 231 (UT); 35 miles west of

Bluff, B.F. Harrison 11947 (BRY); 1 mile east of Moab bridge, Deming 1-24 (BRY); 15 miles south of Blanding, N.D. Atwood 2439 (BRY); Sevier Co., 2 miles north of Elsinore, Reveal, Gentry & Davidge 735 (BRY, UTC); Washington Co., St. George, D.H. Galway s.n. (UT); Diamond Valley, F.W. Gould 1705 (BRY, UT); St. George, M.E. Jones 2034 (UT); Zion Natl. Park, B. Maguire 13575 (UTC); 1 mile east of Hurricane, Maguire & Blood 1534 (UTC); 5 miles west of Springdale, A. Cronquist s.n. (UTC); 32 miles south of Cedar City, B. Maguire 16280 (UTC); Price Bench, R. Hardy s.n. (DIX); St. George, C.W. Cottam s.n. (BRY, DIX); Diamond Valley, D.H. Galway s.n. (BRY); Diamond Valley, W.P. Cottam 4044 (BRY); 4 miles east of Harrisburg, Welsh & Moore 6843A (BRY); 15 miles south of Enterprise, L.C. Higgins 3480 (BRY); Dixie State Park, L.C. Higgins 934 (BRY); Beaverdam Mountains, near the Utah-Arizona border along hwy 91, L.C. Higgins 334 (BRY); about 5 miles west of hwy 91 along the Jackson road, L.C. Higgins 501 (BRY); 4 miles west of Hurricane, L.C. Higgins 4218 (BRY); Diamond Valley, L.C. Higgins 4199 (BRY, WTSU).

17B. *Cryptantha pterocarya* var. *cycloptera* (Greene) Macbr. Contr. Gray Herb. 48:44. 1916. Type: Near Tucson, Arizona. 1884 Pringle.

Krynitzkia cycloptera Greene, Bull. Calif. Acad. Sci. 1:20. 1884.

Cryptantha cycloptera Greene, Pittonia 1:120. 1887.

Nutlets homomorphous, all winged, otherwise like the typical material. Sandy or gravelly deserts. Southern California east to southern Utah, Arizona, New Mexico, and southwestern Texas. April-June. Fig. 27.

Kane Co., Kaiparowits Plateau, about 25 airline miles southeast of Escalante, Holmgren, Reveal & LaFrance 2064 (BRY, UTC); red ledges, north of St. George, D.H. Galway s.n. (BRY).

18. *Cryptantha racemosa* (Wats.) Greene, Pittonia 1:115. 1887. Type: Ehrenberg, Arizona.

Krynitzkia racemosa Greene, Bull. Calif. Acad. Sci. 1:208. 1885.

Eritrichium racemosum Wats. in Gray, Proc. Amer. Acad. 17:226. 1882.

Krynitzkia ramosissima Gray, Proc. Amer. Acad. 20:277. 1885.

Cryptantha suffruticosa Piper, Proc. Biol. Soc. Wash. 32:42. 1919.

Cryptantha racemosa var. *lignosa* Johnst. Univ. Calif. Pub. Bot. 7:445. 1922.

Johnstonella racemosa Brand, Rep. Spec. Nov. 21:249. 1925.

Johnstonella racemosa var. *lignosa* Brand, Rep. Spec. Nov. 21:249. 1925.

Long-lived annual, often decidedly suffruticose near the base, 1-10 dm high; stems single

Washington Co., Black Lava Hill west of St. George, J. W. Harrison s.n. (DIX).

19. *Cryptantha recurvata* Coville, Contr. U.S. Natl. Herb. 4:165. 1893. Type: Surprise Canyon, Panamint Mountains, Coville & Funston 713.

Stems branched from the base, slender, ascending or decumbent at base, 1-3 dm high, strigose, root often dye-stained, basal leaves oblanceolate or spatulate, 1.5-2 cm long, those of the stem remote, linear or lanceolate, 5-10 mm long, rounded or obtuse, rather finely appressed-hispid and minutely pustulate; spikes bractless, slender, loose, 2-10 cm long, solitary or geminate; corolla inconspicuous, about 2 mm long, subtubular, not exerted, lobes short; fruiting calyx slender, asymmetrical, bent and recurved, 3-4 mm long, tardily deciduous, sessile; mature calyx-lobes linear, midrib somewhat thickened and hirsute, rarely merely strigose, axial lobe longest, thickest and most hirsute; ovules 2, nutlet 1, subsistent, oblong-lanceolate, curved inwardly, dull brownish, granulate-muricate, next to the axial calyx-lobe, edges obtusish, groove somewhat oblique, narrow or closed, opening into a small basal areola; gynobase slender, about $\frac{1}{2}$ the length of the matured nutlet and about as long as the abortive ones; style commonly much surpassed by nutlet. Sandy or

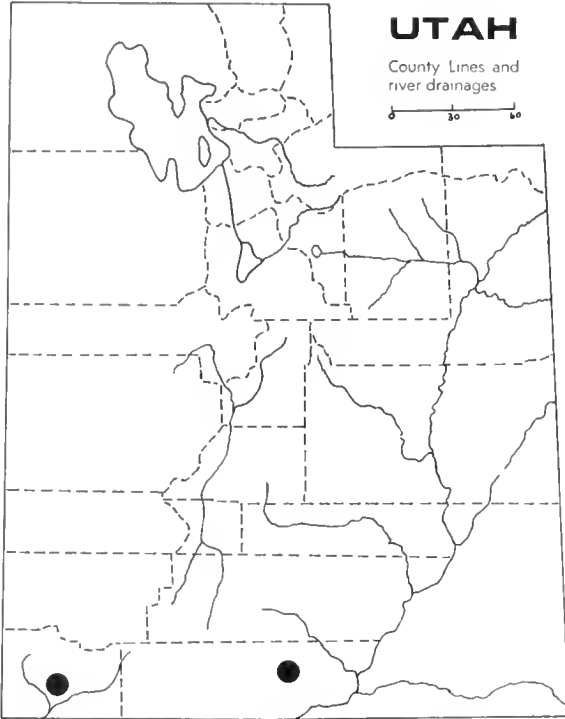


Fig. 27. *Cryptantha pterocarya* var. *cycloptera*

with numerous ascending branches or many and diffusely branched younger parts, green, strigose and commonly hirsute, epidermis at length exfoliating leaving the older woody stems glabrous and brown; leaves oblanceolate, acute, hirsute, pustulate, the early ones 3-6 cm long, 6-12 mm broad; racemes apparently forked and paniculately disposed, minutely bracteate, 3-15 cm long; corolla very inconspicuous, limb about 1 mm wide; fruiting calyces oblong-ovoid, 2-4 mm long, slightly asymmetrical, ascending, tardily deciduous; pedicels usually well developed, 1-4 mm long, slender, frequently nodding; mature calyx-lobes lance-linear, somewhat strigose, hirsute along the thickened midrib; nutlets 4, heteromorphic, triangular-ovate, the acute tips slightly outcurved, groove open or closed above but below broadening out into a shallow broadly triangular areola; odd nutlet next to the abaxial calyx-lobe, 1-2 mm long, somewhat persistent, finely muricate or tuberculate, light or dark, consimilar nutlets 0.8-1.5 mm long, acute, tending to be very narrowly wing-margined, dark with pallid tuberculations; gynobase subulate, $\frac{2}{3}$ length of odd nutlet and about equalling consimilar nutlets; style much surpassing the nutlets. Sandy flats and rocky ridges of the Lower Sonoran Zone. Southwestern Utah, southern Nevada, western Arizona, and southwest to Baja California. March-June. Fig. 28.

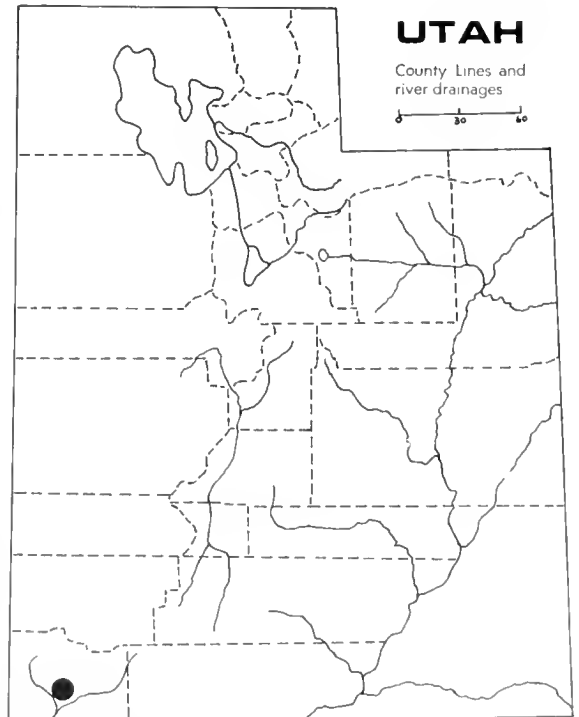


Fig. 28. *Cryptantha racemosa*

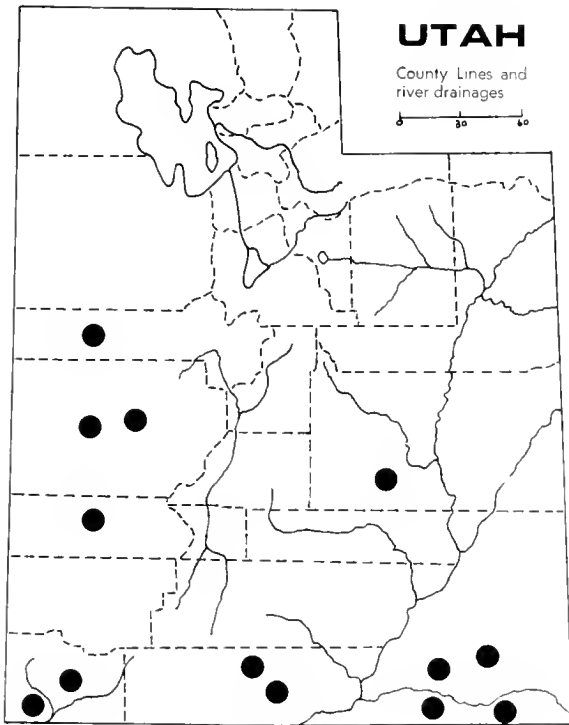


Fig. 29. *Cryptantha recurvata*

gravelly slopes and wash bottoms. Southeastern Oregon to Utah, Nevada, and southern California. April-June. Fig. 29.

Beaver Co., 26 miles north of Milford, B. Maguire 21034 (UTC); Juab Co., 13 miles east of Trout Creek, Maguire & Beecraft 2771 (UTC); north of Fumarole, W.P. Cottam 9647 (UT); Emery Co., Temple Mountain, V.P. Allman s.n. (BRY); Millard Co., 20 miles west of Hineley, B. Maguire 20760 (UTC); 60 miles west of Delta, Maguire & Beecraft 2774 (UTC); Desert Range Exper. Station, R.C. Holmgren 461 (BRY); Kane Co., 6 miles east along road to Warm Creek, from Glen Canyon City, Welsh & Atwood 9811 (BRY); N.E. slope of Kaiparawits, south of Willow Tank, B.F. Harrison 9070B (BRY); San Juan Co., 18 miles northwest of Blanding, A. Cronquist 9016 (UTC); 10 miles west of Bluff, B. Maguire 13541 (UTC); Cottonwood Canyon, Waylands Ranch, B. Maguire 16271 (UTC); 16 miles southwest of Bluff on hwy 163, N.D. Atwood 2474 (BRY); Comb Wash, 7.5 miles west of Bluff, N.D. Atwood 2469 (BRY); along road just west of Monument Valley Hospital, N.D. Atwood 2512 (BRY); 15 miles south of Blanding on road to Bluff, N.D. Atwood 2438 (BRY); Washington Co., 12 miles northeast of St. George, A. Cronquist 10116 (BRY, UTC); north of St. George, D.H. Galway s.n. (DIX); Black Hill west of St. George, D. Hall s.n. (BRY); 4 miles east of Harrisburg, Welsh & Moore 6843 (BRY); 4 miles west of Hurricane L.C. Higgins 4215 (BRY, WTSU); 1 mile southeast of Ivins Reservoir along hwy 91, L.C. Higgins 4126 (BRY, WTSU).

20. *Cryptantha scoparia* A. Nels. Bot. Gaz. 54:144. 1912. Type: Minidoka, Wyoming, Nelson & Macbride 1311.

Cryptantha muriculata var. *montana* Nels. Erythea 7:69. 1899.

Stems with several to many stiffly erect branches 1-3.5 dm high; stems closely short-strigose and frequently also sparsely hispid; leaves linear to lance-linear, 2-4 cm long, obtuse, 1-3 mm broad, strictly ascending, strigose or appressed hirsute, finely pustulate, spikes stiff, bractless, solitary or geminate, 2-10 cm long; corolla inconspicuous, about 1 mm wide, tube about equalling calyx; fruiting calyx ovate-oblong, 5-6 mm long, strictly ascending sessile, slightly asymmetrical, becoming rather obscurely biserial at maturity and 5-10 mm distant; mature calyx-lobes linear-lanceolate, rather stiff, somewhat connivent above with the tips slightly spreading, midrib thickened and hirsute, margins ascending-hispidulous, axial lobe slightly the longest; nutlets 4, homomorphous, lanceolate to broadly lanceolate, 1.8-2.2 mm long, antrorsely spinulose-muriculate, especially toward the apex, margins and base rounded, groove narrow and forked below where occasionally open to form a small triangular areola; gynobase subulate, about 3/4 height of nutlets; style reaching to tips of nutlets. Dry sagebrush plains, usually in sandy soils. Washington and eastern Oregon, also in Idaho, Wyoming, and northern Utah. May-July. Fig. 30.

Weber Co., Ogden Hot Springs, Stokes s.n. (UC).

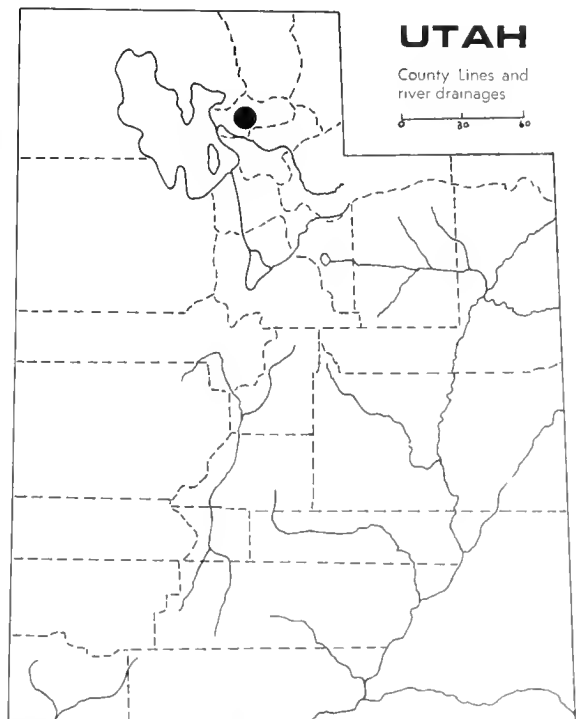


Fig. 30. *Cryptantha scoparia*

21. *Cryptantha torreyana* (Gray) Greene, Pittonia 1:118. 1887. Type: Yosemite Valley, Torrey 337.

Krynitzkia torreyana A. Gray, Proc. Amer. Acad. 20:271. 1885.

Krynitzkia torreyana var. *calycosa* Gray, loc. cit.

Cryptantha torreyana var. *calycosa* Greene, Pittonia 1:119. 1887.

Cryptantha calycosa Rydb. Mem. N. Y. Bot. Gard. 1:331. 1900.

Cryptantha affinis var. *flexuosa* Nels. Bot. Gaz. 30:195. 1900.

Cryptantha flexuosa Nels. New Man. Bot. Cent. Rocky Mts. 416. 1909.

Cryptantha torreyana var. *calistogae* Johnst. Contr. Gray Herb. 74:80. 1925.

Stems erect, 1-4 dm high, solitary or several with erect or more often spreading branches, finely strigose and sparsely hirsutulous; leaves oblanceolate to linear, strict or ascending, 2-5 (7) cm long, 3-6 (8) mm wide, obtuse or rounded, hispid, inconspicuously pustulate if at all so; spikes commonly geminate, bractless, 4-8 (15) cm long, more or less projected from the leafy mass of the plant, very elongate and loosely flowered or congested and glomerate; corolla inconspicuous, about 1 mm broad; fruiting calyx ovoid or oblong-ovoid, 2-7 mm long, ascending, asymmetrical, base rounded or broadly conic; pedicels about 0.5 mm long; mature calyx-lobes lanceolate to linear-lanceolate, connivent above with tips usually spreading, midrib slightly thickened and hispid-hirsute, margins hispid-strigose; nutlets 4, occasionally 1 or more aborted, usually broadly ovate, 1.5-2.2 (2.5) mm long, 0.8-1.3 mm broad, smooth and polished, usually mottled, rarely finely granulate, back low and convex, sides rounded or obtuse, groove broadly forked below and closed throughout; gynobase about $\frac{1}{2}$ height of nutlets, about 1 mm tall; style reaching to $\frac{2}{3}$ height of nutlets or rarely even to their tips. Open slopes or sometimes growing in partial shade, mainly transition zones. Extreme western Wyoming and northern Utah to northern California and northward to British Columbia and Alaska. May-August. Fig. 31.

Box Elder Co. Ralt River Mountains, Dunn Canyon, Maguire & Holmgren 22233 (UTC). Cache Co., Tony Grove Lake, B. Maguire 21665 (UTC); 12 miles southwest of Laketown, Harrison & Larsen 7963 (BRY); Intervale in Providence Canyon, B. Maguire 13838 (UTC); Logan Canyon, H.B. Passey 108 (UTC); Blacksmith Fork Canyon, B. Maguire 3701 (UTC); Wellsville Range, Pine Canyon B. Maguire 3110 (UTC); Davis Co., Lagoon, s.n. (UT); Salt Lake Co., north slope of Mount Olympus, Vickery 832 (UT); Red Butte A.O. Garrett 1869 (UT); Red Butte Canyon, L.

Amow 1534 (UT, BRY); Sanpete Co., vicinity of Ephraim, R. Olsen s.n. (UTC); Sevier Co., 5 miles southeast of Sigurd, B. Maguire 18097 (UTC); Tooele Co., South Willow Creek, B. Maguire 21757 (UTC); Utah Co., north fork of Provo River, S. Flowers 24 (UT); Aspen Grove, A.O. Garrett 3448 (UT); Mount Timpanogos, A.O. Garrett 5551 (UT); 2 miles below Aspen Grove, B.F. Harrison 9392 (BRY); Mount Timpanogos loop road, E. Larsen 7165 (BRY); Aspen Grove, B.F. Harrison 6776 (BRY); American Fork Canyon, I.E. Diehl D3 (BRY); hills around Castilla, I.E. Diehl D4 (BRY); Provo Canyon near Deer Creek, D.H. Galway s.n. (BRY); Aspen Grove, J.D. Walker s.n. (BRY); head of Rock Canyon, B.F. Harrison 9403 (BRY); Washington Co., Pine Valley, W.P. Cottam 8916 (UT); Brouse Area Ranger Station, R.K. Gierisch 332 (UTC); Weber Co., near Ogden, A.O. Garrett 6278 (UT).

22. *Cryptantha utahensis* (Gray) Greene, Pittonia 1:120. 1887. Type: St. George, Palmer 352.

Krynitzkia utahensis Gray, Syn. Fl. N. Amer. 2:427. 1886.

Eritrichium holopterum var. *submolle* Gray, Proc. Amer. Acad. 13:374. 1878.

Cryptantha submollis Coville, Contr. U.S. Natl. Herb. 4:166. 1893.

Plant usually with a main erect stem with a few scattered ascending or erect branches, 1-3 dm high, strigose or appressed short-hispid; leaves not numerous, strongly reduced above,

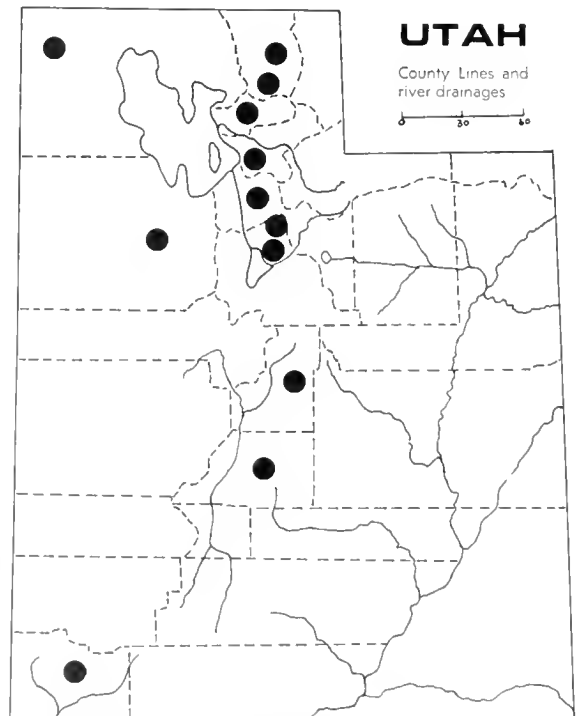


Fig. 31. *Cryptantha torreyana*

linear to oblanceolate-linear, 1-5 (7) cm long, 1-4 mm wide, rounded at apex, commonly pustulate and short-hirsute especially beneath; spikes usually geminate, commonly 1-2.5 (5) cm long, dense, bractless; corolla rather conspicuous, 2-3 mm broad; fruiting calyx ovoid or ovoid-oblong, 2-3 (4) mm long, subsessile, spreading or somewhat recurved, deciduous, usually densely appressed hirsute and silky; mature calyx-lobes lanceolate, connivent, midrib thick and usually brownish, and frequently bearing spreading or recurved hairs; ovules 4, nutlets 1 or rarely 2, next to the abaxial calyx-lobe, 1.7-2.5 mm long, 1-1.5 mm broad, pale, broadly lanceolate, granulate, muricate-papillate or rarely spinulose, back low-convex or flat, margins sharply angled or with a very narrow knifelike margin, groove open, narrow, opening into a small areola below; gynobase subulate, about $\frac{2}{3}$ height of nutlet, not markedly differentiated from style; style usually a trifle shorter than the nutlet. Desert washes and ridges, sandy to rocky soils. Southern Utah and western Arizona, then westward into southern Nevada and the desert regions of California. March-May. Fig. 32.

Washington Co., St. George, Palmer 352 (G); 1 mile east of Hurricane, Maguire & Blood 1532 (UTC); 2 miles north of St. George, E. Cox s.n. (DIX); Terry's Ranch on the Beaverdam Wash, A.H. Barnum 988 (DIX); Terry's Ranch, L.C. Higgins 1225 (BRY); Castle Cliffs, along hwy 91, L.C. Higgins 4168 (BRY).

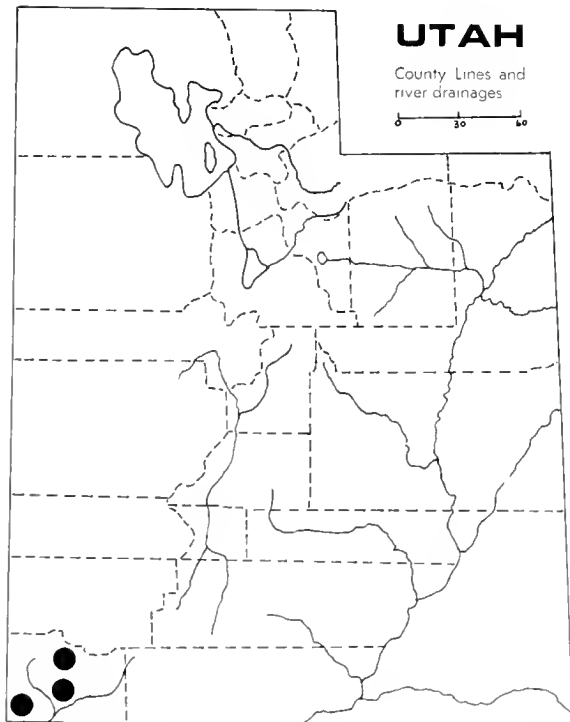


Fig. 32. *Cryptantha utahensis*

WTSU); Terry's Ranch on the Beaverdam Wash, L.C. Higgins 292 (BRY).

23. *Cryptantha watsoni* (Gray) Greene, Pittonia 1:120. 1887. Type: Utah, Wasatch Mountains, Watson 858.

Krynitzkia watsoni Gray, Proc. Amer. Acad. 20:271. 1885.

Cryptantha vincens Nels. & Macbr. Bot. Gaz. 62:143. 1916.

Slender strictly branched hispid herb 1-3 dm high; stems solitary, sparsely or loosely branched, spreading short-hispid; leaves linear to oblanceolate, 1-4 (5) cm long, 1-4 (5) mm broad, obtuse or rounded, ascending hispid, and merely pustulate; spikes solitary or in pairs, 1-4 (6) cm long, bractless or rarely bracted below; corolla inconspicuous, about 1 mm broad; fruiting calyx ovoid to oblong-ovoid, 2-3.5 (4) mm long, subsessile, rounded at base, early deciduous, oldest ones becoming distant; mature calyx-lobes lanceolate, tips usually connivent, hirsute with ascending hairs, the midrib also with a few spreading bristles and scarcely thickened; nutlets 4, homomorphous or practically so, lanceolate, 1.5-2 mm long, about 0.8 mm broad, smooth, shiny or at times dulled by minute granulations, back nearly flat, margins definitely angled, groove closed or nearly so and forked at base; gynobase subulate, about $\frac{2}{3}$ height of nutlets; style equalling nutlets or a trifle surpassed by them. Sandy or rocky slopes and plains of the arid Transition Zone. Eastern Washington, south through Oregon and Nevada to California, and east to Montana, Wyoming, and Colorado. May-September. Fig. 33.

Beaver Co., 11.5 miles east of Milford, B. Maguire 21013 (UTC); Juab Co., Deep Creek Mountains, Maguire & Becraft 2775 (UTC); Tooele Co., near the Great Salt Lake, A.O. Garrett 2864a (UT); Utah Co., Rock Canyon, A.O. Garrett 3316 (UT).

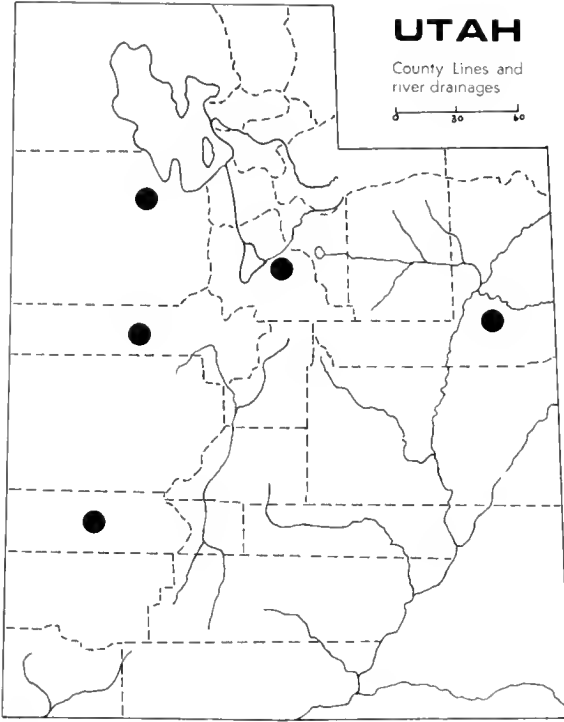
24. *Cryptantha abata* Johnst. Journ. Arn. Arb. 24:240. 1948. Type: Arum, Nevada, Jones 6692.

Krynitzkia depressa Jones, Contr. West. Bot. 13:5. 1910. not *C. depressa* A. Nels.

Oreocarya depressa Macbr. Contr. Gray Herb. 48:32. 1916.

Cryptantha modesta Payson, Ann. Mo. Bot. Gard. 14:278. 1927. Not *C. modesta* Brand.

Plants perennial, arising from a strong, woody taproot, 0.5-1.8 dm high; stems many, 0.2-1.5 dm long, strigose and weakly setose; leaves oblanceolate to spatulate, obtuse, strigose, setose

Fig. 33. *Cryptantha watsoni*

and subtomentose, the petioles ciliate margined, inflorescence narrow, 0.2-0.8 dm long; calyx segments lanceolate to ovate, 2.5-4 mm long in anthesis, in fruit becoming 5-8 mm long, setose; corolla white, the tube 3-4 mm long, crests at base of tube conspicuous, fornices yellow, rounded, papillose, about 0.5 mm long, limb 7-8 mm wide; style exceeding mature fruit 0.5-1 mm; nutlets ovate, 3-3.5 mm long, 2-2.5 mm wide, usually all 4 maturing, margins in contact, obtuse to acute, dorsal surface carinate, tuberculate, muricate and sometimes with low inconspicuous ridges, ventral surface deeply and irregularly rugose, scar open, triangular, surrounded by a slightly elevated margin. Growing on sandy or gravelly soil usually in the Transition Zone, South central Utah, northwestern Arizona, and eastern Nevada. April-July. Fig. 34.

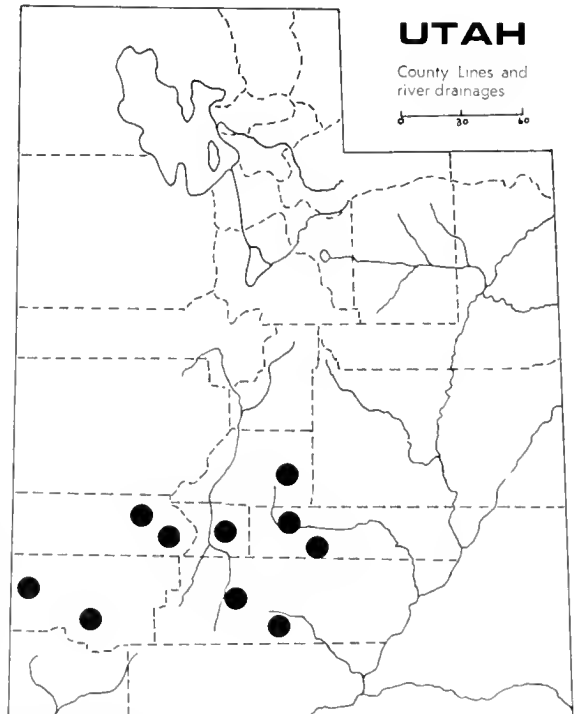
Garfield Co., Bryce Canyon, K.E. Weight B-32 (UT); 25 miles north of Panguitch, B.F. Harrison 9009 (BRY); about 800 yards northwest of Sunset Point, W.S. Boyle 1117 (BRY, UTC); 17 miles southwest of Escalante, A. Cronquist 9152 (UTC); 2.4 miles east of Red Canyon Campground D. Atwood 1888 (BRY); Iron Co., 10 miles northeast of Pinto, P. Plummer 7410 (UT); Pinte Co., Marysville, M.E. Jones 6679 (POM); Sevier Co., about 28.3 miles north of Fremont, Welsh, Atwood & Higgins 8973 (BRY); Wayne Co., 10 miles south of Fish Lake, L.C. Higgins 1015 (BRY); about 5 miles south of Torrey, L.C. Higgins 1016 (BRY); 5 miles north of Fremont, B.F. Harrison 7364 (BRY); about 8 miles west of Loa, L.C. Higgins 1346 (BRY).

25. *Cryptantha bakeri* Payson, Ann. Mo. Bot. Gard. 14:331. 1927. Type: Mancos River sage plains, southern Colorado, Baker, Earle & Tracy 827.

Oreocarya bakeri Greene, Pittonia 4:92. 1899.

Oreocarya eulophus Rydb. Bull. Torrey Club 31:637. 1904.

Biennial or short-lived perennials, 1-4 dm tall; stems 1-4 (6), 0.5-1.5 dm long, spreading setose-hirsute; leaves oblanceolate, obtuse, mostly basal, 3-6 (8) cm long, 0.5-1.2 (2) cm wide, dorsal surface strigose and spreading setose, pustulate, ventral surface uniformly strigose and with few or no pustulate hairs; inflorescence narrow, 0.6-2.5 (3) dm long, setose-hirsute, foliar bracts evident, slightly surpassing the individual cymes; calyx segments broadly lanceolate or ovoid, in anthesis 3.5-4 mm long, in fruit becoming 6-8 mm long, conspicuously setose; corolla white, the tube 4-6 mm long, crests at base of tube lacking, fornices yellow, emarginate, 1-1.5 mm long, limb 6-8 mm broad; nutlets ovate-lanceolate, 2.5-3 mm long, 1.5-2 mm wide, 3 to 4 usually maturing, margins obtuse, nearly in contact, dorsal surface deeply and sharply rugose, scar closed, surrounded by a definitely elevated margin; style exceeding mature fruit 1-2 mm. Growing on sandy or clay soil in the Pin-

Fig. 34. *Cryptantha abata*

yon-Juniper community. Southeastern Utah, southwestern Colorado, northwestern New Mexico, and northeastern Arizona. May-August. Fig. 35.

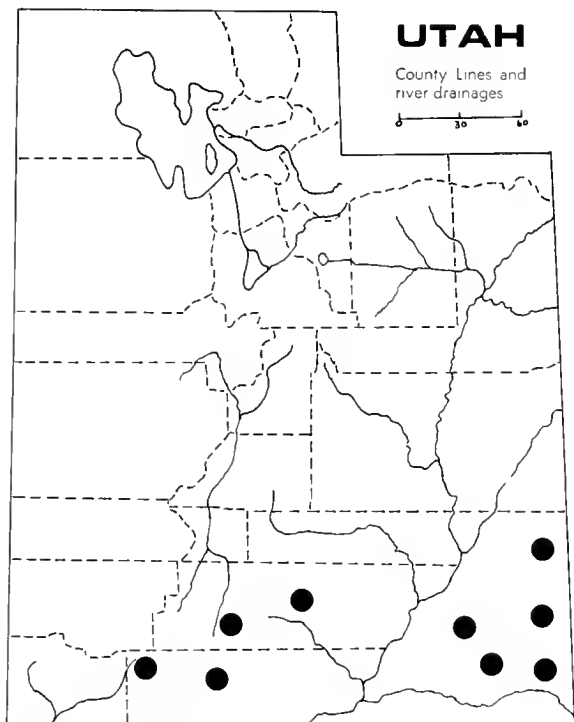


Fig. 35. *Cryptantha bakeri*

Garfield Co., Bryce Canyon Natl. Park, B. Maguire 19101 (UTC); about 17 miles southwest of Escalante, A. Cronquist 9153 (UTC); Bryce Canyon Natl. Park, K. Weight s.n. (BRY); Kane Co., headwaters of the Virgin River, 15 miles north of Orderville, B. Maguire 18855 (UTC); San Juan Co., La Sal Ranger Station, B. Maguire 2059 (UTC); 5 miles west of Blanding, B. Maguire 5102 (UTC); 8 miles north of Blanding, A.H. Holmgren 3374 (BRY, UTC); 18 miles southwest of Blanding, A. Cronquist 9013 (UTC); 12 miles north of junction 47-261, D. Atwood 1539a (BRY); Natural Bridges Natl. Monument, Welsh, Atwood & Higgins 8949 (BRY); about 15 miles south of junction of Utah hwy 95-261, Welsh & Atwood 9979 (BRY); 10 miles south of Monticello, L.C. Higgins 3558 (BRY); 8 miles south of La Sal, L.C. Higgins 3548 (BRY); about 16 miles west of Blanding, Welsh, Atwood & Higgins 8927 (BRY).

26. *Cryptantha barnebyi* Johnst. Journ. Arn. Arb. 29:240. 1948. Type: Uintah County, 30 miles south of Ouray, Ripley and Barneby 8748.

Perennial, 1.5-3.5 dm tall; stems stout, erect, several, 0.8-1.2 dm long, conspicuously yellow-hispid; leaves oblanceolate, thick, acute, 5-9 cm long, 0.5-1.4 cm wide, coarsely appressed hispid-pustulate on both sides, and with some finer

hairs beneath, the petioles conspicuously ciliate; inflorescence narrow, 1-1.5 dm long, densely yellowish-hispid, foliar bracts evident to conspicuous; calyx segments lanceolate, in anthesis 5-7 mm long, in fruit becoming 8-13 mm long, yellowish-hirsute; corolla white or light yellow, the tube 5-7 mm long, crests at base of tube very conspicuous, fornices yellow, emarginate, distinctly papillose, 0.5 mm long, limb 8-11 mm wide; style exceeding mature fruit 5-6 mm; nutlets ovate, 3.5-4 mm long, 2.5 mm wide, all 4 usually maturing, margins of nutlets in contact, acute, smooth and glossy on both surfaces, scar closed, straight, and without an elevated margin. Growing on white barren shale knolls. Endemic to the lower part of the Uintah Basin in Uintah County, Utah. May-June. Fig. 36.

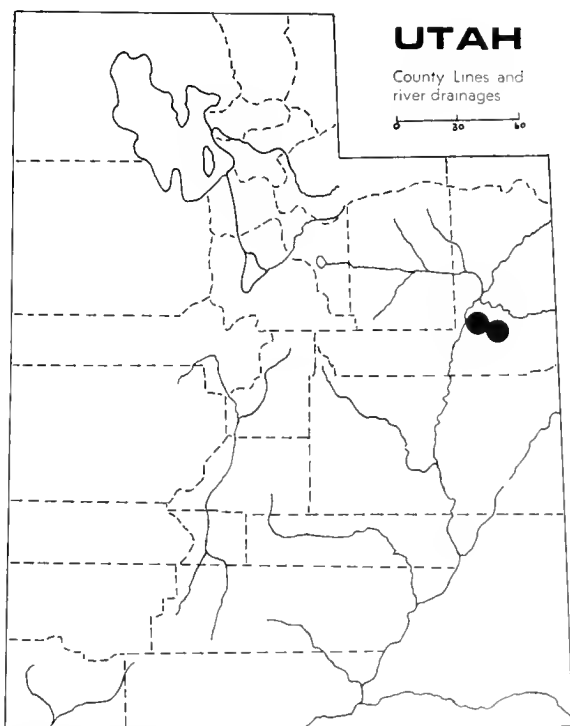


Fig. 36. *Cryptantha barnebyi*

Uintah Co., 8 miles west of Bitter Creek along the Watson-Ouray road, L.C. Higgins 1887 (BBY); about 27 miles south of Ouray along the Hill Creek road, L.C. Higgins 1877 (BRY); along the Watson-Ouray road at Buck Canyon, L.C. Higgins 1884 (BRY); 8 miles west of Bitter Creek, L.C. Higgins 1587 (BRY); about 6.5 miles west of Bitter Creek, L.C. Higgins 1586 (BRY); about 2 miles south of the Knolls, L.C. Higgins 1584 (BRY).

27. *Cryptantha breviflora* (Osterh.) Payson. Ann. Mo. Bot. Gard. 14:318. 1927. Type: 6.5 miles north of Jensen, Uintah County, Utah, G. E. Osterhout 6414.

Oreocarya breviflora Osterh. Univ. Wyo.
Publ. Bot. 1:169. 1926.

Long-lived perennials, 1.6-3 dm tall; stems several, slender, 0.7-1.7 dm long, densely white setose at the base, strigose above; leaves oblanceolate to spatulate, 2.5-9 cm long, 0.4-1.4 cm wide, clustered at the ends of the branched caudices the apices obtuse, dorsal surface densely and uniformly silky-strigose with many very small pustules, ventral surface similar but with fewer pustules; inflorescence in flower narrow but becoming broad and open at maturity, 0.6-2.7 dm long, setose; calyx segments linear-lanceolate, 4.5-6 mm long in anthesis, in fruit becoming 7-9 mm long, setose; corolla white, 3.5-4.5 mm long, crests at base of tube evident, fornicies yellow, rounded, about 0.5 mm long, limb 8-12 mm wide; nutlets lanceolate, 3.4-4 mm long, 2-2.5 mm wide, less than 4 nutlets maturing, margins in contact, knifelike, dorsal surface uniformly muricate or tuberculate, ventral surface similar, scar open, narrowly triangular, margin not elevated; style exceeding mature fruit by 2 mm or less. Growing on heavy clay soils. Northeastern Utah in Duchesne and Uintah counties. May-July. Fig. 37.

Duchesne Co., Red Creek, 3 miles east of Fruitland. L.C. Higgins 1044 (BRY); Bluebell, L.C. Higgins 1060 (BRY); 5 miles east of Red Creek, S.L. Welsh 1774 (BRY); about 2 miles east of Fruitland

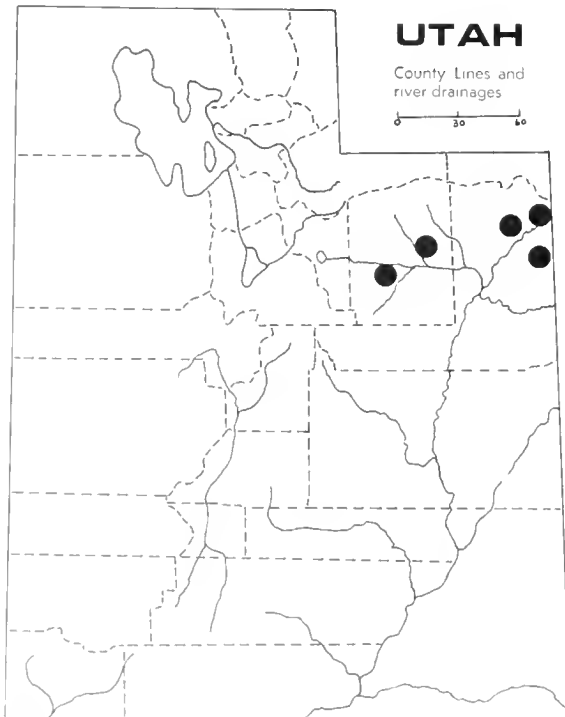


Fig. 37. *Cryptantha breviflora*

Higgins & Welsh 1018 (BRY); Uintah Co., 2 miles north of Brush Creek sheep pens, D. Atwood 1611 (BRY); 3.5 miles north of Brush Creek sheep pens, Higgins & Atwood 1868 (BRY); 8 miles south of hwy 40 on the road to Bonanza, L.C. Higgins 1084 (BRY); Dinosaur Natl. Monument, S.L. Welsh 193 (BRY); Red Wash Oil Field, S.L. Welsh 3901 (BRY); Dinosaur Natl. Monument, J. Brotherson 806 (BRY); Dinosaur Natl. Monument, S.L. Welsh 119, 148 (BRY); Split Mountain Gorge, J. Brotherson 993 (BRY); 14 miles west of Vernal R.C. Rollins 1736 (UTC).

28. *Cryptantha caespitosa* (A. Nels.) Payson, Ann. Mo. Bot. Gard. 14:281. 1927. Type: Point of Rocks, Sweetwater County, Wyoming, Nelson 4749.

Oreocarya caespitosa A. Nels. Erythea 7:65. 1899.

Densely caespitose or mat forming perennials, 0.5-1.5 dm tall; stems 1-many, arising from a much-branched woody caudex, 0.2-0.9 dm long, weakly setose and appressed strigose; leaves oblanceolate to spatulate, 1-3 cm long, 0.3-0.7 cm wide, pubescence of two kinds, strigose and appressed setose, becoming tomentulose toward the petiole; inflorescence narrow, 0.3-1 dm long, foliar bracts inconspicuous; calyx segments lanceolate, in anthesis 3-4 mm long, in fruit becoming 5-8 mm long, strigose and weakly setose, also somewhat tomentulose; corolla white, the tube 3-4 mm long, crests at base of tube conspicuous, fornicies yellow, rounded, about 0.5 mm long, limb 4-7 mm wide; nutlets lanceolate, 3-3.5 mm long, 2-2.5 mm wide, the margins acute, in contact, dorsal surface with low rounded rugae, also tuberculate, and with numerous murications between the ridges, ventral surface muricate, scar open, narrowly triangular, margin of scar not elevated; style equalling or 0.5 mm longer than mature fruit. Growing on heavy clay soils. Southern Wyoming and probably northeastern Utah. May-July. Fig. 38.

Cryptantha caespitosa occurs within a few miles of the Utah border near Mckinnon and Lonetree. With additional collections, this species will without question be found in Utah in either Summit or Daggett counties or maybe both.

29. *Cryptantha capitata* (Eastw.) Johnst. Journ. Arn. Arb. 21:66. 1940. Type: Hermit Trail on the south rim of the Grand Canyon, A. Eastwood 5969.

Oreocarya capitata Eastw. Leaflets West. Bot. 1:9. 1937.

Perennial, 1.5-2.7 dm tall; stems weak, 1-several, 1.2-2.4 dm long, appressed setose; leaves

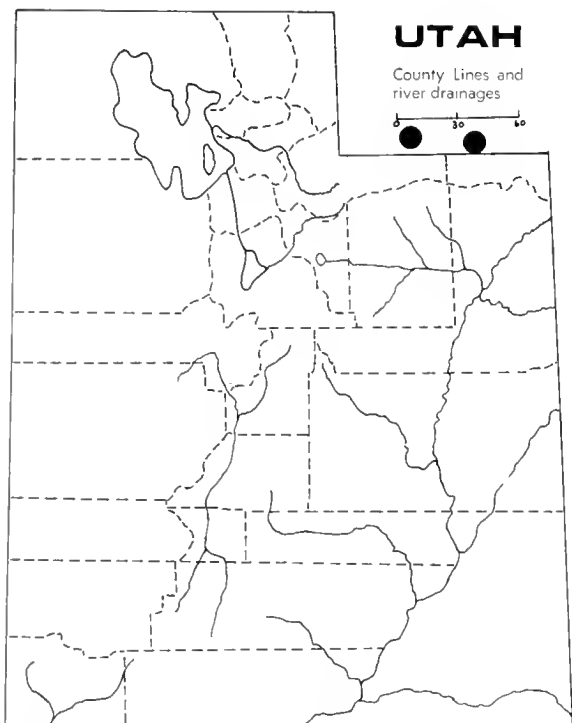


Fig. 38. *Cryptantha caespitosa*

linear or very narrowly oblanceolate, 3-8 cm long, 0.3-0.5 (0.8) cm wide, dorsal surface appressed setose-pustulate, ventral surface uniformly strigose and without pustules; inflorescence capitate, or with 1 or 2 glomerules below the terminal cluster, 0.1-0.4 dm long, spreading white setose; calyx segments linear-lanceolate, 7-9 mm long in anthesis, in fruit becoming 11-16 mm long, conspicuously setose-pustulate; corolla white, the tube 9-12 mm long, crests at base of tube conspicuous, fornicies yellow, emarginate, about 1 mm long, papillose, limb 6-8 mm wide; nutlets lanceolate, 4-5 mm long, 2-3 mm wide, 2-4 usually maturing, the margins in contact, knifelike, both surfaces glossy-smooth, scar closed, straight, and without an elevated margin; style exceeding mature fruit 4-5 mm. Growing in sandy to sandy-loam soil in the transition zone. South central Utah and north central Arizona. April-July. Fig. 39.

Garfield Co., Bull Creek, a little southwest of Bull Mountain, Henry Mountains, 20 miles south of Hanksville, 8,000 feet, Cronquist & Holmgren 9299 (UTC); Wayne Co., with scattered Ponderosa Pine on the northeast slope of Aquarius Plateau southeast of Torrey, Cronquist & Holmgren 9365 (UTC).

30. *Cryptantha compacta* Higgins, Great Basin Naturalist 28:196. 1968. Type: 8 miles west of the Desert Range Experiment Station

Headquarters along hwy 21, L.C. Higgins 1613.

Densely caespitose perennials, 0.3-1 dm tall; stems numerous, arising from a woody root, 0.1-0.4 dm long, tomentose below, weakly strigose above, leaves oblanceolate to spatulate, obtuse, 0.5-1.5 (2) cm long, 0.2-0.4 cm wide, dorsal surface with appressed setose-pustulate bristles, also densely strigose or subtomentose, ventral surface similar but with fewer pustulate hairs, the petioles tomentose; inflorescence narrow, nearly capitate, 1-5 cm long; foliar bracts evident but not conspicuous; calyx segments lanceolate, 2-2.5 mm long in anthesis, in fruit becoming 3.5-4.5 mm long, densely white setose and tomentose; corolla white, the tube 1.8-2.2 mm long, crests at base of tube evident, fornicies yellow, rounded, papillose, about 0.5 mm long, limb 4.5-5.5 mm wide; nutlets lance-ovate, acute, 2.5-3 mm long, 1.5-1.8 mm wide, only 1

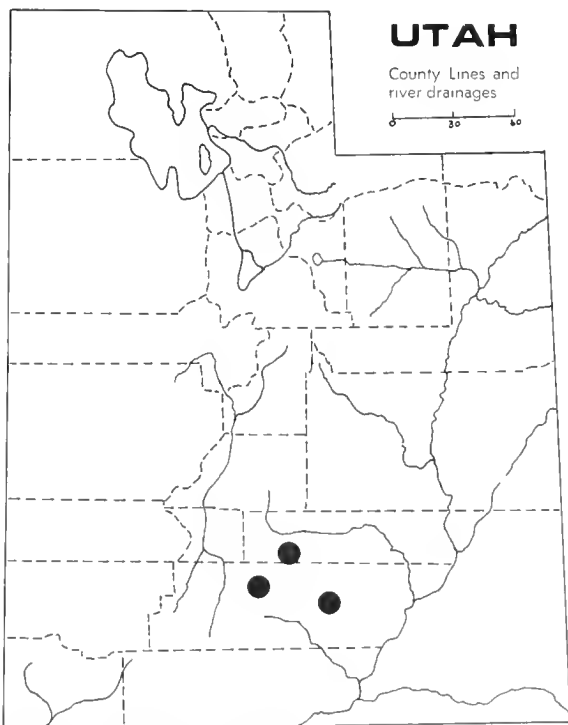
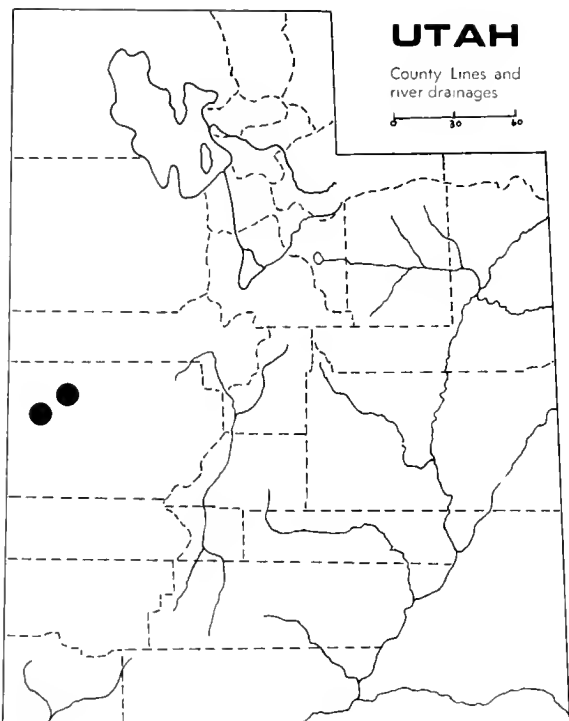


Fig. 39. *Cryptantha capitata*

or 2 maturing, dorsal surface muriccate or weakly tuberculate-rugulose, ventral surface muriccate, scar open, subulate to narrowly triangular, elevated margin lacking; style equalling or shorter than mature fruit. Open slopes and ridges, growing on gravelly loam soil. Known only from southwestern Millard County, Utah. May-July. Fig. 40.

Fig. 40. *Cryptantha compacta*

Millard Co., about 8 miles west of the Desert Range Experiment Station Headquarters along hwy 21. L.C. Higgins 1462, 1613 (BRY); north slope of Pine Valley, R.C. Holmgren 521 (BRY).

31. *Cryptantha confertiflora* (Greene) Payson, Ann. Mo. Bot. Gard. 14:256. 1927. Type: Cushenberry Springs on the north side of the San Bernardino Mountains, S.B. Parish 1316.

Oreocarya confertiflora Greene. Pittonia 3:112. 1896.

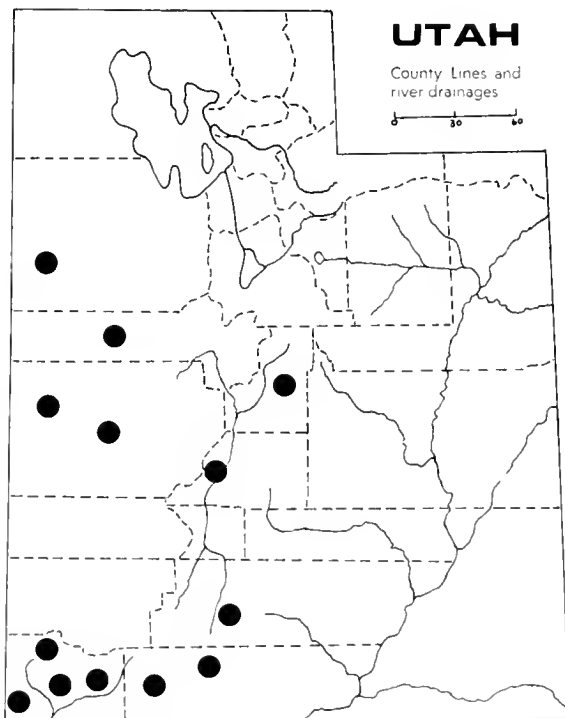
Oreocarya lutea Greene. Muhlenbergia 2:240. 1906.

Oreocarya alata (Jones) Nels. Coult. & Nels. Man. Cent. Rocky Mts. 417. 1909.

Perennial herbs, 1.7-4.3 dm tall; stems 1-7, slender, 1.5-2.5 dm long, tomentose at the base, strigose and setose upward; leaves linear to oblanceolate, 3-12 cm long, 0.2-1.6 cm wide, acute, dorsal surface densely strigose and appressed setose with pustulate bases, ventral surface uniformly strigose, and with few or no pustules; inflorescence subcapitate, 0.3-2 dm long, strigose and with twisted setose hairs, bracts inconspicuous; calyx segments linear-lanceolate, in anthesis 6-8 mm long, in fruit becoming 10-14 mm long, strigose and spreading setose; corolla yellow, the tube 9-13 mm long, fornice broad, emarginate,

about 1 mm long, crests at base of tube evident or sometimes lacking, limb 8-10 mm wide; nutlets triangular or ovate, 3.5-4 mm long, 2.5-3 mm wide, usually all 4 maturing, margins narrowly winged, in contact, surfaces smooth and glossy, sear straight, closed, and lacking an elevated margin; plants distinctly heterostyled. Growing in a wide variety of soil types. Western Utah, northern Arizona, southern Nevada, and west to southern and western California. April-July. Fig. 41.

Garfield Co., about 8 miles southeast of Escalante, Holmgren, Reveal & LaFrance 2036 (BRY); Bryce Canyon Natl. Park, B. Maguire 19100 (UTC); near Granite Ranch, W.P. Cottam 5543 (BRY); Tropic Canyon, H. Buchanan 122 (UT); 5 miles south of Boulder, L.C. Higgins 1013 (BRY); Juab Co., between Callao and Trout Creek, Maguire & Holmgren 21857 (UTC); 15 miles east of Trout Creek, B. Maguire 2753 (UTC); 18 miles east of Trout Creek, B. Maguire 2754 (UTC); Kane Co., Kanab Dunes, J.R. Murdock 101 (BRY); Kanab, Anderson 16 (UTC); Cottonwood Canyon, 20 miles south of Cannonville, L.C. Higgins 1007 (BRY); 6 miles west from head of Collets Wash, D. Atwood 1873 (BRY); Millard Co., north of Paddocks, P. Plummer 131 (UT); Desert Range Experiment Station, M. G. Barlow 84 (BRY); White Sage Valley, B.F. Harrison 6365 (BRY); Sanpete Co., Manti Canyon, 1 mile east of Manti, A.H. Barnum 1291 (DIX); 1 mile northwest of Mayfield, R.S. Bjerregaard 39 (BRY); Sevier Co., west of Richfield, B.F. Harrison 260 (BRY); Washington Co., entrance to Zion Natl. Park, B. Maguire 13557 (UTC); 0.5 miles north of Andersons Ranch, B. Maguire 16289 (UTC); Zion Natl. Park, trail to Angels Landing, B.

Fig. 41. *Cryptantha confertiflora*

Maguire 16287 (UTC); Beaverdam Mountains, B. Maguire 20511 (UTC); 5 miles west of Virgin, C.L. Hitchcock 3015 (UTC); Pine Valley, M. Cox s.n. (DIX); hills north of St. George, V. Worthen 42 (BRY); Santa Clara, W.P. Cottam 1163 (BRY); between Hurricane and Kanab, J.W. Harrison s.n. (DIX); Diamond Valley, F.W. Gould 1550 (BRY, UT, UTC); Diamond Valley, L.C. Higgins 4206 (BRY, WTSU); Zion Natl. Park, B. Johnson s.n. (DIX); 7 miles north of St. George, E. Hawkins s.n. (DIX); Zion Natl. Park, A.M. Woodbury s.n. (DIX); Zion Natl. Park, W.P. Cottam 5149 (UT); Diamond Valley, W.P. Cottam 4038 (BRY); Zion Natl. Park, W.P. Cottam 4754 (BRY); 5 miles south of Veyo, B.F. Harrison 10207 (BRY); 9 miles east of Hurricane, L.C. Higgins 4224 (BRY, WTSU).

32. *Cryptantha elata* (Eastw.) Payson, Ann. Mo. Bot. Gard. 14:285. 1927. Type: on the road to the coal mines, Mesa County, Colorado, Eastwood.

Oreocarya elata Eastw. Bull. Torrey Club 30:241. 1903.

Biennial or short-lived perennials, 3-5 dm tall; stems 1-6, erect, stout, weakly setose with spreading white hairs, 0.9-1.5 dm long; leaves oblanceolate to spatulate, 2-5 cm long, 0.4-1.3 cm wide, apices acute to obtuse, the blade abruptly tapering to the narrow petiole, dorsal surface strigose and appressed setose, ventral surface strigose, both surfaces pustulate; inflorescence spreading or open in age, 1.5-3.5 dm long, setose, foliar bracts inconspicuous; calyx segments lanceolate, in anthesis 3-4.5 mm long, in fruit becoming 7-8 mm long, hirsute; corolla white, the tube 3.5-5 mm long, fornices yellow, rounded, papillose, about 1 mm long, crests at base of tube well developed, limb 6-8 mm wide; nutlets lanceolate-ovate, 4-4.5 mm long, 2-2.5 mm wide, usually all 4 maturing, margins in contract, dorsal surface densely tuberculate and somewhat rugulose, the surface also covered with dense minute papillae, ventral surface similar but the roughenings less prominent, scar closed, or narrowly open at the base, and without an elevated margin; style exceeding mature fruit 0.5-2 mm. Growing on heavy clay soils. Western Colorado and eastern Utah in Grand County, May-June. Fig. 42.

Grand Co., about 3 miles south of U.S. hwy 50-6 along hwy 128, S.L. Welsh 6952 (BRY); near milepost 39 along hwy 128, L.C. Higgins 1479 (BRY).

33. *Cryptantha flava* (A. Nels.) Payson, Ann. Mo. Bot. Gard. 14:259. 1927. Type: Point of Rocks, Sweetwater County, Wyoming, Nelson 3074.

Oreocarya flava Nelson, Bull. Torrey Club 25:202. 1898.

Oreocarya lutescens Greene, Pittonia 4:93. 1899.

Cryptantha confertiflora var. *flava* Brand, Pflanzenreich, (Heft 97) 4, Fam. 252:90. 1931.

Cryptantha confertiflora var. *lutescens* Brand, Pflanzenreich, (Heft 97) 4, Fam. 252:90. 1931.

Perennial, 1.3-4 dm tall; stems many from a multiple caudex, 0.8-2.6 dm long, densely setose, white hairy at the base, becoming setose and strigose upward; leaves narrowly oblanceolate to nearly linear, acute, 2-9 cm long, 0.3-0.8 cm wide, dorsal surface strigose and appressed setose with pustulate hairs, ventral surface almost uniformly strigose, and with the pustulates less conspicuous; inflorescence narrow to somewhat open, 0.5-2.5 dm long, conspicuously yellow setose, the floral bracts inconspicuous; calyx segments linear, in anthesis 8-10 mm long, in fruit becoming 9-12 mm long, densely setose, with yellowish hairs, pedicels 3-5 mm long in fruit; corolla yellow, the tube 9-12 mm long, crests at the base of the tube absent or nearly so, fornices yellow, truncate, emarginate, 1-1.5 mm long, limb 8-10 mm wide; nutlets lanceolate, 3.4-4 mm long, 1.9-2.2 mm wide, 1 or 2 usually maturing, margins acute, in contact when more than 1 nutlet matures, both surfaces of nutlet

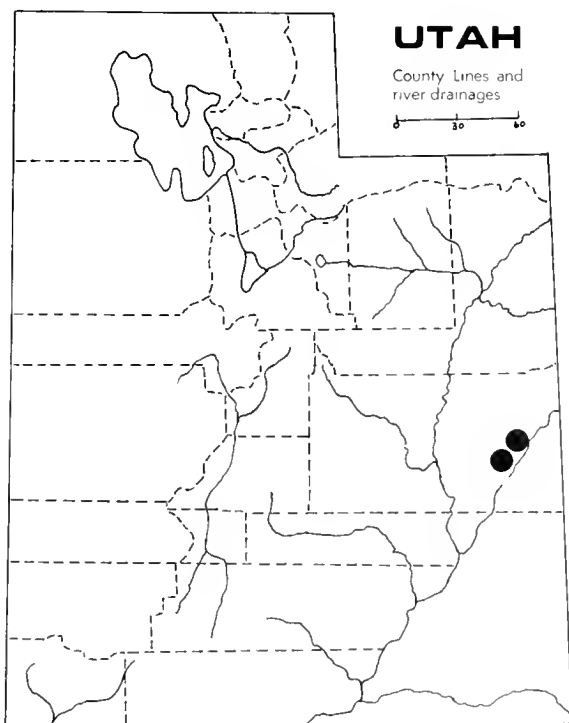


Fig. 42. *Cryptantha elata*

smooth and glossy, scar straight, closed, elevated margin lacking; style exceeding mature fruit 3-7 mm (heterostyled). Usually growing in sandy soils. Southern Wyoming, south through western Colorado and eastern Utah to northern New Mexico and Arizona. April-August. Fig. 43.

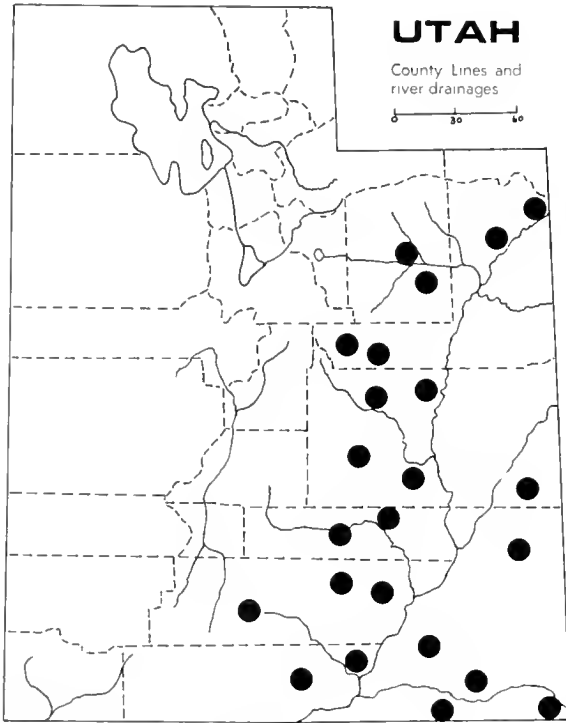


Fig. 43. *Cryptantha flava*

Carbon Co., 2 miles east of roadside geyser, B.K. Vickery 721 (UT); Duchesne Co., 2 miles west of Duchesne, A. Collotzi 545 (UTC); 8 miles north of Duchesne, L.C. Higgins 1057 (BRY); 1 mile west of Duchesne, L.C. Higgins 1051 (BRY); 12 miles north of Duchesne, J. Brotherson 925 (BRY); Emery Co., about 15 miles west of hwy 50-6 along the road to Huntington, L.C. Higgins 1305 (BRY); about 5 miles west of Temple Mountain, L.C. Higgins 1325a (BRY); 50 miles south of Green River, A. Cronquist 9086 (UTC); Goblin Valley, S.L. Welsh 3925 (BRY); San Raphael Swell, B. Maguire 18302 (UTC); 20 miles east of Hanksville, B. Maguire 18211 (UTC); along hwy 24, 10 miles south of San Raphael River bridge, L.B. Barnett 22 (BRY, UTC); Temple Mountain V.P. Allman s.n. (BRY); San Raphael River, B.F. Harrison 8058 (BRY); 18 miles east of Wellington, L.C. Higgins 998 (BRY); Green River, W.P. Cottam s.n. (BRY); east of Wellington, W.P. Cottam 2050 (BRY); 50 miles south of San Raphael River, B.F. Harrison 9627 (BRY); 20 miles east of Price, Welsh & Moore 2791 (BRY); Garfield Co., 25 miles southeast of Hanksville, C. Parry s.n. (UTC); 50 miles southwest of San Raphael, B.F. Harrison 7441 (BRY); about 7 miles south of Trachyte Ranch, S.L. Welsh 3940 (BRY); Sandy Ranch, B.F. Harrison 11489 (BRY, UTC); Calf Creek on the Escalante River, McArthur & Beck 195 (BRY); 23 miles up North Wash from Hite, B.F. Harrison 11550 (BRY);

5 miles south of Boulder, G.E. Bohart s.n. (UTC); east Henry Mountains, near Granite Ranch, B.F. Harrison 5544 (BRY); 14 miles south of the Kane County line on Hole in Rock road, J.B. Karen 89 (BRY); Escalante near town, M.E. Jones 4408 (BRY); Grand Co., Arches Natl. Monument, L.C. Anderson 48 (UTC); Dead Horse Point, A. Carter 1560 (UTC); Arches Natl. Monument, B.F. Harrison 11129 (BRY); Arches Natl. Monument, L.B. Barnett 44, 57 (BRY, UTC); Dead Horse Point, B.F. Harrison 10293 (BRY); Kane Co., Willow Tank, about 17 miles south of Garfield County line, D.H. White 95 (BRY); Glen Canyon area, F. Wright s.n. (ARIZ); about 3 miles north of U.S. hwy 89 in Buckskin Gulch, S.L. Welsh 5319 (BRY); Cockscomb Ridge, about 40 miles east of Kanab, S.L. Welsh 5342 (BRY); Plateau near head of Rock Creek, B.F. Harrison 9033 (BRY); Escalante Desert near Willow Tank, B.F. Harrison 9033 (BRY); San Juan Co., White Canyon, L. O. Wilson 51 (UTC); 5 miles northwest of Mexican Hat, B. Maguire 16290 (UTC); 16 miles east of Hite, A. Cronquist 9023 (UTC); Hatch Rock, S. Flowers 2071 (UT); Rainbow Bridge Trail, J.T. Howell 24617 (ARIZ); about 10 miles east of Halls Crossing, L.C. Higgins 527 (BRY); Natural Bridges Natl. Monument, C. Moore 140 (BRY); Island in the Sky area, C. Moore 190 (BRY); La Sal Range, W.P. Cottam 2197 (BRY); 4 miles above Cow Canyon, L.K. Shumway 64 (BRY); 6 miles south of Bluff, D.E. Bright 114 (BRY); 2 miles northwest of Bluff, B. Maguire 13531 (UTC); 18 miles southwest of Blanding, A. Cronquist 8956 (UTC); 7 miles northeast of Mexican Hat, A. Cronquist 9133 (UTC); Cow Canyon, A.H. Holmgren 3212 (UTC); Robbers Roost, L.A. Stoddart s.n. (UTC); Rock House, Monument Valley, A.H. Holmgren 3220 (UTC); 19 miles south of Blanding, B. Maguire 5104 (UTC); 14 miles south of Bluff, B. Maguire 5103 (UTC); Natural Bridges Natl. Monument, B. Maguire 2058 (UTC); Squaw Canyon, 1 mile west of Cane Spring, Welsh, Moore & Canter 2864 (BRY); about 5 miles north of Bluff, S.L. Welsh 1493 (BRY); about 5.5 miles north of Bluff, C.A. Hanson 81 (BRY); west rim of Browns Canyon, L.K. Shumway 133 (BRY); ledges north of San Juan River just east of Johns Canyon, B.F. Harrison 11954 (BRY, UTC); 10 miles west of Bluff, B.F. Harrison 10363 (BRY); Uintah Co., 14 miles west of Vernal, B.C. Rollins 1734 (UTC); Dinosaur Natl. Monument, I. Brotherson 1100 (BRY); desert west of Vernal, L.O. Williams 619 (UTC); about 5 miles west of Vernal, L.C. Higgins 1069 (BRY); 7 miles south of Fort Duchesne, J. Brotherson 1105 (BRY); about 8 miles south of hwy 40 along the road to Bonanza, L.C. Higgins 1082 (BRY); about 3 miles northwest of Vernal, L.C. Higgins 1073 (BRY); Dinosaur Natl. Monument, S.L. Welsh 176 (BRY); Wayne Co., Fruita Arch Canyon, B. Maguire 18134 (UTC); 17 miles south of Hanksville, B. Maguire 18190 (UTC); 13 miles west of Hanksville, B. Maguire 18149 (UTC); Fruita, DE. Beck s.n. (BBY).

34. *Cryptantha flavocolata* (A. Nels.) Payson. Ann. Mo. Bot. Gard. 14:334. 1927. Type: Piedmont, Wyoming, A. Nelson 4572.

Oreocarya flavocolata A. Nels. Erythea 7:67. 1899.

Oreocarya flavocolata spatulata A. Nels. Erythea 7:67. 1899.

Oreocarya cristata Eastw. Bull. Torrey Club 30:244. 1903.

Oreocarya shockleyi Eastw. Bull. Torrey Club 30:245. 1903.

Oreocarya eastwoodae Nels. & Kenn. Muhlenbergia 3:141. 1908.

Caespitose perennial, 1-3.7 dm tall; stems 1-several, slender, 0.5-2 dm long, strigose and spreading setose with slender bristles; leaves linear-oblongate to spatulate, obtuse or sometimes acute, 3-11 cm long, 0.3-1.5 cm wide, densely strigose and weakly setose, dorsal surface conspicuously pustulate, ventral surface with few pustules or sometimes silky-strigose; inflorescence narrow or sometimes slightly open and lax, 0.5-3 dm long, foliar bracts evident but not conspicuous; calyx segments in anthesis linear-lanceolate, 5-6 mm long, in fruit becoming 8-10 mm long and becoming broadly lanceolate to ovate; corolla white or pale-yellow, the tube 7-10 mm long, crests at base of tube lacking, fornicies yellow, minutely papillose, 1-2 mm long, limb 8-12 mm wide; nutlets lanceolate to lance-ovate, 2.5-3.5 mm long, 1.8-2 mm wide, usually all 4 maturing, margins obtuse, in contact or slightly separated, dorsal surface muricate, tuberculate, and with conspicuous ridges, sometimes nearly foveolate, ventral surface tuberculate, rarely with ridges, scar open, constricted near the middle and surrounded by a highly elevated margin; style exceeding mature fruit 4-8 mm (heterostyled). Open slopes and ridges mostly in the Pinyon-Juniper community. Growing on a wide variety of soils. Southern Wyoming, western Colorado, Utah, Nevada, and southeastern California, south to Arizona and New Mexico. April-July. Fig. 44.

Beaver Co., about 5 miles north of Cove Fort, L.C. Higgins 903 (BRY); Wah Wah Mountains, 4.5 miles up Pine Canyon, B. Maguire 20941 (UTC); Wah Wah Mountains, Pine Grove, W.P. Cottam 8031 (UT); Carbon Co., 5 miles east of Wellington, L.C. Higgins 997 (BRY); near Carbon-Emery county line along hwy 50-6, L.C. Higgins 3324 (BRY); Daggett Co., 2 miles east of Sheep Creek Junction with hwy 44, D. Atwood 1586 (BRY); 15 miles south of Manila, R.C. Rollins 2280 (UTC); Carter Creek, E.E. Jensen s.n. (UTC); Duchesne Co., Indian Canyon, 3.5 miles south of Duchesne, Holmgren, Reveil & LaFrance 1760 (BRY); 27 miles south of Myton, A. Cronquist & Holmgren 9238 (UTC); about 6 miles south of Tabiona, L.C. Higgins 1046 (BRY); about 20 miles south of Myton, L.C. Higgins 1065 (BRY); about 2 miles east of Fruitland, Higgins & Welsh 1020 (BRY); north rim of Nine Mile Creek, Holmgren, Reveil & LaFrance 1950 (BRY, UTC); about 5 miles west of Fruitland, L.C. Higgins 1086 (BRY); about 6 miles west of Duchesne, L.C. Higgins 1049 (BRY); about 2 miles east of Fruitland, L.C. Higgins 1019 (BRY); Red Creek 5 miles north of Fruitland, J. Brotherson 1128 (BRY); Rock Creek, J. Brotherson 965 (BRY); Bluebell, L.C. Higgins 1061 (BRY); Red Creek 3 miles east of Fruitland, L.C. Higgins 1045 (BRY); Emery Co., 10 miles up Huntington

Canyon, B.F. Harrison 8167 (BRY); about 9 miles south of Lawrence, L.M. Pitts 23 (BRY); Grand Co., Arches Natl. Monument, L.B. Barnett 41 (BRY); Iron Co., Kanarrville, W.P. Cottam 5009 (UT); Juab Co., south base of Topaz Mountain, near Thomas Pass, Welsh & Atwood 9667 (BRY); foothills east of Mona, D. Hatch 109 (UTC); Deep Creek Mountains, mouth of Thomas Creek, D.W. Lindsay 206 (UT); Millard Co., Fillmore, D.M. Leidig 237 (UTC); House Range, 44 miles west of Delta, Maguire & Becraft 2755 (UTC); Warm Point, Desert Range Experiment Station, V.B. Matthews 1 (BRY); Warm Point Ridge, F. Coles 6 (BRY); Desert Range Experiment Station, Tunnel Springs, W.P. Cottam 8523 (UT); Pruess Lake, V.B. Matthews 25 (BRY); Rich Co., Stanley Gessell s.n. (UTC); San Juan Co., 10 miles north of Blanding, B. Maguire 13505 (UTC); Natural Bridges Natl. Monument, L.C. Higgins 522 (BRY); head of Gravel Canyon, L.O. Wilson 235 (UTC); 13 miles south of Moab, A. Cronquist 9001 (UTC); 8 miles north of Monticello, B.F. Harrison 5891 (BRY); about 5 miles southwest of Blanding, L.C. Higgins 517 (BRY); Sanpete Co., 0.5 miles north of upper power plant in Ephraim Canyon, T. Jensen s.n. (DIX); Ephraim Canyon, K. Peterson s.n. (DIX); 5 miles east of Ephraim, A.H. Barnum 1259 (DIX); between Ephraim and Great Basin Experiment Station, A.H. Holmgren 7655 (UTC); about 8 miles southeast of Mt. Pleasant, L.C. Higgins 112 (BRY); Sevier Co., Salina Canyon, R. Stevens 33 (BRY); 40 miles north of Fremont, B.F. Harrison 7341 (BRY); 5 miles southeast of Sigurd, B. Maguire 18098 (UTC); Summit Co., 1 mile west of Upton along hwy 133, Welsh & Murdock 6264 (BRY); Tooele Co., Deep Creek Mountains, Johnson Canyon 10 miles southeast of Ibapah, W.P. Cottam 7218 (UT); Stansbury Range, up Willow Creek, B. Maguire 21824 (UTC); Uintah Co., 5 miles northwest of Whiterocks, J. Brotherson 1027 (BRY); between Two Waters Creek

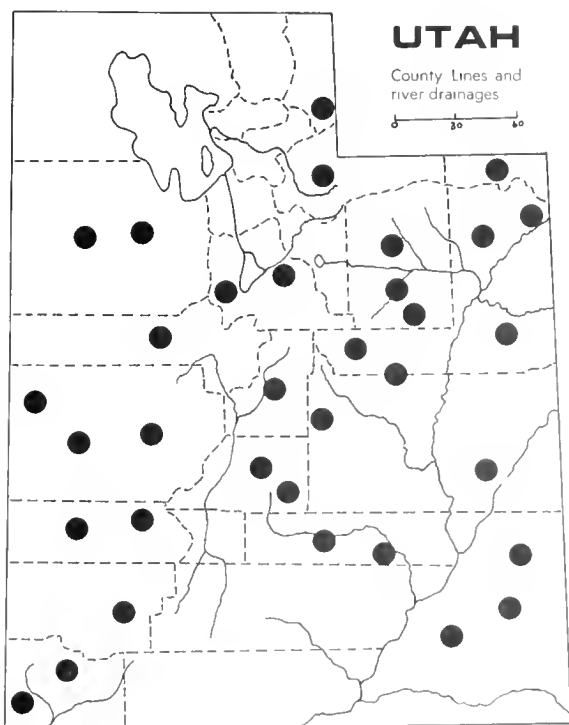


Fig. 44 *Cryptantha flavocolata*

and Willow Creek, Holmgren & Reveal 1857 (BRY, UTC); Seep Canyon, Holmgren & Reveal 1862 (UTC); about 8 miles south of hwy 40 along the road to Bonanza, L.C. Higgins 1083 (BRY); Dinosaur Natl. Monument, S.L. Welsh 92, 92, 155, 272 (BRY); Merkeley Park, Welsh & Moore 1955 (BRY); about 3 miles northwest of Vernal, L.C. Higgins 1072 (BRY); Big Spring, V.A. Murphy 19 (UTC); Utah Co., about 1 mile north of Divide along hwy 50-6, W.R. Buss 61 (BRY); just east of Eureka, J.B. Karen 71a (BRY); Soldier Summit, Holmgren & Boyle 7057 (UTC); Washington Co., Beaverdam Mountains, near summit, L.C. Higgins 557 (BRY); summit of Beaverdam Mountains near television relay tower, L.C. Higgins 3403 (BRY); Wayne Co., Fruita Arch Canyon, B. Maguire 18136 (UTC); 17 miles south of Hanksville, B. Maguire 18170 (UTC).

35. *Cryptantha fulvocanescens* (Wats.) Payson, *Ann. Mo. Bot. Gard.* 14:319. 1927.

Densely caespitose perennials from a strongly lignified taproot, 0.8-3 dm tall; stems many from a multiple caudex, 0.5-1.3 dm long, white hairy at the base, setose-hispid upward; leaves oblanceolate to spatulate, acute to obtuse, 1.5-7 cm long, 0.4-1.2 cm wide, uniformly strigose, pustules mainly confined to the dorsal surface; inflorescence narrow or somewhat open at maturity, 0.3-1.9 dm long, white or yellowish setose, foliar bracts inconspicuous; calyx segments linear, 4-6 mm long in anthesis, in fruit becoming 9-13 mm long, densely white or yellowish setose, pedicels 2-10 mm long; corolla white, the tube 7-11 mm long, crests at base of tube evident or lacking, formices yellow, emarginate or rounded, 0.7-1.3 mm long, limb 7-9 mm broad, nutlets lance-ovate, 3.5-4.5 mm long, 2-3 mm broad, 1 or 2 usually maturing, margins acute to obtuse, in contact when more than 1 nutlet matures, both surfaces densely and uniformly muricate, scar open or nearly closed, elevated margin lacking; style exceeding mature fruit 3-7 mm.

1. Murications on the nutlet rounded; corolla 9-13 mm long; inflorescence narrow, white setose at maturity
35A. var. *fulvocanescens*

1. Murications on the nutlet with 1 or 2 setose projections; corolla 7-9 mm long; inflorescence broader and usually yellowish setose at maturity
35B. var. *echinoides*

35A. *Cryptantha fulvocanescens* (Wats.) Payson, var. *fulvocanescens* Type: near Santa Fe, New Mexico, Fendler 632.

Eritrichium glomeratum var. *fulvocanescens* Wats. *Bot. King Exp.* 243. 1871.

Eritrichium fulvocanescens Gray, *Proc. Amer. Acad.* 10:61. 1875.

Krynitzkia fulvocanescens Gray, *Proc. Amer. Acad.* 20:280. 1885.

Oreocarya fulvocanescens Greene, *Pittonia* 1:58. 1887.

Oreocarya nitida Greene, *Pl. Baker.* 3:21 1901.

Densely caespitose perennial, 1-3 dm tall; inflorescence narrow, white setose; pedicels 2-3 mm long; corolla white, the tube 9-13 mm long, crests at base of tube evident or lacking, formices yellow, rounded to acute; nutlets lanceolate, 3.5-4 mm long, 2-2.5 mm wide, the dorsal surface with rounded murications, scar straight, closed or slightly open. Sandy to sandy clay-loam soils, on open slopes and ridges. Western Colorado, northwestern New Mexico, northeastern Arizona, and southern Utah. April-August. Fig. 45.

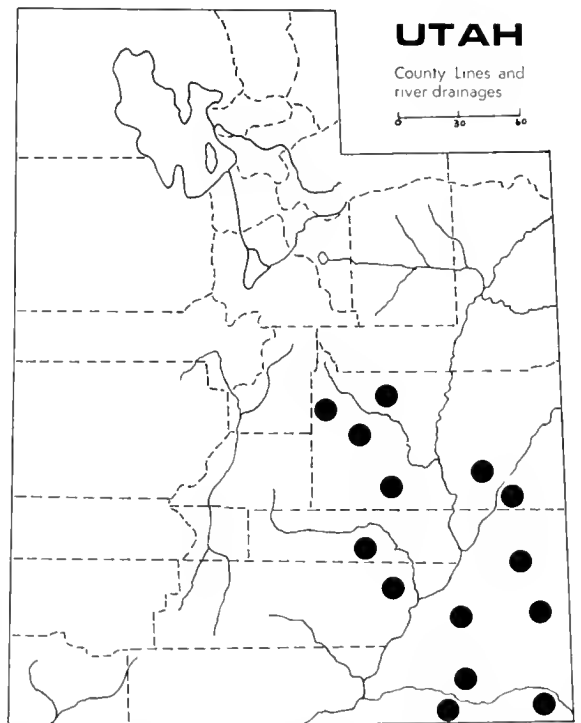


Fig. 45. *Cryptantha fulvocanescens* var. *fulvocanescens*

Emery Co., Mouth of Huntington Canyon, B.F. Harrison 8136 (BRY); about 15 miles west of hwy 50-6 along the road to Huntington, L.C. Higgins 1307 (BRY); Grand Co., about 7 miles south of Moab, L.C. Higgins 999 (BRY); 5 miles south of Moab, B.F. Harrison 10306 (BRY); Arches Natl. Monument, B.F. Harrison 11135 (BRY); Arches Natl. Monument, C.L. Pyrah 48 (BRY); 16 miles northwest of Moab, A. Cronquist 9064 (UTC); Arches Natl. Monument, L.C. Anderson 49 (UTC); San Juan Co., 16 miles east of White Canyon on hwy 95, D.E. Bright 75 (BRY); Squaw Canyon, 1 mile east of Cave Spring, Welsh & Moore 2849 (BRY); 30 miles south of Mexican Hat, J.R. Mordock 308 (BRY); 2 miles west of Bluff, B. Maguire 13530 (UTC); 18 miles southwest of Blanding, A. Cronquist 8949 (UTC); Monument Valley, A.H. Holmgren 3225 (UTC); Wayne Co., 28 miles southeast of Hanksville, A. Cronquist 9181 (UTC); 32 miles east of Fruita, B. Maguire 18156 (UTC).

- 35B. *Cryptantha fulvocanescens* (Wats.) Payson var. *echinoides* (Jones) Higgins, Great Basin Naturalist 29:30. 1969. Type: Pahria Canyon, Kane County, Utah, Jones 5297p. *Krynitzkia echinoides* Jones, Proc. Calif. Acad. Sci. II. 5:709. 1895.
Oreocarya echinoides Macbr. Contr. Gray Herb. 48:31. 1916.
Cryptantha echinoides Payson, Ann. Mo. Bot. Gard. 14:321. 1927.

Caespitose perennials, 0.8-3.6 dm tall; inflorescence narrow to somewhat open at maturity, yellowish setose; pedicels 3-10 mm long; corolla white, the tube 7-9 mm long, crests at base of tube lacking, or sometimes evident, fornicies yellow, emarginate; nutlets lance-ovoid, 4-4.7 mm long, 2.5-3 mm broad, the dorsal surface with 1 or 2 setose projections terminating each murication, scar asymmetrical, and without an elevated margin. Usually growing on heavy clay soils charged with alkali or salts. South central Utah and north central Arizona. April-July. Fig. 46.

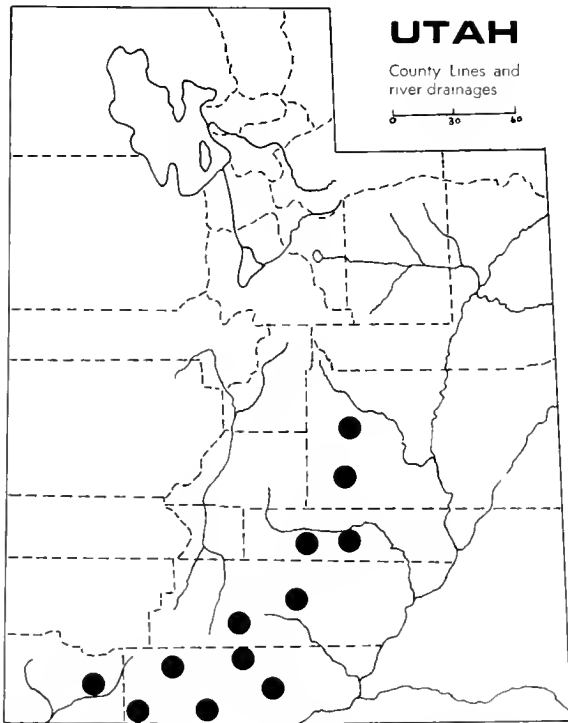


Fig. 46. *Cryptantha fulvocanescens* var. *echinoides*:

Emery Co., near Cedar Mountain, about 39 miles west of Green River along road to Castle Dale, A. Cronquist 9096 (UTC); 50 miles south of San Raphael River, B.F. Harrison 9626 (BRY); Garfield Co., west side of Henry Mountains, B.F. Harrison 11695 (BRY); Kane Co., 5 miles from Mount Carmel, Eastwood & Howell 9265 (UTC); Cottonwood Canyon, 20 miles south of Cannonville, L.C. Higgins 1008 (BRY); 20 miles east

of Kanab, D. Atwood 1792 (BRY); 3.7 miles east of Skutumpah-Alton Junction at head of Johnson Canyon, D. Atwood 1802 (BRY); Washington Co., west entrance to Zion Natl. Park, H.A. Ganning 2288 (ARIZ); Wayne Co., 1 mile east of Bicknell, A. Cronquist 9171 (UTC); 9 miles east of Torrey, B. Maguire 18111 (UTC); about 2 miles west of River Bridge, at junction of Buckhorn Wash and San Raphael River, Welsh & Atwood 9904 (BRY); about 5 miles east of Torrey, L.C. Higgins 1344 (BRY).

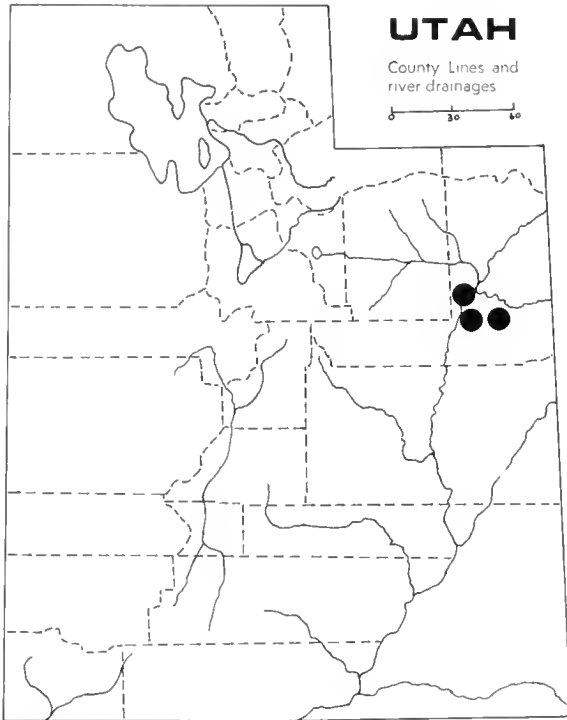
36. *Cryptantha grahamii* Johnst. Journ. Arn. Arb. 20:391. 1939. Type: Bench west of Green River north of mouth of Sand Wash, Uintah County, Utah, Graham 7924.

Long-lived perennial from a thick woody taproot, 1.5-2.5 dm tall; stems several, 0.4-1.2 dm long, weakly spreading setose; leaves spatulate to oblanceolate, 2-4.5 cm long, 0.4-1 cm wide, conspicuously setose pustulate on both surfaces, with some finer pubescence beneath; inflorescence narrow, 0.4-1 dm long setose, foliar bracts evident but not conspicuous; calyx segments lanceolate, in anthesis 5-7 mm long, in fruit becoming 7-9 mm long, very setose; corolla white, the tube 3.5-5 mm long, constricted at the middle, crests at base of tube evident, fornicies yellow, emarginate, papillose, 0.5-1 mm long, limb 11-15 mm wide; nutlets lanceolate, 3-3.8 mm long, 1.7-2 mm wide, 2-4 maturing, margins in contact, acute, both surfaces of nut with inconspicuous, small, low-rounded tubercles, or some of these confluent into short irregular ridges, scar straight, open, narrowly linear, the margin not elevated; style coarse, exceeding mature fruit 1.8-2.2 mm. Found growing only on Green River Shale. Endemic to the Uintah Basin, Uintah County, Utah. May-June. Fig. 47.

Uintah Co., Sunday School Canyon of Willow Creek drainage, Holmgren & Reveal 1879 (BRY, UTC); Willow Creek, R.C. Rollins 1707 (UTC); 30 miles south of Ouray along the Hill Creek Road, Higgins & Atwood 1878 (BRY); Buck Canyon along the Watson-Ouray Road, Higgins & Atwood 1885 (BRY); along Willow Creek 5 miles north of the mouth of Agency Draw, L.C. Higgins 1608 (BRY); 35 miles south of Ouray along the Hill Creek Road, Higgins & Atwood 1881 (BRY); about 18 miles south of Ouray along the Hill Creek Road, Higgins & Atwood 1876 (BRY).

37. *Cryptantha humilis* (Gray) Payson, Ann. Mo. Bot. Gard. 14:278. 1927.

Perennials, more or less densely caespitose, 0.5-3 dm tall; stems many, arising from the ends of the branched caudex, 0.2-1.5 dm long, strigose to spreading setose; leaves oblanceolate to spatulate, 1-6 cm long, 0.2-1.2 cm wide, strigose, setose or subtomentose, pustulate on both surfaces; inflorescence narrowly cylindrical to open and lax, 0.2-1.8 dm long, tomentose to conspicuously

Fig. 47. *Cryptantha grahamii*

setose; calyx segments linear-lanceolate, in anthesis 2.5-4.5 mm long, in fruit becoming 6-13 mm long, setose or tomentose; corolla white, the tube 2.5-4.5 mm long, crests at base of tube conspicuous to nearly obsolete, fornicies yellow, more or less papillose, rounded, about 0.5 mm long, limb 7-10 mm wide; nutlets lanceolate to ovate-lanceolate, 3-4.5 mm long, 1.8-3.2 mm wide, 1 to 4 of them maturing, margins in contact, acute to somewhat obtuse, dorsal surface muricate, tuberculate, or somewhat rugulose, ventral surface indistinctly muricate or tuberculate, scar open, triangular, margin not elevated; style from shorter than to longer than the mature fruit by 2.5 mm.

1. Leaves strigose and setose but not conspicuously tomentose; calyx evidently setose (2).
1. Leaves densely strigose as well as tomentose; calyx setose and subtomentose (3).
2. Style exceeding the mature nutlets 1-1.5 mm; the inflorescence open and broad; plants loosely tufted
37A. var. *commixta*
2. Style not or only slightly surpassing the nutlets; inflorescence congested, even in fruit; plants densely caespitose
37B. var. *nana*
3. Style scarcely exceeding the mature nutlets; inflorescence somewhat open at maturity
37C. var. *shantzii*
3. Style exceeding the mature fruit 0.5-1.5 mm; inflorescence cylindrical and congested in fruit
37D. var. *ovina*

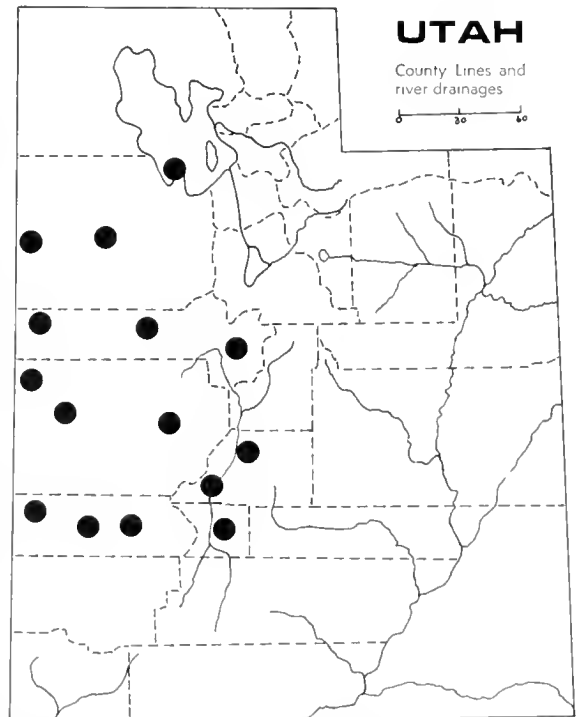
37A. *Cryptantha humilis* (Gray) Payson, var. *commixta* (Macbr.) Higgins, Brigham Young Univ. Sci. Bull. Vol. 13, No. 4:36. 1971 Type: Juab, Juab County, Utah Goodding 1074.

Oreocarya commixta Macbr. Contr. Gray Herb. 48:33. 1916.

Cryptantha nana var. *commixta* Payson, Ann. Mo. Bot. Gard. 14:312. 1927.

Caespitose perennials, 1-2.7 dm tall; stems 1-several, arising from the ends of the branched caudex, 0.3-1 dm long, weakly strigose and spreading setose; leaves spatulate to broadly oblanceolate, 2.5-6 cm long, 0.5-1.2 cm wide, strigose and spreading setose; inflorescence open, 0.8-1.8 dm long, foliar bracts evident on lower part of stem; calyx segments linear-lanceolate, in anthesis 3.5-4.5 mm long, in fruit becoming 7-10 mm long, setose; nutlets lance-ovate, 3.5-4 mm long, muricate, tuberculate, or sometimes with the murications joined to form short irregular ridges, scar subulate or nearly closed; style exceeding mature fruit 0.7-1.6 mm. Usually growing on gravelly soil or talus slopes in the Pinyon-Juniper community, Central Utah to eastern Nevada. May-July. Fig. 48.

Beaver Co., Summit of Wah Wah Mountains along hwy 21, L.C. Higgins 1617 1468 (BRY); Juab Co., Juab, Goodding 1074 (RM); Millard Co., Ca. 70 miles west

Fig. 48. *Cryptantha humilis* var. *commixta*

of Delta, L.C. Higgins 1612 (BRY); Pavant Butte, 17 miles northwest of Fillmore, Cottam & McMillan 9592 (UT); Piute Co., Marysvale, M.E. Jones 5388 (UT); 6 miles east of Kingston along hwy 62, L.C. Higgins 1618 (BRY); Sevier Co., near the Big Rock Candy Mountain, L.C. Higgins 1620 (BRY); Tooele Co., Stansbury Island, G. Saccomanno 7680 (UT).

37B. *Cryptantha humilis* (Gray) Payson, var. *nana* (Eastw.) Higgins, Brigham Young Univ. Sci. Bull. Vol. 13, No. 4:37. 1971. Type: near Grand Junction, Colorado, Eastwood s.n. 1892.

Oreocarya nana Eastw. Bull. Torrey Club 30:243. 1903.

Cryptantha nana (Eastw.) Payson, var. *typica*, Ann. Mo. Bot. Gard. 14:315. 1927.

Caespitose perennial, 0.5-1.5 dm tall; stems several, 0.2-0.7 dm long, setose; leaves oblanceolate to spatulate, 0.5-4 cm long, 0.2-0.6 cm wide, strigose to subtomentose, spreading setose; inflorescence narrow, cylindrical, 0.2-1 dm long, setose; calyx segments linear-lanceolate, in anthesis 2.5-3.5 mm long, in fruit becoming 6-8 mm long, setose; corolla white, the tube 2.5-3.5 mm long, crests at base of tube evident; nutlets muricate or sometimes tuberculate or rugulose; style shorter to slightly longer than mature fruit. Growing mostly in heavy clay soils but occasionally on sandy-loam soil. Western Colorado and eastern Utah. April-July. Fig. 49.

Duchesne Co., west of Duchesne, Ripley & Barneby 4675 (CAS); north of Duchesne, G.E. Osterhout 6200 (RM); Summit Co., Echo Canyon, G.E. Osterhout 6231 (RM); San Juan Co., 13 miles south of Moab, A. Cronquist 9108 (NY); Uintah Co., 1 mile west of Red Pine, Book Cliffs, L.C. Higgins 1598 (BRY).

37C. *Cryptantha humilis* (Gray) Payson, var. *shantzii* (Tidest.) Higgins, Brigham Young University Sci. Bull. Vol. 13, No. 4. pp. 37. 1971. Type: Grant's station south of the Great Salt Lake, Kearney & Shantz 3098.

Oreocarya shantzii Tidestr. Proc. Biol. Soc. Wash. 26:122. 1913.

Oreocarya dolosa Macbr. Contr. Gray Herb. 48:32. 1916.

Cryptantha nana var. *shantzii* Payson, Ann. Mo. Bot. Gard. 14:313. 1927.

Caespitose perennial, 1-2 dm tall; stems 1-many from the ends of the much-branched caudex, 0.3-1 dm long, weakly setose and strigose; leaves spatulate to oblanceolate, obtuse, 2-5 cm long, 0.3-0.7 cm wide, tomentose and appressed setose, with slender more or less appressed bristles; inflorescence usually narrow, but the

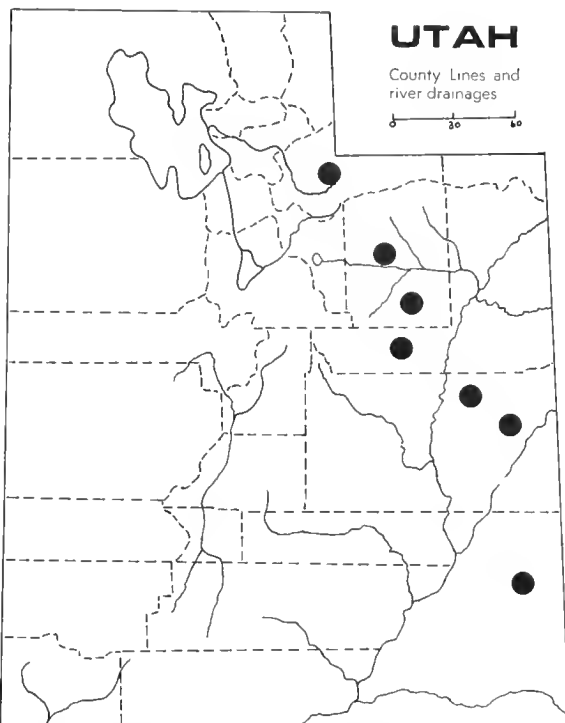


Fig. 49. *Cryptantha humilis* var. *nana*

cymules slightly elongating, lower foliar bracts rather conspicuous in the young inflorescence; calyx segments densely setose and subtomentose; style scarcely exceeding the nature, muricate nutlets. Open, sandy to gravelly slopes and ridges. Southwestern Montana, eastern Idaho, and northern Utah. April-July. Fig. 50.

Box Elder Co., Kelton Pass, Maguire & Holmgren 26247 (UTC); Raft River Mountains, S.J. Preece 889 (UT); Cache Co., Providence Canyon, B. Maguire 12952 (UTC); College Bench, B. Maguire 3700 (UTC); College Bench, L.C. Higgins 1087 (BRY); Logan River Bench, W.C. Muenscher 2415 (UTC); Davis Co., Mueller Park, K. Brizzee 7876 (UT); Salt Lake Co., City Creek Canyon, s.n. (UT); Bonneville Terrace, S. Flowers 444 (UT); City Creek, M.E. Jones s.n. (RM); Dry Fork Canyon, P.C. Farnsworth s.n. (UT); Utah Co., west side of Mount Timpanogos, R. Goutley 8086 (UT).

37D. *Cryptantha humilis* (Gray) Payson, var. *ovina* (Payson) Higgins, Brigham Young University Sci. Bull. Vol. 13, No. 4:37. 1971. Type: Vicinity of Current, Nye County, Nevada, G. H. Bentley s.n.

Cryptantha nana (Eastw.) Payson, var. *ovina* Payson, Ann. Mo. Bot. Gard. 14:314. 1927.

Densely caespitose long-lived perennials, 0.5-1.5 dm tall; stems several, 0.2-0.7 dm long; leaves spatulate to oblanceolate, obtuse, 2-4 cm

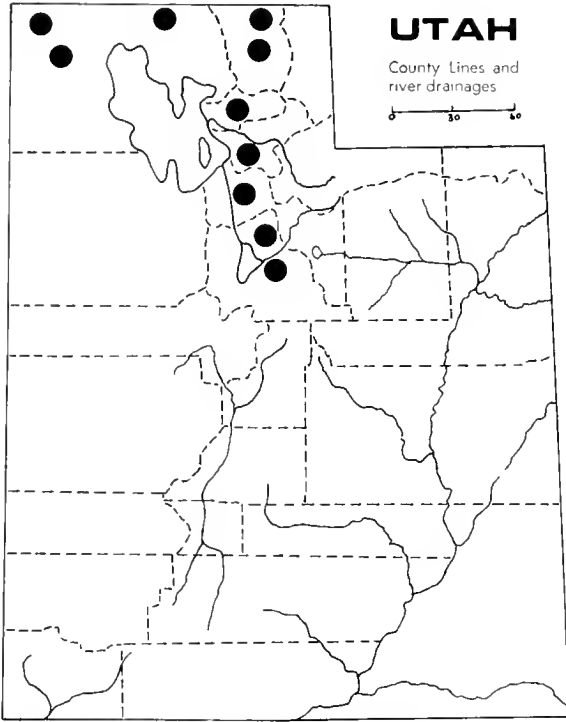


Fig. 50. *Cryptantha humilis* var. *shantzii*

long, tomentose and appressed setose with rather weak bristles; inflorescence narrow, cylindrical, lower foliar bracts inconspicuous; calyx segments linear-lanceolate, densely setose and tomentose; style exceeding the mature fruit 0.5-1 mm. Growing on gravelly loam to clay soils, in the Pinyon-Juniper community. Southwestern Utah, southern Nevada, and southeastern California. April-July. Fig. 51.

Only a few of the several hundred specimens of the various varieties of *C. humilis* have been cited in this paper for two reasons: (1) most collections are so immature that it is almost impossible to assign them to a particular variety; (2) in order to conserve space in the paper. Future collections of *Cryptantha* would be much more adequate if fruiting plants rather than flowering specimens were collected, particularly with members of this species.

Washington Co., Beaverdam Mountains, L.C. Higgins 1234 (BRY); summit of the Beaverdam Mountains, L.C. Higgins 1409 (BRY).

35. *Cryptantha jamesii* (Torr.) Payson, *Ann. Mo. Bot. Gard.* 14:242, 1927.

Perennials, 1-6 dm tall; stems 1-many, 0.4-4 dm long, glabrous to conspicuously hirsute; leaves linear to broadly oblanceolate, obtuse to acute, 2-15 cm long, 0.2-1.5 cm wide, glabrous

to hirsute, usually pustulate dorsally, ventral surface lacking pustules or the pustules very inconspicuous; inflorescence open, cymules usually elongating, tomentose to setose-hirsute, floral bracts inconspicuous to very conspicuous; calyx segments ovate-lanceolate, acute, in anthesis 3-4 mm long, in fruit 5-7 mm long, subtomentose to setose-hirsute; pedicels 1-3 mm long; corolla white, the tube 2.5-3 mm long, crests at base of tube conspicuous, fornicee light yellow, emarginate, 0.5-1 mm long, limb 5-8 mm broad; fruit oblate=ovoid, 1-4 nutlets maturing, ovate-lanceolate, margins acute, 2-2.5 mm long, 1.5-2 mm wide, the margins not in contact, both surfaces smooth and glossy, scar straight, closed, extending from the base to near the apex; style exceeding mature fruit 1-3 mm.

1. Ventral surface of the leaves glabrous, the petioles not ciliate-margined, nor the leaves tufted at the base 38A. var. *pustulosa*
1. Ventral surface of the leaves strigose or setose, the petioles ciliate-margined; leaves tufted at the base (2).
2. Stems simple, not branched above the base (3).
2. Stems branched from the base as well as above 38B. var. *disticha*
3. Stems 1-4.4 dm long, usually twice as long as the basal tuft of leaves 38C. var. *multicaulis*
3. Stems 0.2-0.9 dm long, usually not exceeding the basal tuft of leaves 38D. var. *setosa*

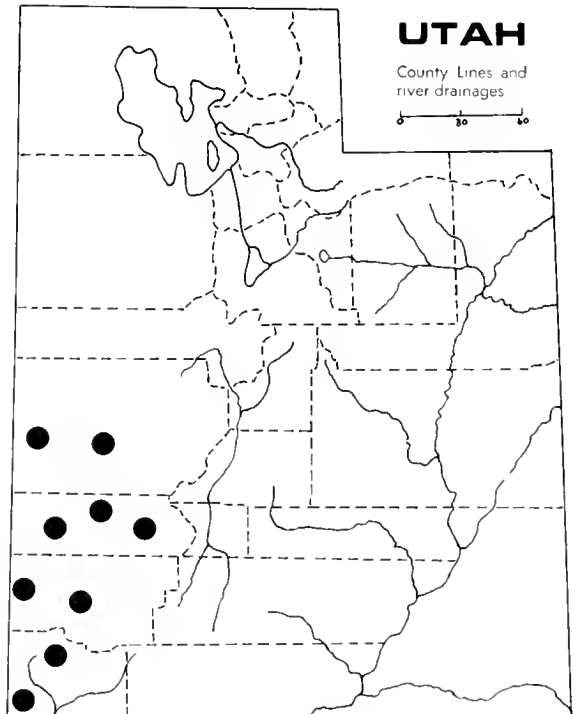


Fig. 51. *Cryptantha humilis* var. *ovina*

38A. *Cryptantha jamesii* (Torr.) Payson, var. *pustulosa* (Rydb.) Harringt. Man. P. Colo. 466, 641. 1954. Type: San Juan County, Utah.

Oreocarya pustulosa Rydb. Bull. Torrey Club 40:480. 1913.

Cryptantha pustulosa (Rydb.) Payson, Ann. Mo. Bot. Gard. 14:252. 1927.

Erect perennials, 2-5.8 dm tall, branched from the base, simple above; stems slender, 1-3.9 dm long, glabrous or finely strigose; leaves linear to broadly oblanceolate, 2-9 cm long, 0.4-1.5 cm wide, the dorsal surface appressed setose-pustulate, ventral surface glabrous, the petioles not ciliate-margined; inflorescence open, 0.4-2 dm long, floral bracts inconspicuous. Sandy to gravelly soils, mainly in the Pinyon-Juniper community. Southwestern Colorado, northwestern New Mexico, northeastern Arizona, and southeastern Utah. May-August. Fig. 52.

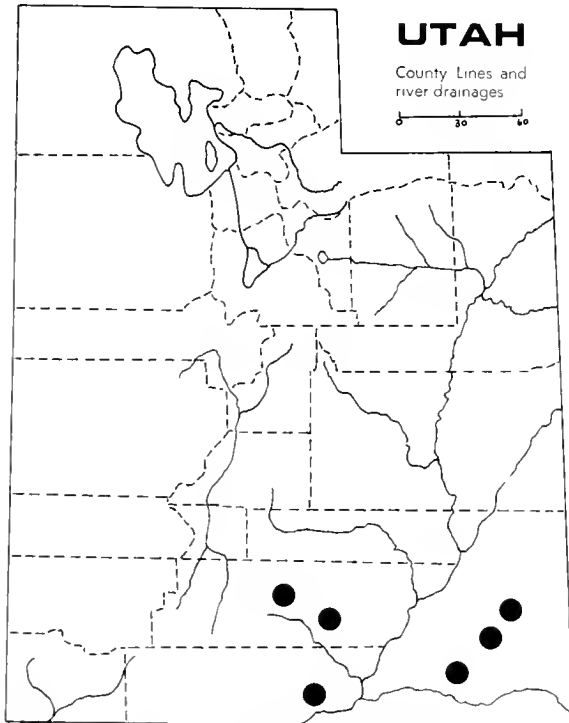


Fig. 52. *Cryptantha jamesii* var. *pustulosa*

Garfield Co., King Ranch, Boulder, Utah, Beck & Tanner 8204 (BRY); about 4 miles south of Boulder, D. Atwood 1864 (BRY); Kane Co., Mokie Tanks, DE. Beck s.n. (BRY); San Juan Co., east slope of Elk Ridge, Maguire & Redd 2065 (UTC); between Blanding and Kigalia Ranger Station, A.H. Holmgren 3489 (BRY); 10 miles west of Blanding, D. Henriques H-9 (UT); Hammond Canyon, Elk Mountains, Rydberg & Garrett 9569 (UT); Arch Canyon, 18 miles west of Blanding, Cronquist & Holmgren 9372 (UTC); bottom of

Comb Wash about 20 miles west of Blanding along hwy 95, Welsh, Atwood & Higgins 8933 (BRY).

38B. *Cryptantha jamesii* (Torr.) Payson, var. *disticha* (Eastw.) Payson, Ann. Mo. Bot. Gard. 14:248. 1927. Type: Bartons Range, San Juan County, Utah, Alice Eastwood 90.

Oreocarya disticha Eastw. Bull. Torrey Club 30:238. 1903.

Erect perennials, branched from the base as well as above, 2.5-4.2 dm tall; stems somewhat woody near the base, 1.2-2.9 dm long, strigose and weakly setose; leaves narrowly oblanceolate, 3-12 cm long, dorsal surface setose-pustulate and strigose, ventral surface strigose to setose or silky-strigose, without pustulate hairs or the pustules inconspicuous, the petioles ciliate-margined; inflorescence open, 0.5-2 dm long, foliar bracts not very conspicuous. Southwestern Colorado, northeastern Arizona, northwestern New Mexico, and southeastern Utah. Usually found growing on sandy soils. April-September. Fig. 53.

Emery Co., 4 miles up Calf Spring Wash, San Raphael Swell, B. Maguire 18446 (UTC); first fork of Calf Spring Canyon, San Raphael Swell, B. Maguire 18298 (UTC); Buckhorn Wash, B.F. Harrison 9643 (BRY); junction of Buckhorn Wash and San Raphael River, Welsh & Atwood 9829 (BRY); Garfield Co., 5 miles south of Boulder, L.C. Higgins 1011 (BRY); 4

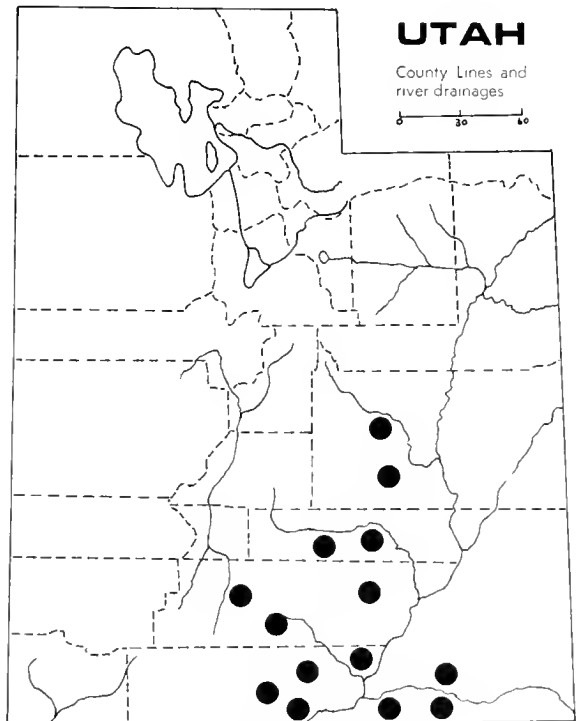


Fig. 53. *Cryptantha jamesii* var. *disticha*

miles south of Henrieville, L.C. Higgins 1010 (BRY); 16 miles west of Bryce Canyon Natl. Park, R.C. Rollins 2449 (UTC); 5 miles east of Escalante, A.H. Holmgren 7716 (UTC); 10 miles east of Escalante, A.H. Holmgren 7748 (UTC); Kane Co., 3.7 miles east of Skutumpah-Alton junction at head of Johnson Canyon, D. Atwood 1804 (BRY); about 7 miles east of Skutumpah-Alton junction, D. Atwood 1807 (BRY); one half mile west of Paria River bridge along hwy 89, Welsh & Atwood 9748 (BRY); 47 miles east of Kanab, B.F. Harrison 12092 (BRY); San Juan Co., bottom of Comb Wash along hwy 47 west of Bluff, Welsh & Atwood 9970 (BRY); Monument Valley, Eastwood & Howell 6674 (UTC); near summit of Navajo Mt., A.H. Holmgren 10661 (UTC); Mexican Hat, B. Maguire 16291 (UTC); Monument Valley, A.H. Holmgren 3243 (BRY, UTC); 10 miles west of Bluff, C.A. Hanson 87 (BRY); mesa north of Bluff, B. Maguire 5101 (UTC); head of Cow Canyon, 2 miles north of Bluff, A.H. Holmgren 3213 (UTC); Wayne Co., junction of road to Ekkers Ranch, Welsh & Atwood 9859 (BRY); 3 miles north of Grover, D. Atwood 1862 (BRY); 3 miles southeast of Torrey, Holmgren, Reveal & LaFrance 1091 (BRY, UTC); about 2 miles south of Lyman, L.C. Higgins 1014 (BRY); 5 miles east of Teasdale, Holmgren, Reveal & LaFrance 2551 (BRY).

38C. *Cryptantha jamesii* (Torr.) Payson, var. *multicaulis* (Torr.) Payson, Ann. Mo. Bot. Gard. 14:244. 1927. Type: New Mexico near Santa Fe, Fendler 636.

Eritrichium multicaule Torr. in Marcy, Expl. Red River 262. 1854.

Oreocarya multicaulis (Torr.) Greene, Pittonia 3:114. 1896.

Oreocarya suffruticosa (Torr.) Payson, var. *multicaulis* (Torr.) Payson, Univ. Wyo. Publ. Bot. 1:171. 1926.

Hemisphaerocarya suffruticosa (Torr.) Brand, var. *multicaulis* (Torr.) Brand, Rep. Spec. Nov. 24:60. 1927.

Perennial, 2-5.5 dm tall, branched from the base, simple above; stems slender, 1-4.4 dm long, weakly strigose-setose; leaves mostly basal, oblanceolate, 5-15 cm long, 0.4-1 cm wide, dorsal surface strigose and appressed setose, or sometimes setose-hirsute, pustulate, ventral surface uniformly strigose or subtomentose, without pustules, or the pustules small and inconspicuous, the petioles conspicuously ciliate on the margins; inflorescence open, 0.5-1.5 dm long, bracts inconspicuous. Growing on a wide variety of soils, but mainly in sands in Utah. Southern Colorado and eastern New Mexico, south to western Oklahoma and Texas into northern Mexico, and north through central Arizona to southern Utah. April-September. Fig. 54.

Garfield Co., canyon above Tropic, M.E. Jones 5300 (US); Kane Co., 4 miles north of Kanab, Ripley & Barneby 4851 (GH); plateau near head of Rock Creek, B.F. Harrison 9040 (BRY); on slopes southeast of dunes, Knudsen 44 (BRY); Coral Pink Sand Dunes,

S.L. Welsh 5299 (BRY); 23 miles south of Alton, A. Cronquist 10191 (UTC); Johnson Canyon, D. Atwood 1789C (BRY); Washington Co., Zion Canyon Natl. Park, east tunnel road, W.P. Cottam 4763 (BRY); Zion Natl. Park, Clear Creek Canyon, Eastwood & Howell 9219 (GH).

38D. *Cryptantha jamesii* (Torr.) Payson, var. *setosa* (Jones) Johnst. ex Tidest. Proc. Biol. Soc. Wash. 48:42. 1935. Type: Cove Fort, Utah, Jones s.n.

Oreocarya cinerea Greene, Pittonia 3:113. 1896.

Krynitzkia multicaulis var. *setosa* Jones, Contr. West. Bot. 13:4. 1910.

Oreocarya lemmoni Eastw. Bull. Torrey Club 30:239. 1903.

Oreocarya multicaulis var. *cinerea* (Greene) Macbr. Proc. Amer. Acad. 51:54. 1916.

Oreocarya suffruticosa var. *cinerea* (Greene) Payson, Univ. Wyo. Publ. Bot. 1:171. 1926.

Hemisphaerocarya suffruticosa var. *setosa* (Jones) Brand, Rep. Spec. Nov. 24:60. 1927.

Hemisphaerocarya cinerea (Greene) Brand, Rep. Spec. Nov. 24:61. 1927.

Cryptantha jamesii var. *cinerea* (Greene) Payson, Ann. Mo. Bot. Gard. 14:246. 1927.

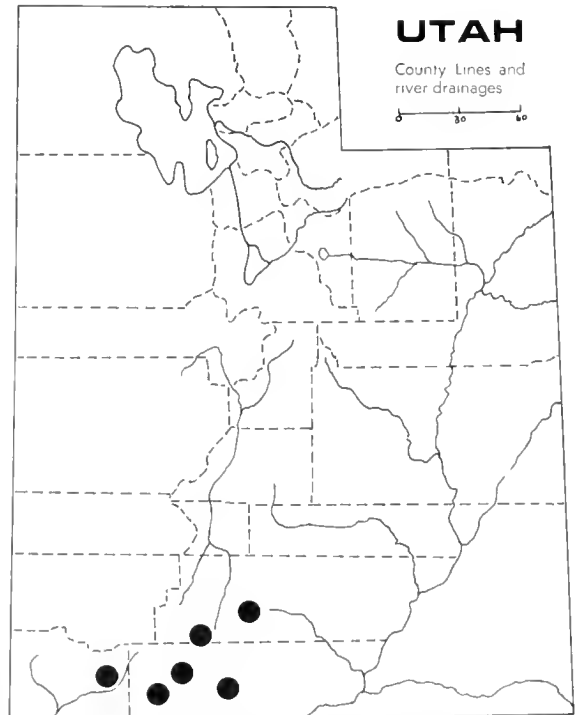


Fig. 54. *Cryptantha jamesii* var. *multicaulis*

Perennial, 1-3 dm tall, branched from the base, simple above; stems slender, 0.2-0.9 dm long, strigose and weakly setose; leaves mostly basal, oblanceolate, obtuse, 3.5-13 cm long, 0.4-1.5 cm wide, dorsal surface finely strigose, usually conspicuously pustulate, ventral surface uniformly and densely strigose, the petioles conspicuously ciliate on the margins; inflorescence open, 0.4-2 dm long, bracts evident, especially near the base of the inflorescence. Growing on a wide variety of soils, especially in the Piñon-Juniper community. South central Colorado, northern New Mexico, northern Arizona, eastern Nevada, and southern Utah. May-September. Fig. 55.

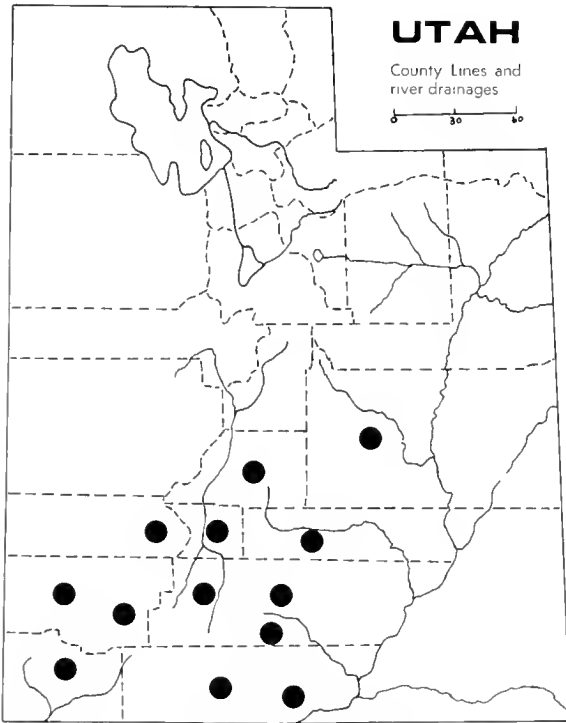


Fig. 55. *Cryptantha jamesi* var. *setosa*

Emery Co., about 10 miles south of the San Raphael River bridge, San Raphael Swell, L.C. Higgins 1321 (BRY); Garfield Co., near milepost 41 south of Circleville, L.C. Higgins 1352 (BRY); head of Red Canyon, B. Maguire 19053 (UTC); 5 miles south of Panguitch, B. Maguire 18706 (UTC); Iron Co., Beryl Desert, C. Lambert 34L (BRY, UT); Kane Co., 20 miles east of Kanab, D. Atwood 1792A (BRY); 4 miles south of Cannonville, A. Cronquist 10213 (UTC); 24 miles west of Collets Wash, D. Atwood 1873A (BRY); about 32 miles southeast of Kanab, D. Atwood 1535 (BRY); Cottonwood Canyon, 20 miles south of Cannonville, L.C. Higgins 1009 (BRY); Sevier Co., Fish Creek Canyon, A.O. Garrett 2557 (UT); Washington Co., Mountain Meadows, W.P. Cottam 3351 (BRY); Mountain Meadows, W.P. Cottam 6770 (UT); Wayne Co., 7 miles southeast of Teasdale, B.F. Harrison 7529 (BRY); 1

mile west of Bicknell, R.K. Vickery 604 (UT); 1 mile southeast of Torrey, L.C. Higgins 1345 (BRY).

39. *Cryptantha johnstonii* Higgins, Great Basin Naturalist 28:195. 1968. Type: About 15 miles west of hwy 50-6 along the road from Woodside to Huntington, Emery County, Utah, L.C. Higgins 1310.

Caespitose perennial 1-2.5 dm tall; stems several, arising from the branched caudex, 0.6-1.3 dm long, very weakly strigose; leaves oblanceolate, the apices obtuse to acute, 2-6.5 cm long, 0.4-1 cm wide, dorsal surface strigose with conspicuous pustulate hairs; inflorescence somewhat open, 0.5-2 dm long; floral bracts evident but not conspicuous, 1-2 cm long; calyx segments linear-lanceolate, in anthesis 5-6 mm long, in fruit becoming 8-10 mm long, strigose and spreading white-setose; pedicels 0.5-1 mm long; corolla white, the tube 12-15 mm long, flaring in the throat, crests at base of tube lacking, fimbriae yellow, 1-1.5 mm long, emarginate, papillose, limb 13-17 mm broad; nutlets ovate, 3-3.5 mm long, 2.3-2.7 mm wide, usually all 4 maturing, margins acute and knifelike, in contact, both surfaces smooth and glossy, scar straight, closed, elevated margin lacking; style exceeding mature fruit 3-8 mm (heterostyled). Growing in clay or clay-loam soils. Known only from the type locality near the head of Cottonwood Wash on the San Raphael Swell. May-June. Fig. 56.

Emery Co., about 15 miles west of hwy 50-6 along the road from Woodside to Castle Dale, L.C. Higgins 1310 (BRY); San Raphael Swell, B.F. Harrison 5628 (BRY); about 6 miles down Cottonwood Wash, L.C. Higgins 3522 (BRY); San Raphael Swell, at the north end of Cottonwood Wash, L.C. Higgins 3520 (BRY, WTSU).

40. *Cryptantha jonesiana* (Payson) Payson, Ann. Mo. Bot. Gard. 14:323. 1927. Type: San Raphael Swell, Emery County, Utah, M. E. Jones s.n.

Oreocarya jonesiana Payson, Univ. Wyo. Publ. Bot. 1:168. 1926.

Coarse caespitose perennials, 0.5-1.5 dm tall; stems many, arising from a thick woody multiple caudex, 0.2-0.7 dm long, setose; leaves spatulate, 1-4 cm long, 0.4-1.3 cm wide, coarsely appressed setose-pustulate, leaf bases also setose with dense white hairs; inflorescence narrow, somewhat capitate, with 1-3 flowers in the axils of the bracts below the terminal cluster; calyx segments lanceolate to nearly linear, in anthesis 5-7 mm long, in fruit becoming 7-10 mm long, densely setose, with ascending yellowish bristles; corolla white, the tube 10-15 mm long, campanu-

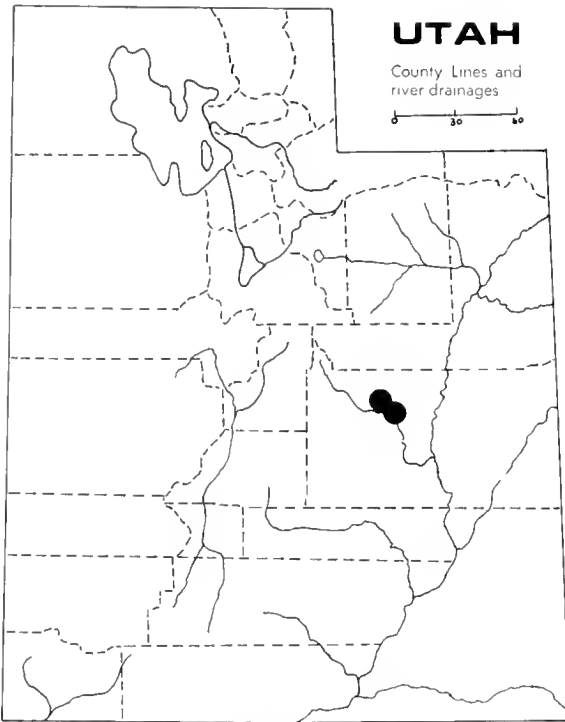


Fig. 56. *Cryptantha johnstonii*

late in the throat, fornicies low and broad, papillose, crests at base of tube lacking, limb 9-13 mm wide; nutlets lanceolate, 3.5-4.5 mm long, densely and uniformly muriculate, or with a few short, low ridges, scar narrow, open, and without an elevated margin; style exceeding mature fruit 4-6 mm. Barren clay hills. Endemic to the San Raphael Swell, Emery County, Utah. April-May. Fig. 57.

Emery Co., San Raphael Swell, W.P. Cottam 5247 (UT); about 10 miles south of the San Raphael River bridge, San Raphael Swell, L.C. Higgins 1322 (BRY); about 15 miles west of hwy 50-6 along the road from Woodside to Castle Dale, L.C. Higgins 1308 (BRY); San Raphael Swell, about 1 mile south of river bridge, Higgins & Reveal 1265 (BRY); San Raphael Swell, D. Atwood 1301 (BRY).

41. *Cryptantha longiflora* (A. Nels.) Payson, Ann. Mo. Bot. Gard. 14:326. 1927. Type: Palisades, Mesa County, Colorado, C. S. Crandall s.n.

Oreocarya longiflora A. Nels. Erythea 7:67. 1899.

Oreocarya horridula Greene, Pl. Baker. 3:20. 1901.

Short-lived perennial or possibly biennials, 0.5-3 (5) dm tall; stems 1-several, 0.5-1 dm long, setose and spreading hirsute; leaves spatulate, obovate or oblanceolate, 2-7 cm long, 0.5-1.5

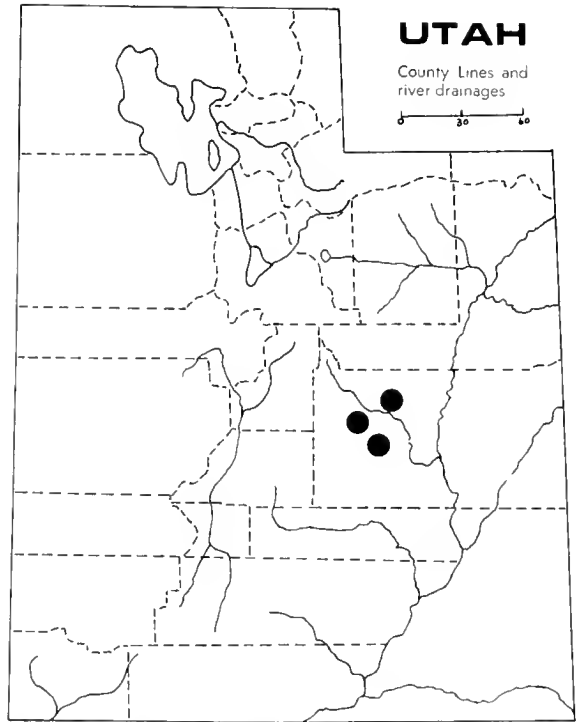


Fig. 57. *Cryptantha jonesiana*

em wide, both surfaces strigose and strongly hirsute, pustulate; inflorescence broad and open, 0.7-2.5 dm long, setose, foliar bracts inconspicuous; calyx segments linear-lanceolate, in anthesis 7-10 mm long, in fruit becoming 10-16 mm long, setose; corolla white, the tube 12-14 mm long, crests at base of tube lacking, fornicies yellow, emarginate, broad, rounded, papillose, 0.5-1 mm long, limb 9-11 mm wide; style exceeding mature fruit 4-9 mm (heterostyled); nutlets lanceolate-ovate 3-4 mm long, 2.2-2.6 mm wide, 2-4 maturing, both surfaces with tubercles and low rounded ridges, scar straight, closed or very narrowly open, with a slightly elevated margin. Sandy to clayey open ridges and flats. Western Colorado and eastern Utah along the Colorado River drainage. May-June. Fig. 58.

Grand Co., bluffs along the Colorado River, about 10 miles south of U.S. hwy 50-6 along hwy 24, S.L. Welsh 6966 (BRY); Morrison Formation along the Colorado River about 32.5 miles from Moab, S.L. Welsh 6989 (BRY); near Cisco, L.C. Higgins 3314 (BRY); near milepost 32 along hwy 128, L.C. Higgins 1478 (BRY).

42. *Cryptantha mensana* (Jones) Payson, Ann. Mo. Bot. Gard. 14:333. 1927. Type: Emery County, Utah. M. E. Jones 5445p.

Oreocarya mensana (Jones) Payson, Univ. Wyo. Publ. Bot. 1:171. 1926.

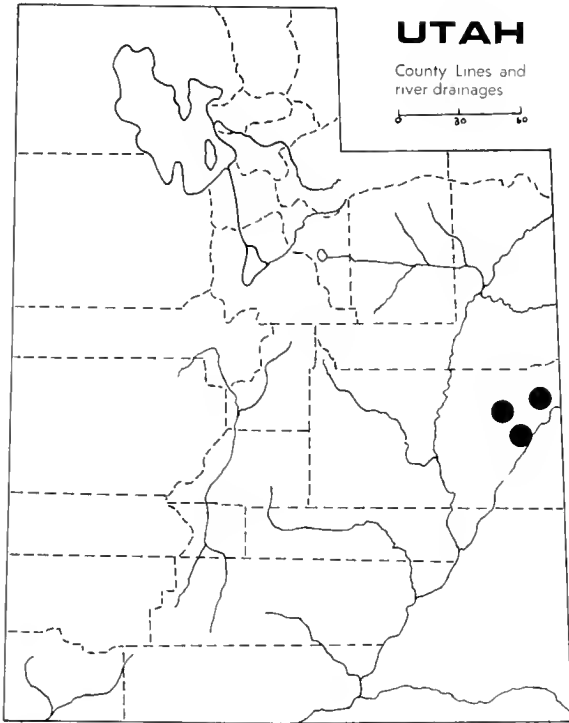


Fig. 58. *Cryptantha longiflora*

Krynitzkia mensana Jones, Contr. West. Bot. 13:4. 1910.

Short-lived perennials, 1-1.5 (2) dm tall; stems 1-several, 0.5-1.2 dm long, setose-hirsute, with some finer strigose hairs beneath; leaves oblanceolate to spatulate, obtuse, 3-8 cm long, 0.5-1.4 cm wide, lower surface setose with pustulate hairs, also finely strigose, ventral surface strigose, less setose and with fewer pustules; inflorescence broad, open, 0.4-1.2 dm long, setose, foliar bracts well developed; calyx segments lanceolate, in anthesis 4-5 mm long, in fruit becoming 7-8 mm long, setose-hirsute; corolla white, the tube 3-4 mm long, crests at base of tube lacking or nearly so, fornicies yellow, rounded, slightly papillose, about 0.5 mm long, limb 5-8 mm wide; nutlets ovoid, 3-3.5 mm long, 1.6-1.9 mm wide, margins obtuse, not in contact, dorsal surface rugose, tuberculate and somewhat muricate, ventral surface conspicuously tuberculate, scar open, constricted at the middle and surrounded by a high, elevated margin; style exceeding mature fruit 1.5-2 mm. Clay to clay-loam soils. Central and eastern Utah in Emery, Carbon, and Grand counties. April-July. Fig. 59.

Carbon Co., 20 miles north of Wellington, B. Maguire 18536 (UTC); left fork of Minnie-Maud Creek, B. Maguire 18596 (UTC); West Tavaputs Plateau, B. Maguire 18503 (UTC); 5 miles east of Wellington, L.C.

Higgins 996 (BRY); 5 miles east of Wellington, Higgins & Welsh 1043, 1041 (BRY); near Carbon-Emery County line along hwy 50-6, Higgins 3323 (BRY, WTSU); Emery Co., about 15 miles west of hwy 50-6 along the road from Woodside to Castle Dale, L.C. Higgins 1306 (BRY); about 7 miles south of the San Raphael River bridge, San Raphael Swell, L.C. Higgins 1318 (BRY); Carbon-Emery County line along hwy 50-6, Higgins & Welsh 1039 (BRY); San Raphael River, B.F. Harrison 8060 (BRY); about 9 miles south of Lawrence, G.L. Pyrah 15 (BRY); Grand Co., vicinity of Sego, about 5 miles north of Thompson, S.L. Welsh 6915 (BRY); Wayne Co., 5 miles east of Buckhorn Wash, Welsh & Atwood 9908 (BRY).

43. *Cryptantha ochroleuca* Higgins, Great Basin Naturalist 28:197. 1968. Type: Garfield County, Utah, on outcrop 100 meters south of Red Canyon Campground along hwy 12, L. C. Higgins 1788.

Low caespitose perennial, 0.2-1.3 dm tall; stems several, 0.1-0.4 dm long, strigose and weakly setose; leaves linear-oblanceolate to oblanceolate, the apices acute or sometimes obtuse, 1-2.5 mm long, 0.1-0.3 cm wide, basal leaves uniformly and densely strigose, sparsely setose, the petioles white-hairy, cauline leaves strigose and with some setose-pustulate bristles; inflorescence narrow, 0.2-0.7 dm long, weakly setose; calyx segments linear-lanceolate, 2-2.5 (3) mm long in anthesis, in fruit becoming 4-6 mm long, setose; corolla pale-yellow, the tube 2-2.5 mm long,

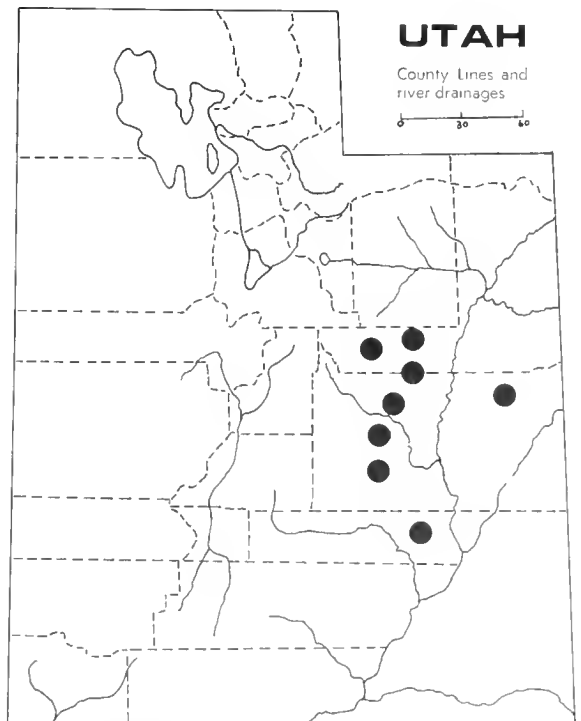


Fig. 59. *Cryptantha mensana*

crests at base of tube conspicuous, fornicies yellow, rounded, about 0.3 mm long, limb 4-5 mm wide; nutlets lanceolate, 2.5-3 mm long, 1.4-1.6 mm wide, usually only 1 maturing, margin acute, dorsal surface irregularly rugose with low rounded ridges, ventral surface only slightly uneven, scar open, narrowly triangular, extending $\frac{3}{4}$ the length of the nutlet, and lacking an elevated margin; style scarcely surpassing the mature fruit. Limited to the red Wasatch Formation near Red Canyon Campground in southwestern Garfield County, Utah. May-August. Fig. 60.

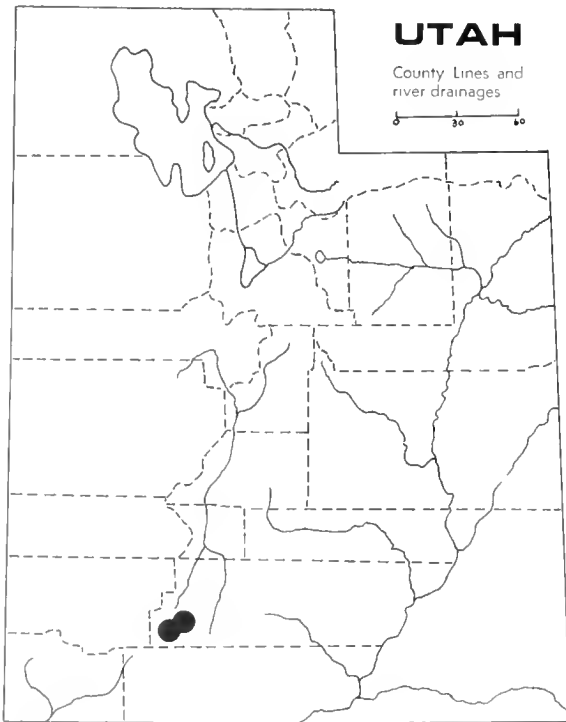


Fig. 60. *Cryptantha ochroleuca*

Garfield Co., on outcrop 100 meters south of Red Canyon Campground, L.C. Higgins 1788 (BRY); Red Canyon Campground, Reveal & Reveal 1031 (BRY); Rocky outcrops north of Red Canyon Campground, D. Atwood 1891 (BRY); 2.4 miles east of Red Canyon Campground, D. Atwood 1879 (BRY).

44. *Cryptantha osterhoutii* (Payson) Payson, Ann. Mo. Bot. Gard. 14:329. 1927. Type: Monument Park, near Grand Junction, Colorado, G. E. Osterhout 6138.

Oreocarya osterhoutii Payson, Univ. Wyom. Publ. Bot. 1:167. 1926.

Densely caespitose perennials, 0.7-1.2 dm tall; stems slender, many, arising from the densely branched multiple caudex, 0.3-0.6 dm long, strigose and spreading setose; leaves spatulate to oblanceolate, obtuse, 1-3 cm long, 0.3-0.8 cm

wide, dorsal surface strigose and appressed setose, pustulate, ventral surface strigose, not pustulate or the pustules inconspicuous, the petioles ciliate-margined; inflorescence open, 0.3-0.8 dm long, weakly white setose, foliar bracts inconspicuous; calyx segments lanceolate, in anthesis 2.5-4 mm long, in fruit becoming 5-6.5 mm long, strigose and spreading white setose; corolla white, the tube 2-3 mm long, crest at base of tube usually evident but poorly developed, fornicies yellow, broad, emarginate, papillose, about 0.5 mm long, limb 5-7 mm wide; nutlets lanceolate, 2.7-3.2 mm long, 1.8-2.2 mm broad, usually less than 4 nutlets maturing, margins obtuse, not in contact, dorsal surface carinate, sharply tuberculate and rugose, ventral surface sharply tuberculate, scar open, constricted above the base, elevated margin evident but not conspicuous; style exceeding mature fruit 0.2-0.7 mm. Sandy soil or rocky ledges and slopes of the Pinyon-Juniper community. Mesa County, Colorado, Wayne and San Juan counties, Utah. May-June. Fig. 61.

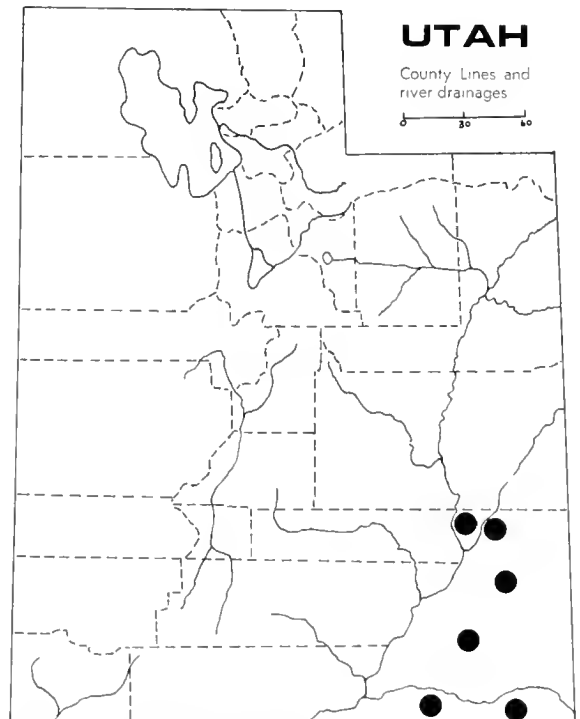


Fig. 61. *Cryptantha osterhoutii*

San Juan Co., Elephant Hill, Canyonlands Natl. Park, Welsh Atwood & Higgins 8875 (BRY); 25 miles west of Bluff near Johns Canyon, B.F. Harrison 11923 (BRY); nine miles north of junction 47-261 at summit of dugway, D. Atwood 1538A (BRY); Wayne Co., North Point, about 8 miles northwest of road to Flint Trail, above Orange Cliffs, Welsh & Atwood 9872 (BRY).

45. *Cryptantha paradoxa* (A. Nels.) Payson, *Ann. Mo. Bot. Gard.* 14:330. 1927. Type: Paradox Valley, Montrose County, Colorado, E. P. Walker 91.

Oreocarya paradoxa A. Nels. *Bot. Gaz.* 56:69. 1913.

Oreocarya gypsophila Payson, *Bot. Gaz.* 60:380. 1915.

Caespitose perennial, 0.4-1.2 dm tall; stems 1-many, slender, 0.2-0.8 dm long, subtomentose near the base, weakly setose above; leaves oblanceolate to spatulate, usually folded, obtuse, 1.5-4 cm long, 0.2-0.4 cm wide, dorsal surface with appressed setose-pustulate hairs, ventral surface uniformly strigose and without pustulate hairs, the petioles ciliate-margined; inflorescence subcapitate, 0.1-0.4 dm long, setose, foliar bracts inconspicuous; calyx segments linear-lanceolate in anthesis 5-6 mm long, in fruit becoming 6-8 mm long, weakly setose; corolla white, usually with a yellow tube 10-12 mm long, crests at base of tube lacking, fornices yellow, broad, emarginate, papillose, about 0.5 mm long, limb 10-12 (15) mm wide; nutlets lanceolate, turgid, 2-3 mm long, 1.3-1.6 mm wide, all 4 usually maturing, margins acute to obtuse, not in contact, dorsal surface densely tuberculate and conspicuously rugose, ventral surface tuberculate, also somewhat rugulose, scar open, constricted below the middle, the margin elevated; style exceeding mature fruit 4-9 mm. Sandy to heavy clay soils on flats and open ridges. Western Colorado, northwestern New Mexico, and eastern Utah. May-June. Fig. 62.

Emery Co., 5 miles south of the San Raphael River, B.F. Harrison 9607 (BRY); San Raphael Swell, 50 miles north of Hanksville, A. Cronquist 9204 (UTC); San Raphael Swell, B. Maguire 18282 (UTC); 3 miles south of San Raphael River Bridge, San Raphael Swell, L.C. Higgins 1314 (BRY); 10 miles south of the San Raphael River Bridge, San Raphael Swell, L.C. Higgins 1319 (BRY).

46. *Cryptantha rollinsii* Johnst. *Journ. Arn. Arb.* 20:391. 1939. Type: on Thornes Ranch near Willow Creek, 22 miles south of Ouray, Uintah County, Utah, R. C. Rollins 1715.

Biennial herbs, 1-3.5 dm tall; stems 1-several, 0.2-1 dm long, setose, leaves clustered at the base, gradually reduced upward, oblanceolate to spatulate, obtuse to acute, 2-5 cm long, 0.5-1.5 cm wide, setose and hispid, pustulate on both surfaces; inflorescence narrow to somewhat open at maturity, cylindrical or obovoid, racemes in dense glomerules, 3-6 flowered, hispid, 0.5-2 dm long; calyx segments linear, in anthesis 7-8 mm long, in fruit becoming 8-10 mm long, hispid;

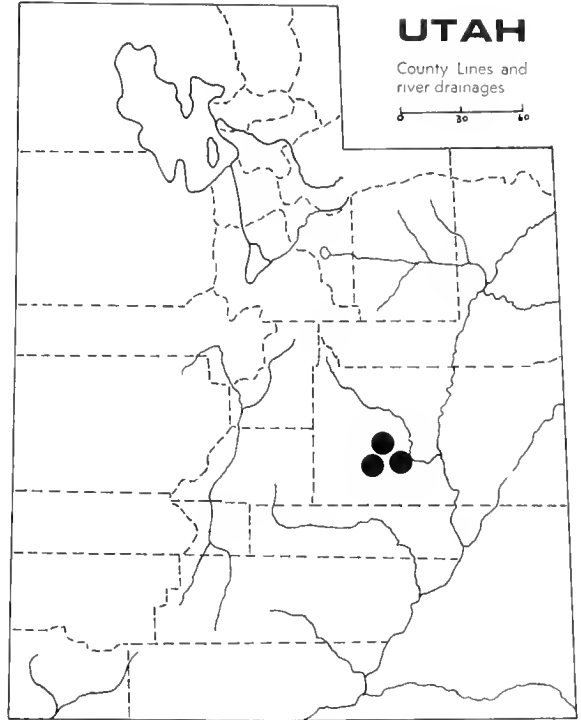
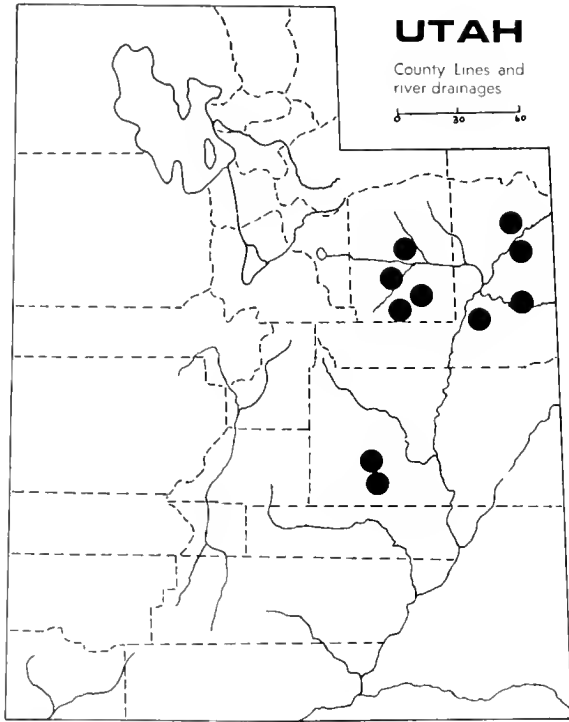


Fig. 62. *Cryptantha paradoxa*

corolla white, campanulate, the tube 7-9 mm long, crests at base of tube evident, fornices yellow, papillose, about 0.5-1 mm long, limb 7-8 mm wide; plants slightly heterostyled; nutlets lanceolate, 3-4 mm long, 1-1.5 mm wide, obscurely rugulose and tuberculate on the dorsal surface, ventral surface smooth, scar closed, and without an elevated margin. Open hills and ridges, growing on white or red shale. Central and northeastern Utah in Emery, Uintah, and Duchesne counties. May-July. Fig. 63.

Duchesne Co., about 10 miles south of Myton, L.C. Higgins 1067 (BRY); 10 miles south of Duchesne, L.C. Higgins 1052 (BRY); Indian Canyon, 10 miles south of Duchesne, B.F. Harrison 400II (BRY); between Myton and Wellington, 19 miles south of junction with U.S. hwy 40, Holmgren, Reveal & LaFrance 1946 (BRY); 2 miles south of Bridgeland, L.C. Higgins 1068 (BRY); 20 miles south of Myton, L.C. Higgins 1063 (BRY); Parley Canyon, tributary to Argyle Canyon, south end of county, Welsh & Christensen 6622 (BRY); 1 mile south of Duchesne, L.C. Higgins 1056 (BRY); about 8 miles north of Duchesne, L.C. Higgins 1058 (BRY); Emery Co., near Temple Mountain, L.C. Higgins 1324 (BRY); west of Hidden Splendor Mine, D. Atwood 1846 (BRY); 8 miles north of Goblin Valley turnoff on Temple Mountain road, D. Atwood 1859 (BRY); about 5 miles east of Buckhorn Wash, along road north of San Raphael River, Welsh & Atwood 9843 (BRY); 11 miles north of Goblin Valley turnoff on Temple Mt. road, thence 40 miles west-southwest on mining road, D. Atwood 1858 (BRY); Uintah Co., Hill Creek, about 12 miles south of Ouray, J. Brotherson 541 (BRY); Hill Creek, 33 miles south of Ouray, J. Brotherson 473

Fig. 63. *Cryptantha rollinsii*

(BRY); about 5 miles south of White River bridge, D. Atwood 1617, 1618A (BRY); Dinosaur Natl. Monument, Split Mountain Gorge Campground, J. Brotherson 994 (BRY); 18 miles south of Ouray, L.C. Higgins 1875 (BRY); 3 miles west of Bitter Creek, L.C. Higgins 1581 (BRY).

47. *Cryptantha rugulosa* (Payson) Payson, Ann. Mo. Bot. Gard. 14:295. 1927. Type: Fish Springs, Juab County, Utah, M. E. Jones s.n. *Oreocarya rugulosa* Payson, Univ. Wyom. Publ. Bot. 1:166. 1926.

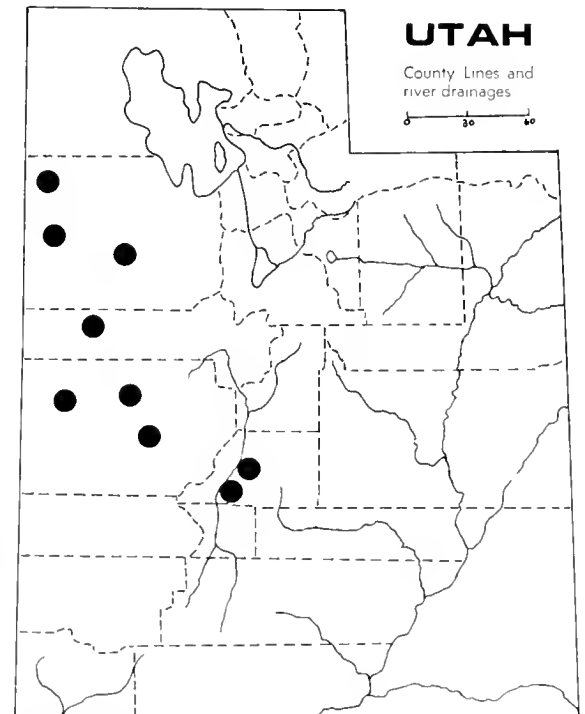
Biennial or short-lived perennial, 1.2-3 dm tall; stems slender, 1-several, 0.8-1.6 dm long, spreading setose-hispid; leaves oblanceolate to spatulate, obtuse to acute, strigose and conspicuously setose-hispid, pustulate on both surfaces; inflorescence 0.2-2 dm long, hispid; foliar bracts inconspicuous; calyx segments linear-lanceolate, in anthesis 4-5 mm long, in fruit becoming 7-9 mm long, strigose and spreading hirsute; corolla white, the tube 3-4 mm long, crests at base of tube conspicuous, fornicies rounded, distinctly papillose, about 0.5 mm long, limb 5-7 mm broad, nutlets lanceolate, 2.5-3.2 mm long, 1.3-1.7 mm wide, all 4 usually maturing, margins in contact, acute, dorsal surface with short low ridges, also somewhat tuberculate, ventral surface smooth or nearly so, scar open, subulate, without an elevated margin; style exceeding

mature fruit 1-1.5 mm. Upper Sonoran Zone in gravelly loam to clay soils. Central Utah to northeastern Nevada. May-July. Fig. 64.

Juab Co., 7 miles east of Trout Creek, Maguire & Becraft 2761 (UTC); 13 miles east of Trout Creek, Maguire & Becraft 2760 (UTC); near Topaz Reservoir, B.F. Harrison 11796 (BRY); Millard Co., Desert Range Experiment Station, W.P. Cottam 8523 (UT); 10 miles west of Fillmore, Ice Spring Crater, W.P. Cottam 9569 (UT); 26 miles west of Delta, Maguire & Becraft 3943 (UTC); 9 miles north of Desert Range Experiment Station Headquarters, R.C. Holmgren 519 (BRY); 1 mile south of Grady, B.F. Harrison 11658 (BRY); Cinder Cones, W.P. Cottam 8003 (UT); House Range, 37 miles west of Delta, Maguire & Becraft 2758 (UTC); Cowboy Pass, Q. A. Hare 130F (UTC); 20 miles west of Hinckley, B. Maguire 20759 (UTC); about 15 miles west of Desert Range Experiment Station, L.C. Higgins 1614, 1463 (BRY); Sevier Co., about 1 mile southeast of Sigurd, L.C. Higgins 1623 (BRY); 6 miles south of Big Rock Candy Mountain, D. Atwood 1787 (BRY); 1 mile south of Sevier, L.C. Higgins 1474, 1621 (BRY); Tooele Co., 4 miles north of Gold Hill, B. Maguire 22021 (UTC); 2 miles west of Gold Hill, Maguire & Becraft 2762 (UTC); near Ibapah, W.P. Cottam 3159 (BRY); about 3 miles east of Wendover, L.C. Higgins 1720 (BRY).

48. *Cryptantha semiglabra* Barneby, Leaf. West. Bot. 3:197. 1943. Type: Arizona, about 2 miles east of Fredonia, Ripley & Barneby 8429.

Erect perennials, 2-3 (4) dm tall; stems 1-several, 0.9-1.8 (2) dm long, retrorsely strigose

Fig. 64. *Cryptantha rugulosa*

and weakly spreading setose; leaves oblanceolate, acute, 3-7 cm long, 0.3-0.6 cm wide, dorsal surface appressed setose-pustulate, ventral surface glabrous, the old leaf bases long white-hairy; inflorescence narrow to somewhat open, 0.4-1.3 dm long, foliar bracts slightly surpassing the cymes, 1.5-2 cm long; calyx segments lanceolate, in anthesis 5-8 mm long, in fruit becoming 10-13 mm long, setose; pedicels 1-2 mm long; corolla white, the tube 10-12 mm long, crests at base of tube conspicuous, fornices yellow, rounded, 1-1.2 mm long, obscurely papillose, limb 8-10 mm wide; nutlets ovate, 3.5-4 mm long, 2-2.5 mm wide, usually all 4 maturing, margins acute, in contact, both surfaces smooth and glossy, scar closed, elevated margin lacking, style surpassing the mature fruit 5-7 mm. Clay soils, Upper Sonoran Zone. Northern Arizona and southwestern Utah. May-July. Fig. 65.

Washington Co., Galagers Hill. Hurricane-Kanab road, J.W. Harrison s.n. (DIX).

49. *Cryptantha sericea* (Gray) Payson, Ann. Mo. Bot. Gard. 14:286. 1927. Type: Bridger Pass, Wyoming, H. Engelmann s.n.

Krynitzkia sericea Gray, Proc. Amer. Acad. 20:279. 1885.

Oreocarya sericea Greene, Pittonia 1:58. 1887.

Oreocarya affinis perennis A. Nels. Erythea 7:67. 1899.

Oreocarya argentea Rydb. Bull. Torrey Club 31:637. 1904.

Oreocarya perennis Rydb. Bull. Torrey Club 33:150. 1906.

Oreocarya proccra Osterh. Bull. Torrey Club 47:211. 1920.

Cryptantha sericea var. *perennis* (Nels.) Payson, Ann. Mo. Bot. Gard. 14:288. 1927.

Perennials, 1.5-4.3 (5) dm tall; stems 1-several, branched from near the base, 0.5-1.2 (3) dm long, setose with spreading hairs; leaves oblanceolate to spatulate, obtuse, 2.5-10 (15) cm long, 0.5-2 cm wide, dorsal surface strigose and weakly appressed to spreading setose, pustulate, ventral surface silky-strigose, pustules lacking or very inconspicuous; inflorescence narrow to somewhat open, 0.5-3.2 dm long, setose-hispid, foliar bracts 2-5 cm long; calyx segments lanceolate, 2.5-4 mm long in anthesis, in fruit becoming 6-8 mm long; pedicels 0.5-1 mm long; corolla white, the tube 2.5-3.5 mm long, crests at base of tube conspicuous, fornices yellow, broad, depressed, 0.5-0.6 mm long, limb 7-9 mm wide; nutlets lanceolate, 2.5-3.5 mm long, 1.5-2 mm wide, usually all 4 maturing, margins acute or narrowly winged, in contact, dorsal surface with low rounded tuberculations, also somewhat rugulose and muriculate, ventral surface similar but the markings less evident, scar straight, closed and without an elevated margin; style exceeding mature fruit 0.5-1.3 mm. Growing on heavy clay soils in the Pinyon-Juniper community. Southwestern Wyoming, northwestern Colorado, and northeastern Utah. May-August. Fig. 66.

Carbon Co., West Tavaputs Plateau. Welsh & Christensen 6572 (BRY); Daggett Co., 7 miles south of Manila, R.C. Rollins 1772 (UTC); 6 miles south of Manila, B. Maguire 12378 (UTC); Duchesne Co., Indian Canyon, A.O. Garrett 8330 (UT); Indian Canyon, R.S. Ferris 11331 (UTC); about 2 miles south of Duchesne, L.C. Higgins 1055 (BRY); 10 miles east of Fruitland, L.C. Higgins 1048 (BRY); about 14 miles west of Duchesne, Higgins & Welsh 1023 (BRY); Rich Co., about 5 miles west of Evanston just across the Utah line, L.C. Higgins 1571 (BRY); Uintah Co., Brush Creek, 1 mile east of sheep corrals, D. Atwood 1585 (BRY); 1 mile north of Brush Creek sheep pens, D. Atwood 1589 (BRY); 5 miles west of White River bridge, D. Atwood 1620 (BRY); about 1 mile west of Rainbow, Holmgren, Reveal & LaFrance 1806 (BRY); 3 miles north of Brush Creek sheep corrals, L.C. Higgins 1867 (BRY); Book Cliffs, about 8 miles south of the junction to Cook Ridge, L.C. Higgins 1596 (BRY).

50. *Cryptantha setosissima* (Gray) Payson, Ann. Mo. Bot. Gard. 14:268. 1927. Type: Fish Lake, Sevier County, Utah, L. F. Ward 646.

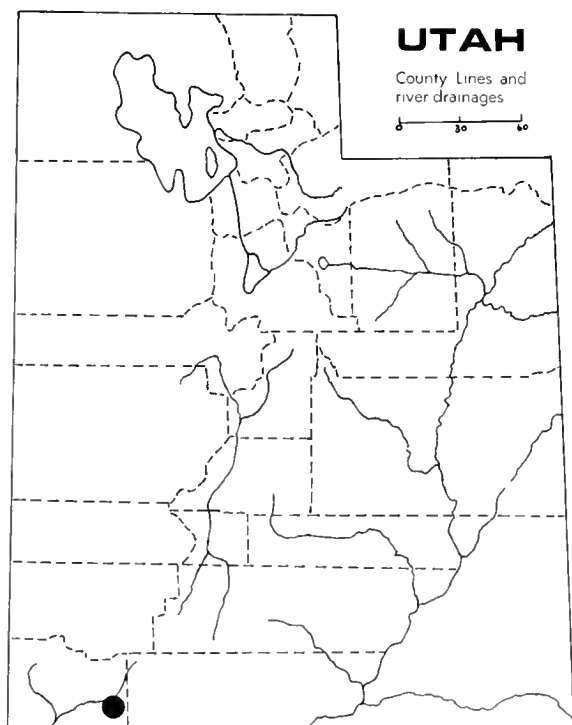


Fig. 65. *Cryptantha semiglabra*

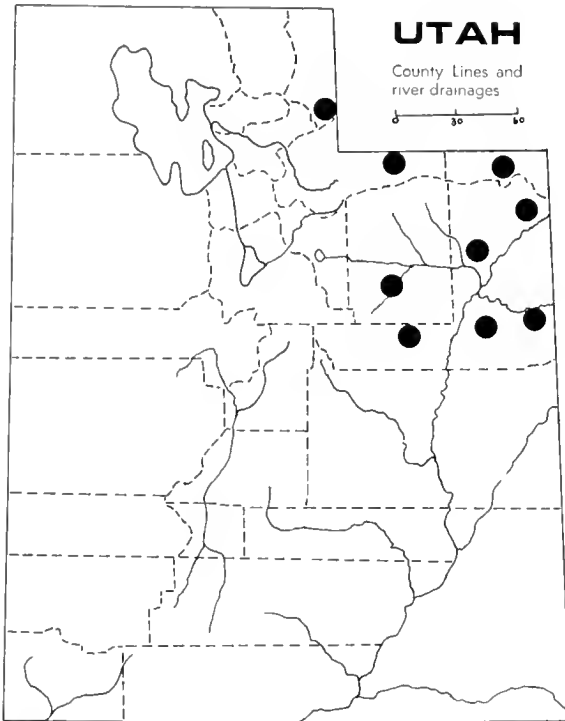


Fig. 66. *Cryptantha sericea*

Eritrichium setosissima Gray, Proc. Amer. Acad. 12:80. 1877.

Krynitzkia setosissima Gray, Proc. Amer. Acad. 20:276. 1885.

Oreocarya setosissima (Gray) Greene, Pittonia 1:58. 1887.

Biennial or short-lived perennials, 3-10 dm tall; stems usually 1-3, erect, 1.5-5 (6) dm long, hirsute; leaves clustered at the base, reduced upward, oblanceolate, the apices obtuse to acute, 3-13 cm long, 0.5-1.5 cm wide, setose, and with some linear twisted pubescence beneath, pustulate hairs numerous on both surfaces; inflorescence broad-topped due to the elongation of the scorpioid racemes, 1-5 dm long; calyx segments broadly lanceolate, 4-6 mm long in anthesis, in fruit becoming 9-11 mm long, setose, and strigose; corolla white, the tube 3-5 mm long, constricted above the ovary by the conspicuous ring of crests, fornicees yellow, emarginate, 0.5 mm long, limb 7-9 mm broad; nutlets ovate, 5-6 mm long, 3.5-4.5 mm wide, papery, with a broad, winged margin, dorsal surface muricate, and inconspicuously rugulose or tuberculate, ventral surface smooth or nearly so, scar straight, narrow, slightly open, elevated margin lacking; style exceeding mature fruit 1-2 mm. Sandy to gravelly soils in the Transition Zone, Central Utah, south through most of Arizona in the mountain-

ous areas, west to Nye County, Nevada. June-September. Fig. 67.

Garfield Co., east side of Mount Ellen, Henry Mountains, W.D. Stanton 516 (UT); Piute Co., 10 miles west of junction along hwy 153, L.C. Higgins 1785 (BRY); Sevier Co., Bowery Camp, Fish Lake, B. Maguire 19890 (UTC); Fish Lake, Bowery Creek Campground, L.C. Higgins 1117 (BRY); Fish Lake, Main Lodge, L.C. Higgins 1125 (BRY); Washington Co., about 6 miles west of the town of Pine Valley, L.C. Higgins 1440 (BRY).

51. *Cryptantha strict* (Osterh.) Payson, Ann. Mo. Bot. Gard. 14:264, 1927. Type: Some distance south of the Yampa or Bear River along the Victory highway, Moffatt County, Colorado, G. E. Osterhout 6195.

Oreocarya stricta Osterh. Bull. Torrey Club 50:217. 1923.

Strict perennial, 1-3.9 dm tall; stems 1-several, 0.4-2 dm long, strigose and conspicuously setose-hispid; leaves mostly basal, reduced upward, oblanceolate, acute, 2-7 cm long, 0.4-0.9 cm wide, retrorsely strigose and spreading setose-hispid, pustulate; inflorescence narrow, interrupted below the terminal cluster, 0.5-2 dm long, setose-hispid, foliar bracts conspicuous, especially near the base; calyx segments lanceolate, 4-6 mm long in anthesis, in fruit becoming 7-9 mm long, setose-hispid; corolla white, the

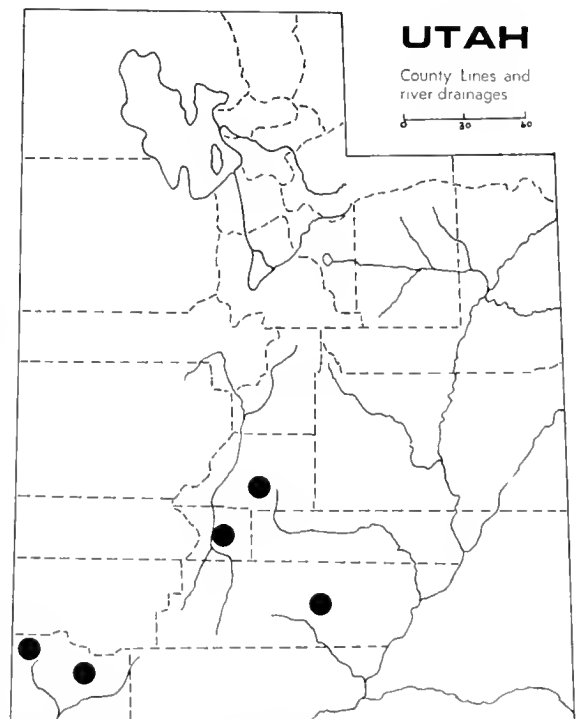


Fig. 67. *Cryptantha setosissima*

tube 3-4 mm long, crests at base of tube conspicuous, fornices yellow, rounded, papillose, limb 7-10 mm wide; nutlets lanceolate to elliptic, 3-3.5 mm long, 1.5-2 mm wide, usually all 4 maturing, margins in contact, knifelike, dorsal surface with definite transverse ridges, also somewhat tuberculate or nearly smooth, ventral surface smooth or nearly so, scar open, very narrowly linear, elevated margin lacking; style exceeding mature fruit 1-1.5 mm. Growing on clay or shale in the Transition Zone. Southwestern Wyoming, northwestern Colorado, and northeastern Utah. June-August. Fig. 68.

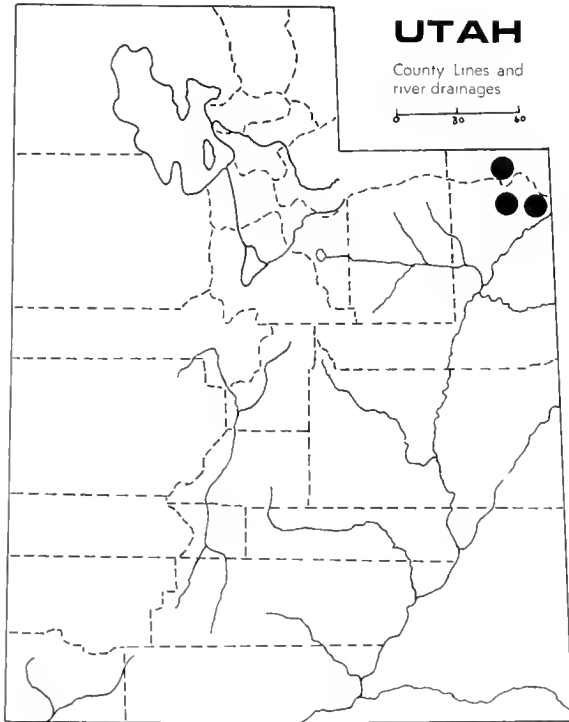


Fig. 68. *Cryptantha stricta*

Daggett Co., Flaming Gorge, L. Williams 489 (RM); Summit Co., about 10 miles south of Lonetree, Wyoming, Welsh & Moore 6714 (BRY); Uintah Co., 2 miles north of Brush Creek on the Manila-Vernal highway, D. Atwood 1609 (BRY); 3.6 miles north of Brush Creek along the Manila-Vernal highway, L.C. Higgins 1869 (BRY); 2.5 miles north of Brush Creek, L.C. Higgins 1874 (BRY).

52. *Cryptantha tenuis* (Eastw.) Payson, Ann. Mo. Bot. Gard. 14:327. 1927. Type: Court House Wash, Grand County, Utah, Alice Eastwood s.n.

Oreocarya tenuis Eastw. Bull. Torrey Club 30:244. 1903.

Caespitose perennials, 1.3-2.5 dm tall; stems slender, 1-many, 0.8-1.2 dm long, strigose and

weakly spreading setose; leaves linear-spatulate, mostly basal, obtuse, 2-5 cm long, 0.3-0.6 cm wide, dorsal surface strigose and weakly spreading setose, conspicuously pustulate, ventral surface uniformly strigose and without pustules; inflorescence narrow, interrupted, 0.6-1.4 dm long, weakly setose, foliar bracts inconspicuous; calyx segments linear-lanceolate, in anthesis 4.5-6 mm long, in fruit becoming 7-9 mm long, white setose; corolla white, the tube 5.5-7 mm long, crests at base of tube lacking or sometimes evident, fornices yellow, broad, emarginate, papillose, about 0.5 mm long, limb campanulate, 5-8 mm wide; nutlets lanceolate, 3-4 mm long, 1.8-2 mm wide, all 4 nutlets usually maturing, margin acute to somewhat obtuse, nearly in contact, dorsal surface carinate, sharply and deeply rugose, ventral surface rugose, scar open, constricted above the base, and with an elevated margin; style exceeding mature fruit 3-4 mm. Sandy or sandy-loam soils in the Upper Sonoran Zone. Southeastern Utah in Emery, Grand, Wayne, and San Juan counties. April-July. Fig. 69.

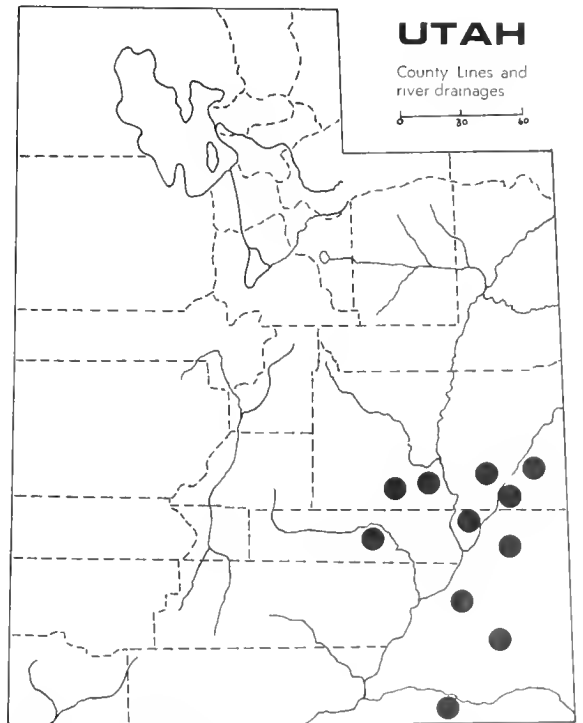


Fig. 69. *Cryptantha tenuis*

Emery Co., about 5 miles southwest of Temple Mountain, L.C. Higgins 1326 (BRY); about 26 miles southwest of Green River along hwy 24, Higgins & Reveal 1281 (BRY); Grand Co., 10 miles northwest of Moab, B.F. Harrison 5967 (BRY); Headquarters, Arches Natl. Monument, Welsh & Moore 2801 (BRY); 1 mile west of Delicate Arch, B.F. Harrison 11258 (BRY); White Canyon, B.F. Harrison 11576 (BRY); Fisher

Towers, Welsh & Atwood 9961 (BRY); Castle Valley, Welsh & Atwood 9950 (BRY); northeast of Moab, just below Salt Wash, A. Cronquist 8978 (UTC); 1 mile east of Moab bridge, Bryan & Moab School s.n. (UTC); San Juan Co., 14 miles southeast of Moab along power transmission line, L.C. Higgins 3547 (BRY, WTSU); 2 miles west of Hite, Welsh, Atwood & Higgins 8952 (BRY); Fry Canyon, Welsh, Atwood & Higgins 8951 (BRY); about 2 miles west of Dugout Rock, Welsh, Atwood & Higgins 8883 (BRY); 1 mile southeast of Natural Bridges Natl. Monument visiting center, D. Atwood 1511 (BRY); north slope of divide into Monument Valley, A.H. Holmgren 3237 (UTC); 10 miles east of Hite, A. Cronquist 9035 (UTC); about 12 miles south of Moab, L.C. Higgins 1000 (BRY); 19 miles west of Fry Canyon Post Office, L.C. Higgins 537 (BRY); 2 miles up road to Dead Horse Point, R.K. Vickery 751 (UT); Wayne Co., about 1 mile east of Hanksville, L.C. Higgins 1334 (BRY); Three Canyon, along road about 25 miles south of Green River along county road, Welsh & Atwood 9895 (BRY).

53. *Cryptantha virginensis* (Jones) Payson, Ann. Mo. Bot. Gard. 14:274. 1927. Type: Laverkin, Washington County, Utah, M. E. Jones 5195A.

Krynitzkia glomerata var. *virginensis* Jones Contr. West. Bot 13:5. 1910.

Oreocarya virginensis (Jones) Macbr. Proc. Amer. Acad. 51:547. 1916.

Biennial, 1.5-3.5 (4) dm tall; stems 1-several, arising from a stout taproot, 0.3-0.6 dm long, setose-hirsute; leaves oblanceolate to spatulate, obtuse, 3-10 (12) cm long, 0.5-1.5 cm wide, dorsal surface sparsely setose, pustulate, also with some fine tangled hair beneath, ventral surface subtomentose and weakly appressed setose, with only a few pustulate hairs; inflorescence a broad thyrsus with the individual cymes much elongating, 0.5-3 dm long, foliar bracts conspicuous, 2-4 cm long; calyx segments linear-lanceolate, in anthesis 3-4 mm long, in fruit becoming 7-11 mm long, hirsute; corolla white, the tube 3-4 mm long, crests at base of tube conspicuous, fornices yellow, emarginate, papillose, about 1 mm long, limb 7-9 mm broad; nutlets ovate, 3.3-4.5 mm long, 2.4-2.6 mm wide, usually only 1-2 nutlets maturing, margins in contact, acute, dorsal surface with a distinct ridge, the surface tuberculate and usually rugulose, ventral surface very uneven with indeterminate rugae and tubercles, scar open and triangular with an elevated margin; style exceeding mature fruit 1-1.5 mm. Usually growing on clay or clay-loam soils in the Lower Sonoran Zone, Southwestern Utah, southern Nevada, northwestern Arizona, and southeastern California, March-July. Fig. 70.

Washington Co., about 5 miles southwest of St. George, L.C. Higgins 1243 (BRY); Beaverdam Mountains, L.C. Higgins 1232 (BRY); 11 miles east of St. George, F.W. Gould 1580 (BRY, DIX); north of Gun-

lock, P. Nyberg s.n. (DIX); 4 miles west of St. George, A. Terril s.n. (DIX); near the Shivwitt Indian Reservation, E. Hawkins s.n. (DIX); Beaverdam Mountains, R.W. Christian 863 (UT); 8 miles north of Santa Clara, A.H. Holmgren 8224 (UTC); Virgin River above Hot Mineral Springs, Laverkin, Utah, B. Maguire 4470 (UTC); Jackson Wash, Beaverdam Mountains, D.H. Nish 36 (UTC); about 4 miles west of the Shivwitt Indian Reservation, L.C. Higgins 4151 (BRY, WTSU).

54. *Cryptantha wetherillii* (Eastw.) Payson, Ann. Mo. Bot. Gard. 14:324. 1927. Type: Court House Wash near Moab, Grand County, Utah, Alice Eastwood s.n.

Krynitzkia glomerata var. *acuta* Jones, Zoe 2:250. 1891.

Oreocarya wetherillii Eastw. Bull. Torrey Club 30:242. 1903.

Biennial or short-lived perennials, 1-3.5 (4) dm tall; stems 1-6, 0.5-0.8 dm long, branched from the base with 1 stout and usually several low slender ascending stems; leaves clustered at the base, gradually reduced upward, spatulate to broadly oblanceolate, the apices obtuse to rounded, 2.5-5 cm long, 0.7-1.6 cm wide, strigose and appressed setose, dorsal surface conspicuously pustulate, ventral surface with few or no pustules; inflorescence becoming broad in age due to the elongation of the cymes, 0.6-3 dm long, calyx segments lanceolate, in anthesis 5-7 mm long, in fruit becoming 7-13 mm long,

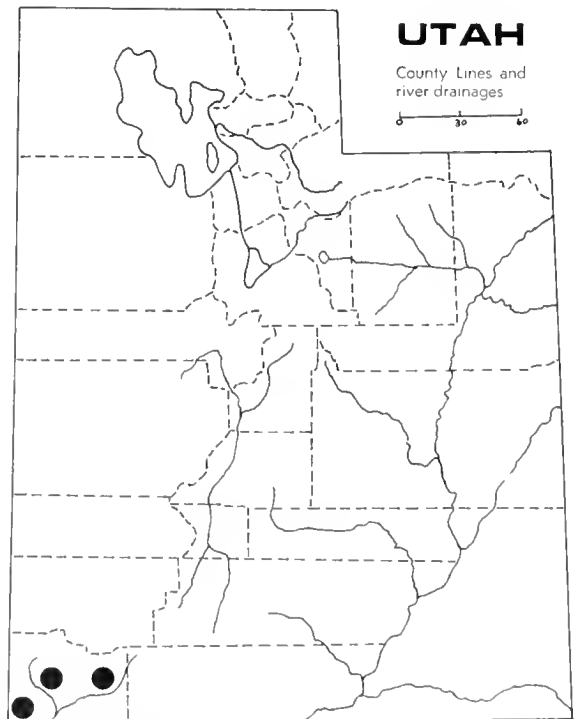


Fig. 70. *Cryptantha virginensis*

white setose; corolla white, the tube 7-10 mm long, crests at base of tube lacking, fornicies light-yellow, emarginate, papillose, about 1 mm long, limb 6-13 mm wide; nutlets lanceolate, or ovate-lanceolate, 3.5-4 mm long, 2-2.5 mm wide, usually all 4 maturing, margins acute, in contact, dorsal surface distinctly tuberculate and often rugulose as well, scar open, linear, surrounded by a slightly elevated margin; style exceeding mature fruit 3-5 mm. Usually growing on heavy clay soils associated with *Atriplex*. East central Utah in Grand, Carbon, Emery, Wayne, and Garfield counties. April-June. Fig. 71.

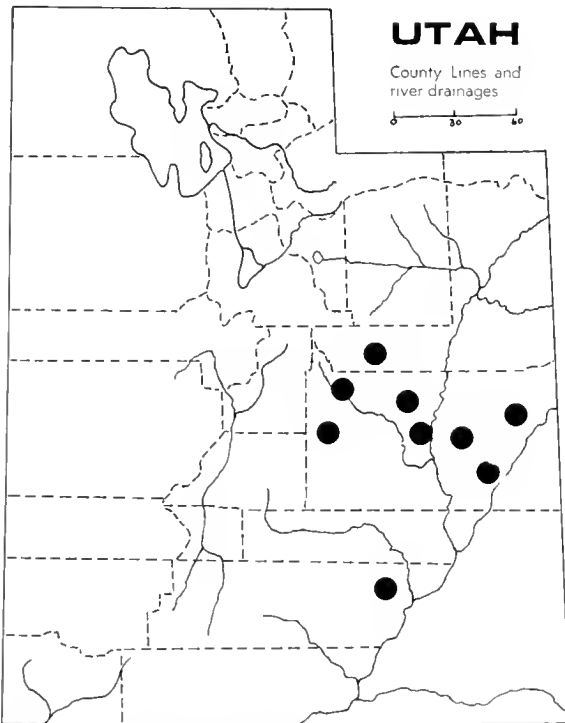


Fig. 71. *Cryptantha wetherillii*

Carbon Co., Price, W.P. Cottam s.n. (UT); Wellington, W.P. Cottam 2031 (BRY); 2 miles south of Price, B. Maguire 18264 (UTC); Emery Co., 9 miles north of Green River, B. Maguire 18229 (UTC); Green River, W.P. Cottam 2073 (BRY); Big Springs Wash, 25 miles south of the Carbon County line. Welsh & Moore 2786 (BRY); Carbon-Emery County line, Higgins & Welsh 1042 (BRY); 7 miles south of Huntington, L.C. Higgins 1017 (BRY); Gunnison Butte, O.S. Walsh 29 (UT); 6 miles north of Woodside, B.F. Harrison 10412 (BRY); along hwy 24, 3-6 miles north of San Raphael River bridge, G.L. Pyrah 21 (BRY, UTC); 10 miles south of Woodside, J. Brotherson 90 (BRY); 7 miles west of Lawrence, D. Atwood 1839 (BRY); Garfield Co., Henry Mountains, W.D. Stanton s.n. (BRY); Grand Co., 4 miles south of Crescent Junction, Welsh & Higgins 8874 (BRY); 10 miles east of Green River, C.A. Hanson 64 (BRY); 10 miles east of Green River, D.E. Bright 26 (BRY); about 6 miles east of Thompson along hwy 50-6, L.C. Higgins 1476 (BRY).

7. *Cynoglossum* (Tourn.) L.

Cynoglossum (Tourn.) L., Sp. Pl. 134. 1753, and Gen. Pl. 65. 1754.

Biennial or perennial or rarely annuals; leaves alternate, the basal ones long petioled; racemes elongating, usually without bracts, or rarely bracted at base; calyx cut to beyond the middle, somewhat accrescent, segments often spreading or reflexed in fruit; corolla cylindrical or funnel-form, the tube short, lobes broad, spreading, imbricate, throat with trapeziform oblong or subulate appendages; stamens included; filaments short, anthers oblong or elliptic; ovules 4; nutlets 4, equally divergent, depressed ovoid or orbicular, glochidiate, back flat or convex, frequently with an elevated margin, attached by a small or large medial to apical scar to a convex or pyramidal gynobase and frequently with a free subulate prolongation decurrent on the short entire style.

Type Species: *Cynoglossum officinale* L. A cosmopolitan genus of about 50 species.

1. *Cynoglossum officinale* L. Sp. Pl. 134. 1753. Type: Europe.

Biennial, villous-tomentose throughout; stems stout, erect, leafy to the top, 4-5 dm high; lower leaves oblong to oblong-lanceolate, slender petiolate, 15-30 cm long, 2-7 cm wide; upper leaves lanceolate, acute or acuminate, sessile or the upper mostly clasping; racemes several to many, simple or branched, sparingly bracted or bractless; much elongating in fruit; pedicels 5-12 mm long; calyx segments ovate-lanceolate, obtuse to acutish, 5-7 mm long in fruit, corolla reddish-purple, the broad tube 3-5 mm long, the limb 6-8 mm broad; nutlets ascending on the pyramidal gynobase, about 6 mm high, flattish on the upper surface and margined, splitting away from the gynobase at maturity but hanging attached to the subulate style. Native to Europe and Asia but widely distributed over North America. May-July. Fig. 72.

Box Elder Co., Perry Canyon, Cottam. Allen & Rowland 16231 (UT); Blue Creek, W.P. Cottam 2838 (BRY); Cache Co., Twin Creek drainage of Cache Natl. Forest, C.O. Baker 125 (UTC); fields and waste places, N.H. Holmgren 40 (UTC); Logan, B. Maguire 3716 (UTC); Paradise-Hyrum road, C.P. Smith 1744 (UTC); Logan, D. Hobson 13770 (UTC); 2 miles west of Logan, B. Maguire 3717 (UTC); Duchesne Co., 18 miles north of Duchesne, J. Brotherson 829 (BRY); Juab Co., 8 miles west of sand dune on the road to Calico, J. Anderson 842 (BRY); Mount Nebo, Cottam & Anderson 15105 (UT); Millard Co., 9 miles east of Fillmore, G. Worthen 248 (UT); Confusion Range, 21.8 miles east of the Utah-Nevada line, J. Gentry 2006 (BRY, UTC); Salt Lake Co., Red Butte Canyon, G. Swanson 288 (UT); Emigration Canyon, E.B. Robinson

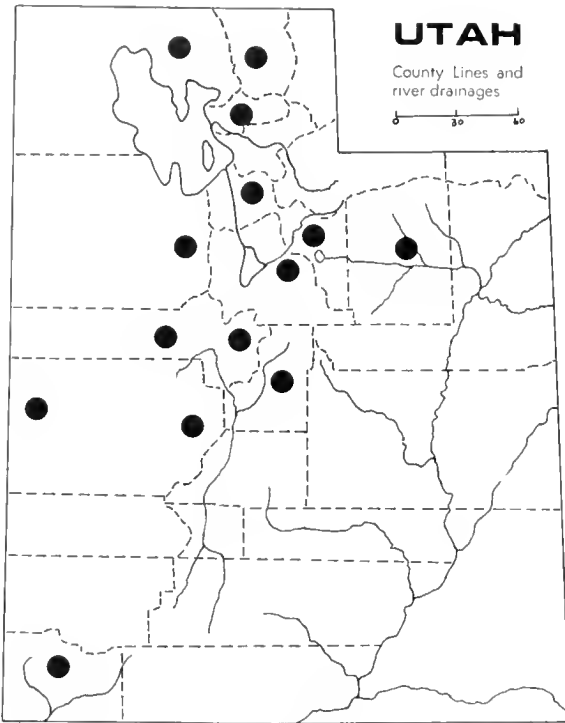


Fig. 72. *Cynoglossum officinale*

s.n. (UT); Sanpete Co., Ephraim Canyon, A.H. Barnum s.n. (DIX); 4 miles east of Ephraim, R. Stevens 30 (BRY); 5 miles up Manti Canyon, A. Collotzi 511 (UTC); Tooele Co., south of Vernon, R.H. Foster 22 (BRY); Utah Co., Timp Haven, K. Shaw 95 (BRY); 2 miles east of Thistle, J. Gentry 2001 (UTC); Wasatch Co., 5.7 miles east of Heber, L. Arnow 676 (UT); 5 miles southwest of Heber, L.C. Higgins 1863 (BRY); Washington Co., no locality, J.W. Harrison s.n. (BRY); Weber Co., Weber River, W.S.F. 755 (UT); Ogden, on south Harrison Blvd., A. Collotzi 51 (UTC).

8. *Echium* L.

Echium L. Sp. Pl. 139. 1753, and Gen. Pl. 68. 1754.

Biennial or possibly perennial, hispid, herbaceous plants; leaves alternate, entire; flowers blue to violet-purple, in leafy bracted scorpioid, spikelike racemes; calyx 5-parted; corolla tubular-funnelform, irregular, usually 5-lobed, the throat not appendaged; stamens unequal, at least the longer ones exerted on long filaments; ovary 4-lobed, these separating in fruit; style 2-cleft at apex; nutlets erect, rugose, attached by their bases to a flat gynobase, the scar flat or somewhat concave, not leaving a pit.

Type Species: *Echium italicum* L.

1. *Echium vulgare* L. Sp. Pl. 139. 1753.

Stems 3-9 dm tall, erect, solitary or occasionally several, finely hispid-villous as well as

shaggy coarse-hirsute; leaves appressed-hispid and along the margin and midrib somewhat hirsute, with a strong midrib but very obscure or absent veins; lower leaves 8-16 cm long, oblanceolate, broadly stalked, forming a rosette which withers away at anthesis; cauline leaves reduced up the stem, the middle ones linear-lanceolate, 3-9 cm long, contracted to a rounded sessile base; racemes short, lateral, disposed in a long narrow thyse or open panicle; corolla bright blue, rarely rose or white, pubescent and sparsely setose, rather firm in texture, 10-15 mm long, the tube about equaling the calyx; stamens very unequal, the two pair slightly unequal but both surpassing the lower corolla lobe, the odd stamen included; nutlets about 2 mm long, erect, rugose. Native of Europe, introduced into eastern United States where it has spread westward to the Rocky Mountains. June-August. Fig. 73.

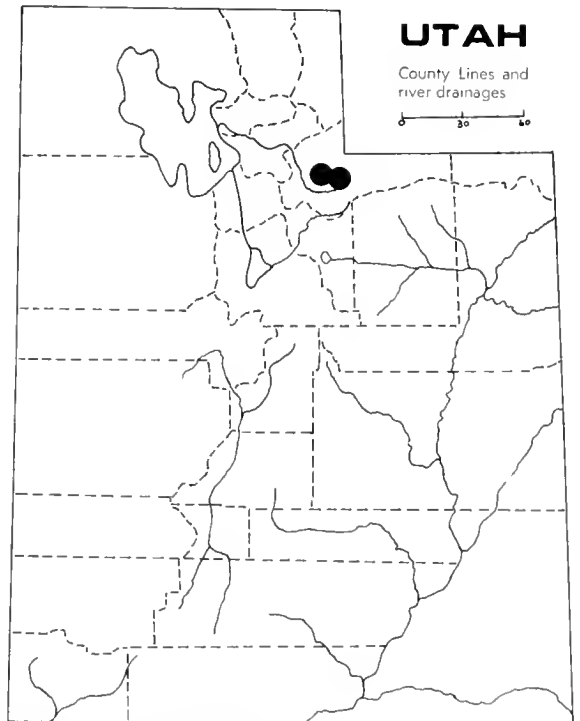


Fig. 73. *Echium vulgare*

Summit Co., Echo Canyon, C.H. Field 37 (UTC); Echo Canyon, 2 miles above town of Echo on old road, J.R. Moore s.n. (UTC); Echo Canyon, S. Flowers s.n. (UT).

9. *Eritrichium* Schrad.

Eritrichium Schrad. in Gaud. Fl. Helv. 2:57. 1828.

Low depressed cushion-like perennials, with the short stems densely clothed with small often

imbricate leaves; flowers few in a racemelike cluster terminating the slender flowering stem; calyx-lobes ascending, linear; corolla blue, funnelliform, with a short tube; nutlets obliquely attached to the conical gynobase, smooth, the apex obliquely truncate, with a distinct, entire or toothed margin.

Type Species: *Eritrichium nanum* Schrad.

1. *Eritrichium nanum* (Vill.) Schrad. var. *elongatum* (Rydb.) Cronq. Vasc. Pls. Pacif. N. W. 4:203. 1959.

Eritrichium argenteum Wight, Bull. Torrey Club 29:411. 1902.

Eritrichium elongatum Wight, Bull. Torrey Club 29:408. 1902.

Eritrichium elongatum var. *argenteum* I. M. Johnst. Contr. Gray Herb. 70:53. 1924.

Oreocarya pulvinata A. Nels. Bot. Gaz. 40:63. 1905.

Plants villous often silvery looking, forming a tuft about 2-4 cm tall (not counting the flowering branches); leaves closely overlapping, 5-10 mm long, narrowly ovate to oblong or oblanceolate, 1.5-2 mm broad, acute or obtuse, pilose, especially on the margins and tips, with long white hairs; flower cluster compact when sessile among the leaves or sometimes raceme-like when borne on a leafy flowering branch up to 7 cm long; calyx-lobes linear, 1.5-3 mm long; corolla tube equalling the calyx-lobes, limb variable in size (1) 4-5 (7) mm broad, bright blue (rarely white), crests in the throat puberulent; nutlets smooth, with an entire margin to the truncated oblique portion, rarely with a few obscured teeth. Rocky ridges in high alpine areas, 10,000 to 13,000 feet. Oregon, east to Idaho, Montana, Wyoming, Utah, and Colorado. July-September. Fig. 74.

Box Elder Co., Raft River Range, W.P. Cottam 2849 (BRY, UT); Raft River Mountains, S.J. Preece 640 (UT); Duchesne Co., Uintah Mountains, J.R. Murdock 554 (BRY); Summit of Mt. Agazziz, W.P. Cottam 3718 (UT); Summit Co., Upper Henrys Fork, north of Lake Blanchard, B. Maguire 14346 (UTC); about Henrys Fork Lake, B. Maguire 14385 (UTC).

10. *Hackelia* Opiz in Bercht.

Hackelia Opiz in Bercht. Fl. Boehm. 2 pt. 2:146. 1839.

Coarse biennial or perennial or rarely annual herbs; leaves alternate, broad and veiny; flowers in naked or inconspicuous bracted racemes paniculately disposed; pedicels slender, recurving in fruit; calyx cut to the base into spreading ovate

to oblong or lanceolate lobes; corolla white or blue, with a short or elongate tube, lobes rounded, imbricate; throat with trapeziform intruded appendages; stamens included, affixed at middle of tube; filaments slender, short; anthers oblong to elliptic; style slender, scarcely if at all surpassing the nutlets; stigma capitate; ovules 4; nutlets 4, erect, ovate, affixed ventrally to the pyramidal gynobase by a broad medial or submedial areola, margin with subulate glochidiate appendages which are frequently confluent at the base, back smooth or with glochidiate appendages.

Type Species: *Hackelia deflexa* (Wahl.) Opiz (*Myosotis deflexa* Wahl.)

1. Surface of nutlet more or less ridged but without prickles; branches many flowered 1. *H. floribunda*
1. Surface of nutlet more or less prickly (may be ridged); branches fewer and with fewer flowers (2)
2. Nutlets broadly ovate; basal leaves few, stems leafy above, not conspicuously reduced in size; corolla blue 2. *H. jessicae*
2. Nutlets narrowly ovate; basal leaves many, stem leaves few and reduced in size; corolla white 3. *H. patens*

1. *Hackelia floribunda* (Lehm.) Johnst. Contr. Gray Herb. 68:46. 1923. Type: "Lake Pentagishene to the Rocky Mountains, Drum-

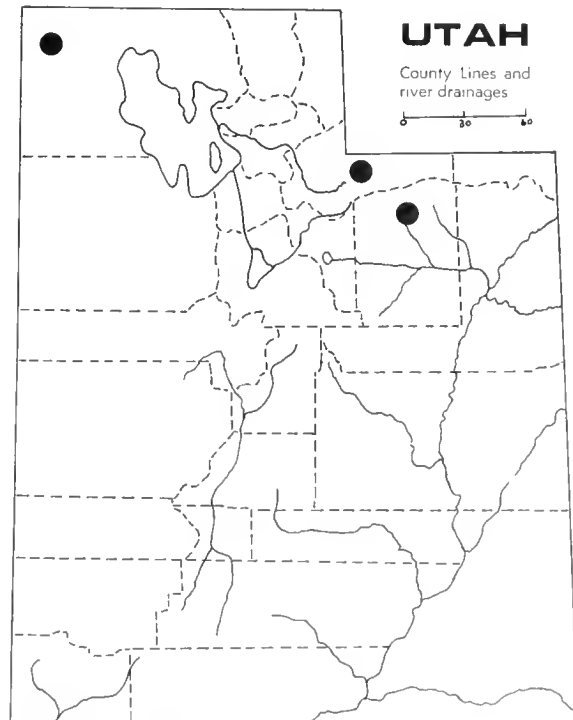


Fig. 74. *Eritrichium nanum*

mound" according to Lehmann in Hooker Fl. Bor. Amer. 2:84. 1838.

Echinosperrnum floribundum Lehm. Stirp. Pub. 2:24. 1830.

Lappula floribunda (Lehm.) Greene, Pittonia 2:182. 1891.

Stem erect, stout, from a short-lived perennial root, 5-12 dm high, the rough pubescence deflexed, mixed with some spreading hairs; leaves oblanceolate to linear or oblong, hirsutulous-appressed, the basal leaves petiolate, with spreading hairs, the stem leaves sessile above; racemes of the inflorescence many, rather strict, densely flowered, pedicels short, 5-7 mm long in fruit; corolla blue, 4-7 mm broad, appendages small, obscurely papillate, not closing the throat; nutlets 3-5 mm long, the face with a medial ridge, muriculate, hirsutulous, without short glochidiate prickles, the marginal spines much flattened at base, distinct or somewhat confluent, 4 to 6 on each side, mostly exceeding in width the face of the nutlet. Brushy slopes and edge of woods. Mostly western United States and Canada, east to Ontario and Minnesota to western Texas. June-August. Fig. 75.

Cache Co., Logan, C.P. Smith 1766b (UTC); Logan Canyon, B. Maguire 12981 (UTC); Tony Grove, Logan Canyon, F.B. Wann 3705 (UTC); City Park, Logan Canyon, B. Maguire 21540 (UTC); West Hodges pasture, Logan Canyon, H.B. Passey 2 (UTC); Logan,

Logan River, Northrop & Crockett s.n. (UTC); Emery Co., Huntington Canyon, W.P. Cottam 7437 (UT); Garfield Co., Henry Mountains, 22.9 miles south of Hanksville, J. Gentry 1753 (UTC); east slope of Mount Ellen, B. Maguire 19322 (UTC); 15 miles southwest of Escalante, H. Hall s.n. (UT); Henry Mountains, W.D. Stanton 4888 (BRY); Juab Co., Thoms Creek, W.P. Cottam 3244 (BRY); Salt Lake Co., Little Cottonwood Canyon, W.P. Cottam 3543 (BRY); Sanpete Co., vicinity of Ephraim, R. Olsen s.n. (UTC); 10 miles up Ephraim Canyon, J.D. Walker s.n. (BRY); Sevier Co., Fish Lake, Maguire & Richards 12982 (UTC); 20 miles west of Richfield, F. Coles 53 (BRY); Wasatch Co., Cascade Terraces, E.C. Davenport 23 (BRY); Utah Co., Mount Timpanogos, B. Maguire 3704 (UTC); Mount Timpanogos, W.P. Cottam 1265 (BRY).

2. *Hackelia jessicae* (McGregor) Brand, Pflanzenreich 4, 252:132. 1931. Type: Halfmoon Lake, Eldorado County, California.

Lappula micrantha Eastw. Bull. Torrey Club 30:497. 1903, not *Hackelia micrantha* Opiz.

Lappula jessicae McGregor, Bull. Torrey Club 37:262. 1910.

Hackelia castwoodiae I. M. Johnst. Contr. Gray Herb. 68:47. 1923.

Lappula floribunda var. *jessicae* Jepson & Hoover in Jepson Fl. Calif. 3:307. 1943.

Stems erect or ascending from a stout root, sparsely to rather densely villous-hirsute; basal leaves 8-15 cm long, the blades oblanceolate, 15-20 mm wide, narrowed to a winged petiole of about equal length; upper stem leaves sessile, lanceolate, acute, the reduced ones subtending the lower racemes often ovate-lanceolate; racemes several in an open panicle; pedicels slender, at length recurved reflexed, 5-10 mm long; calyx-lobes oblong to oblong-lanceolate, 2-3 mm long; corolla small, pale blue, 3.5-5 mm broad, tube often whitish, 1.5-2 mm long, lobes oblong-ovate, crests yellowish, rounded, puberulent; nutlets 4-6 mm long, marginal prickles broadly dilated at base, about 10, distinct, often with a shorter one in between; dorsal face broadly ovate, usually flattened with a distinct median ridge, puberulent and in age more or less muriculate, usually with 1 or more short barbed prickles near the center. Usually on moist banks or slopes. British Columbia, Washington, and Idaho, south to Utah, Nevada, and California. May-August. Fig. 76.

Cache Co., 5 miles up road to Tony Grove, Gentry & Davids 1729 (UTC); Pine Canyon, B. Maguire 3101 (UTC); Logan Canyon, C.P. Smith 2227 (UTC); Sardine Canyon, B. Maguire 12985 (UTC); 12 miles up Smithfield Canyon, B. Maguire 13777 (UTC); Davis Co., Centerville Canyon, A.C. Hull s.n. (UTC); Salt Lake Co., Little Cottonwood Canyon, R.D. Day 35 (BRY); Summit Co., north slope of Big Mountain, D.H. Galway 2382 (BRY); Utah Co., divide between Ameri-

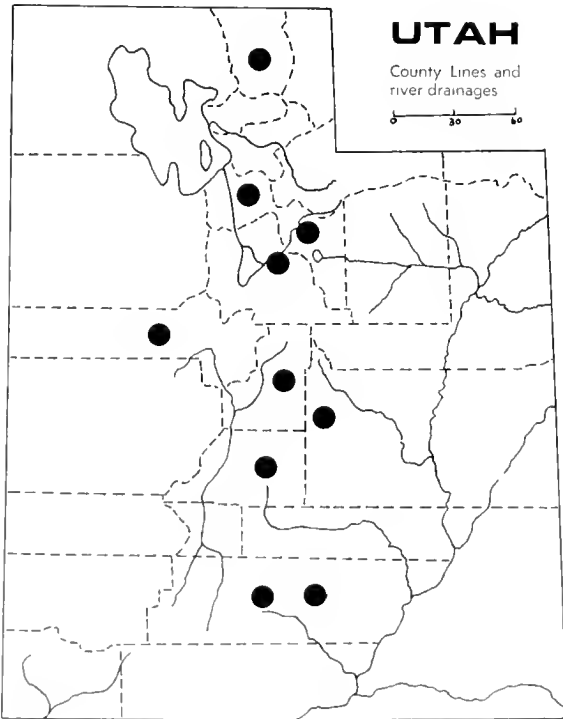


Fig. 75. *Hackelia floribunda*

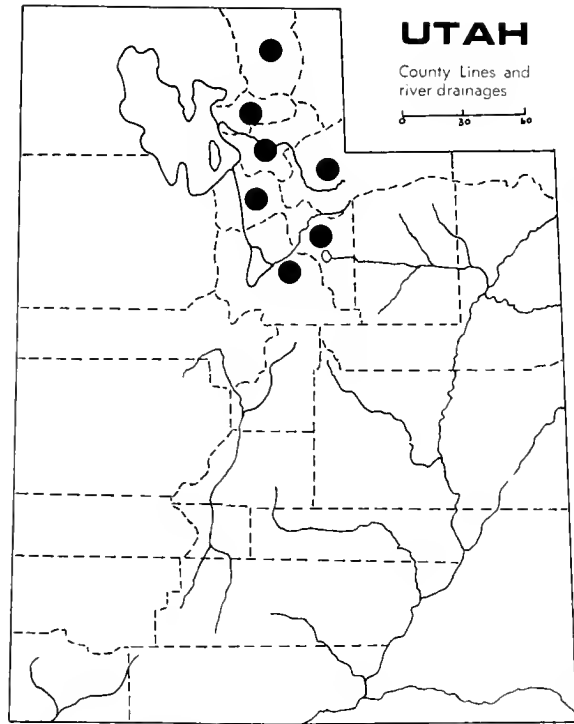


Fig. 76. *Hackelia jessicae*

can Fork and Snake Creek canyons, Welsh, Murdock & Stocks 6348 (BRY); Mount Timpanogos, Little Basin above falls, B. Maguire 17496 (UTC); Wasatch Co., Daniels Canyon, B.F. Harrison 8717 (UTC); Strawberry Valley, D.H. Galway 8717 (BRY).

3. *Hackelia patens* (nutt.) Johnst. Journ. Arn. Arb. 16:194. 1935. Type: Near the Flathead River. Collected by Wyeth.

Rochelia patens Nutt. Journ. Acad. Phila. 7:44. 1834.

Lappula coerulescens Rydb. Mem. N. Y. Bot. Gard. 1:328. 1900.

Stems 2 or 3 short, deflexed hirsute, with some hairs spreading, arising from a woody caudex covered with old leaf bases; basal leaves many, oblanceolate to lanceolate, stem leaves reduced upward, pubescence rather dense, short, appressed; branches of the inflorescence 5-10 flowered, pedicels short, elongating somewhat in fruit; corolla whitish or light blue, usually quite large, appendages somewhat broader than long, obscurely papillose; nutlets small, marginal glochidiate prickles 3-5 on each side, a few short prickles interspersed, the longest prickles surpassing the body of the nutlet; face of nutlet with a faint median ridge, muricate and occasionally bearing 1 or 2 prickles. Sandy or gravelly slopes and foothills. Western Montana and Idaho to Utah and Nevada. May-August. Fig. 77.

Box Elder Co., Cold Water Canyon, L. Williams 636 (UTC); Bench east of Honeyville, M. Burke 3102 (UTC); Smithfield junkpile, D. Stocks 12 (BRY); Raft River Mountains, J. Berryman 35 (UT); Perry Canyon, Cottam, Allen, & Rowland 16244 (UT); Beaver Co., Pine Canyon Pass, south ridge, B. Maguire 20962a (UTC); Cache Co., vicinity of Green Canyon, Maguire & Piranian 12987 (UTC); ½ mile east of the fish hatchery, B. Maguire 3708 (UTC); Sardine Canyon, B. Maguire 12986 (UTC); mouth of Logan Canyon, C.P. Smith s.n. (UTC); Intervale, Logan Canyon, Muencher & Maguire 2422 (UTC); Providence Bench, Logan, C.P. Smith 1593 (UTC); 4 miles up Logan Canyon, B. Maguire 12988 (UTC); Logan Bench, B. Maguire 13771 (UTC); Davis Co., mouth of Holbrook Canyon, R. & B. Anderson s.n. (UTC); Muchler Park, Cottam s.n. (UT); Garfield Co., Henry Mountains, (UT); Juab Co., Granite Canyon, Trout Creek, Maguire & Becraft 2779 (UTC); Deep Creek, W.P. Cottam 3231 (BRY, UT); Iron Co., 12 miles east of Cedar City, B. Maguire s.n. (UTC); Kane Co., vicinity of Glendale, F.B. Wann 36 (UTC); Millard Co., Confusion Range, 21.8 miles east of the Utah-Nevada line, J. Gentry 2003 (UTC); Salt Lake Co., Mill Creek Canyon, L. Eyre 37 (BRY); Jordan Narrows, E. Young s.n. (BRY); Dry Creek Canyon, J. Ludwig 193 (UT); City Creek Canyon, R.K. Vickery 1918 (UT); Big Cottonwood Canyon, H.K. Harrison 68 (UT); Fort Douglas, R.K. Vickery 563 (UT); Sanpete Co., 8 miles southeast of Mt. Pleasant, L.C. Higgins 1095 (BRY); 10 miles west of Moroni, B. Maguire 18657 (UTC); Tooele Co., Intermountain Forest and Range Experiment Station, N. Frischknecht 25 (UTC); Benmore Experiment Station, W.H. Blackburn 39 (BRY); Utah Co., 3 miles south of Thistle, B. Maguire s.n. (UTC); Rock Canyon, P.A. Replogle 80 (BRY); Y Mountain, Decker & Eggertson 347 (BRY); Wasatch Co., 1 mile east of Heber City,

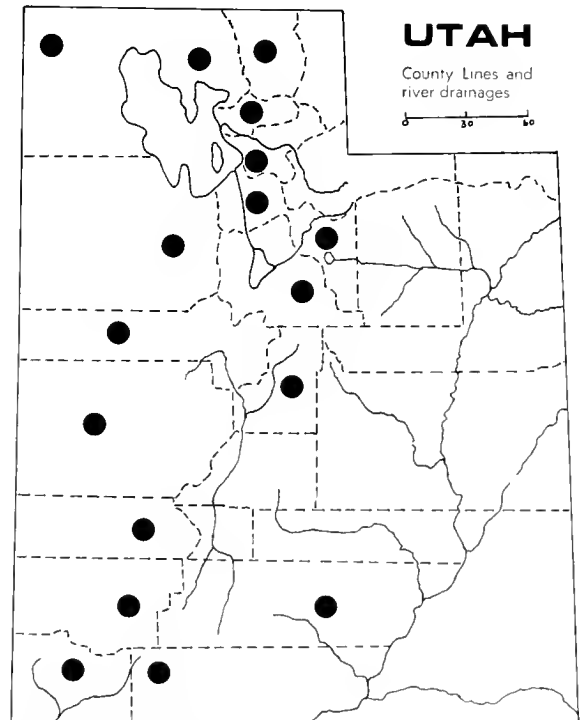


Fig. 77. *Hackelia patens*

B.F. Harrison 8709 (BRY); Weber Co., Ben Lomond Trail, W. Calif 17 (UT); North Ogden, A. Collotzi 77 (UTC).

The following citations are for the variety *harrisonii* Gentry, which has recently been described. Utah Co., near Tucker, Spanish Fork Canyon, L. Mason 4323 (BRY); hogs back between right fork of Hobble Creek and Shingle (Mill) Creek, B.F. Harrison 8323 (BRY); Spanish Fork Canyon, 2 miles east of Thistle, J. Gentry 2000 (UTC); Washington Co., Pine Valley, 1.5 miles up Forsyth Trail, J. Gentry 2002 (UTC).

11. *Heliotropium* L.

Heliotropium L. Sp. Pl. 1:130. 1753, and Gen. Pl. 130. 1754.

Annual or perennial, herbaceous or more or less shrubby plants; leaves small to large, sessile or petiolate; cymes unilateral and usually distinctly scorpioid, with or without bracts; corolla white, yellow or purple, variable in form, throat frequently pubescent inside; anthers included, filaments extremely short; style present or absent; stigma usually frustumlike or conic, mostly sterile, receptive only in a band around the base; fruit dry, at maturity breaking up into 4 single-seeded or 2 biseminiferous nutlets; seeds with a thin endosperm. A large genus widely distributed in the warmer parts of the world, also arid regions.

Type species: *Heliotropium europaeum* L.

1. Plant not succulent, hairy, never glaucous; fruit 2-lobed, each lobe splitting into 2 nutlets; stigma capped by a tuft of bristles 1. *H. convolvulaceum*
 1. Plants very succulent, glabrous, usually glaucous; fruit not lobed, stigma discoid, naked; perennials (2).
 2. Fruit 2.5 mm wide; corolla 5-16 broad, at most only purplish-tinged at the throat 2a. *H. curassavicum* var. *obovatum*
 2. Fruit 1.5-2 mm wide; corolla 3-5 (7) mm broad, usually becoming distinctly purple or purplish at the throat 2b. *H. curassavicum* var. *oculatum*
1. *Heliotropium convolvulaceum* (Nutt.) Gray, Mem. Amer. Acad. Sci. 6:403. 1859. Type: Sandy banks of the Arkansas, Nuttall
Euploca convolvulacea Nutt. Trans. Amer. Phil. Soc. 2, 5:190. 1837.
Batschia albiflora Raf. New Fl. No. Amer. 4:19. 1836. Not *H. albiflorum* Engler, 1924.
Euploca albiflora (Raf.) Johnst. Contr. Gray Herb. 70:53. 1924.
Euploca grandiflora Torr. in Emory. Notes Mil. Recon. 147. 1848.

Annual, 1-4 dm tall, stems at first usually simple, but later developing elongate branches, which are ascending or sprawling; strigose and cinereous; leaves numerous, strigose, pustulate, lanceolate to ovate, 10-14 mm long, 4-15 mm broad, apex acute, base acute to rounded, petiole slender, 3-8 mm long, midrib evident; flowers extra axillary, appearing to be borne along the elongating leafy branches, bracts leaflike, numerous; calyx 5-lobed, at anthesis 4-6 mm long, becoming 6-9 mm long at maturity; lobes linear-lanceolate or linear, unequal; pedicels at anthesis 1-3 mm long, in fruit 3-5 mm long, corolla white with a yellow throat, fragrant, opening during the morning and evening, limb widely funnelform, expanded, 15-22 mm broad, not lobed pentagonal, plicate in the bud with the sinus inflexed; tubular portion of corolla 8-11 mm long, strigose on the outside; anthers lanceolate, basifixed, 2-2.5 mm long; filaments about 1 mm long; ovary globose, glabrous; style slender, 3-4 mm long; stigmatic head with a prominent stigmatic band 0.5 mm in diameter at the base, and this surmounted by a truncate appendage bearing a cluster of hairs; fruit laterally compressed, hairy, 2-lobed, 3-4 mm long, 2-2.5 mm thick, 2-2.5 mm high; at maturity first dividing transversely and the lobes separating, forming halves, each with a broad flat commissural face; each half next dividing on the narrow longitudinal axis to form the asymmetrical single seeded nutlets. In sandy soils. Nebraska and Wyoming, south to northern Chihuahua and Texas, and westward into Arizona and Nevada. June-September. Fig. 78.

Emery Co., 20 miles north of Hanksville, B. Maguire 19397 (UTC); San Raphael Desert, A. Smith s.n. (UTC); 25 miles southwest of Green River, W.P. Cottam 17740 (UT); Garfield Co., 30 miles south of Hanksville, Cronquist & Holmgren 9316 (UTC); 8 miles down Shita Marine Creek, J.C. Pederson 16 (BRY); Hite, D. Lindsay 2 (UT); Grand Co., 5 miles west of Moab, Maguire & Redd 2067 (UTC); north of Moab, B.F. Harrison 12024 (BBY); Juab Co., near Champlin railroad stop, B.F. Harrison 352 (BRY); Millard Co., sand dunes, W.P. Cottam 3792 (UT); San Juan Co., Bluff Cemetery, Holmgren & Hansen 3442 (UTC); ½ mile north of Chocolate Drop Butte, L.O. Wilson 155 (UTC); 5 miles east of Hite, Holmgren & Maguire 10615 (UTC); 8 miles northeast of Hite, Cronquist & Holmgren 9490 (UTC); Bluff, W.P. Cottam 2547 (BRY, UT); Bluff, W.C. Twiss s.n. (UT); Tooele Co., Dugway Valley, S. Flowers 46 (UT); Wayne Co., 5½ miles north of Hanksville, Cronquist & Holmgren 9424 (UTC); between Hanksville and Hite, A.H. Holmgren 7799 (UTC); 10 miles north of Hanksville, S. Flowers 57 (UT); Washington Co., 2.5 miles west of Toquerville, Maguire & Piranian 12316 (UTC); 2 miles south of Anderson's Ranch, Maguire & Richards 15927 (UTC); Santa Clara W.P. Cottam 1519 (BRY); Leeds, W.P. Cottam 5391 (UT); Gumlock, W.P. Cottam 5718 (UT); Santa Clara Bench, W.P. Cottam 12752 (UT); Zion Natl. Park, W.P. Cottam (UT).

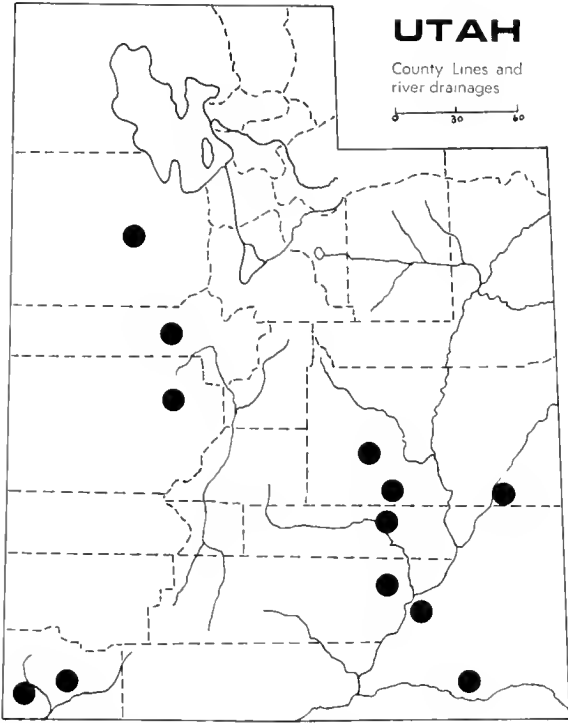


Fig. 78. *Heliotropium concobulaceum*

2. *Heliotropium curassavicum* L. Sp. Pl. 130. 1753.

Annual or short-lived perennial, fleshy, glaucous, glabrous throughout, stems diffusely branched, 1-6 dm long; leaves succulent, varying from linear to obovate, but commonly spathulate, 1-4 cm long, obtuse, narrow to a thick petiole; spike mostly in pairs, sometimes 3-5, often 6-12 cm long; calyx-segments ovate-lanceolate, acute, 2-3 mm long; corolla 3-5 mm long, white with a violet-purple eye on the throat; stigma glabrous; stamens included, the anthers subsessile; fruit subglobose, at length separating into 4 nutlets.

2A. *Heliotropium curassavicum* var. *obovatum* A. DC. Prod. 9:538. 1845. Type: Columbia River, probably near the Blue Mountains, Oregon

Heliotropium spathulatum Rydb. Bull. Torrey Club 30:262. 1903.

Leaves spathulate to obovate; corolla white or slightly tinged with purple, 6-8 mm long, the limb about as broad; nutlets 2.5-3 mm long. Alkaline or saline places. Eastern Washington, eastern Oregon, and northwestern Nevada, east to the Rocky Mountains. June-October. Fig. 79.

Box Elder Co., Bear River Refuge, D. Hobson 14839 (UTC); Knudsen Marsh, Jensen & Dargan s.n.

(UTC); Cache Co., Pelican Pond, J. Thieret 60 (UTC); Daggett Co., Linwood Bridge, S. Flowers 127 (UT); Garfield Co., Bakers Ranch, B. Markham B-9 (UTC); Millard Co., between Delta and Hinekley, Maguire & Becraft 3941 (UTC); Salt Lake Co., Salt Lake City, W.P. Cottam s.n. (UT); Tooele Co., Smelter Bench, C.P. Smith 1893 (UTC); Utah Co., near Provo, W.P. Cottam 3171 (UT); Uintah Co., 8.5 miles north of Ouray, N. Folks 235 (UTC).

2B. *Heliotropium curassavicum* var. *oculatum* (Heller) Johnst. ex Tidestr. Proc. Biol. Soc. Wash. 48:42. 1935. Type: Sand along the Russian River near Healdsburg, Sonoma County, California.

Heliotropium oculatum Heller, Muhlenbergia 1:58. 194.

Heliotropium spathulatum subsp. *oculatum* Ewan. Bull. So. Calif. Acad. 4:56. 1942.

Middle cauline leaves oblanceolate to spathulate, smaller lower and upper ones commonly oblong and acutish; corolla limb about 4 mm wide, the lobes white or bluish and the throat with a violet-purple eye. Southwestern Utah, south to Baja California, and east to New Mexico and Texas. March-September. Fig. 80.

Washington Co., Arizona Strip, B. McAllister s.n. (UTC); St. George, F.B. Wann 32 (UTC); Santa Clara, W.P. Cottam 6900 (UT); 2 miles southeast of Santa Clara, R. Christian 934 (UT); St. George, W.P. Cot-

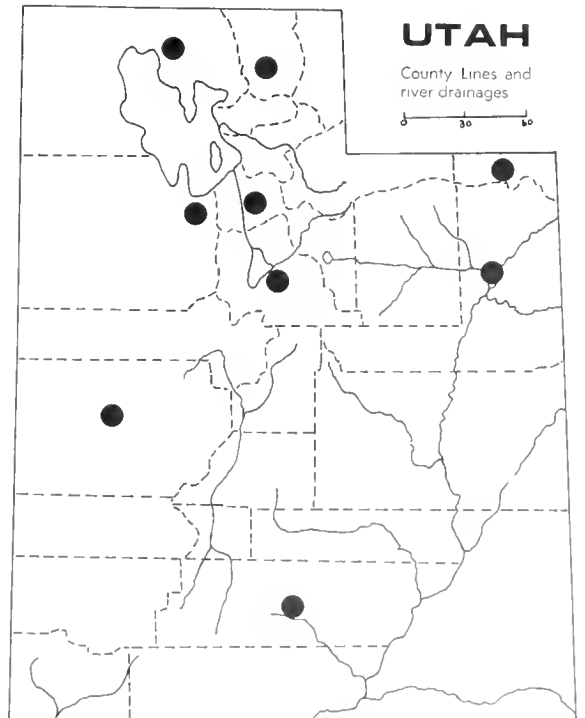


Fig. 79. *Heliotropium curassavicum* var. *obovatum*

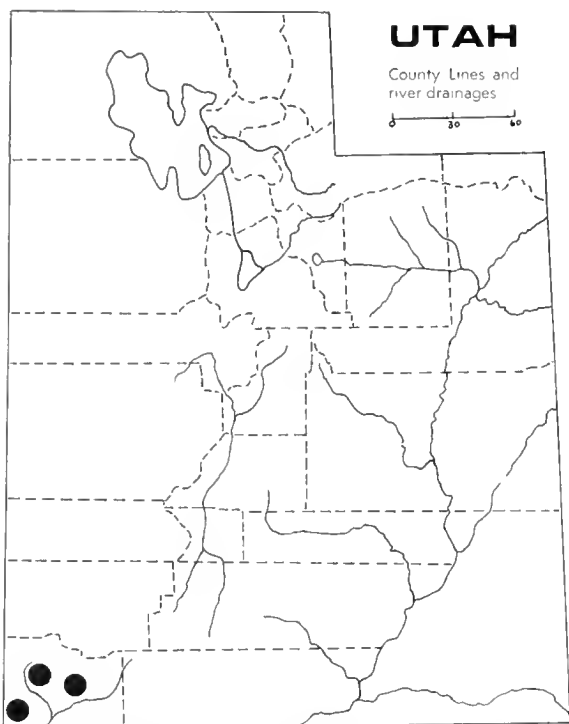


Fig. 80. *Heliotropium curassavicum* var. *oculatum*

tam 3386 (UT); Beaverdam Wash, K.R. Kelson s.n. (UT); Terry's Ranch, S.L. Welsh 5270 (BRY); Terry's Ranch, in the bottom of Beaverdam Wash, L.C. Higgins 513 (BRY).

12. *Lappula* Moench

Lappula Moench, Meth. 416. 1794.

Annual herbs; leaves alternate, usually narrow, firm and veinless; flowers small, blue or white, on usually erect pedicels or rarely subsessile, in bracted racemes; calyx 5-parted into spreading lanceolate lobes; corolla with a rather short tube; lobes rounded, ascending imbricate; throat closed by intruded appendages; stamens affixed in the tube, included; filaments slender, short; anthers oblong, obtuse; style short, surmounting the subulate-columnar gynobase, commonly surpassing the mature nutlets; stigma subcapitate; ovules 4; nutlets 4, erect, smooth or verrucose, narrowly but firmly attached to the gynobase along the length of the well-developed ventral keel, back angulate or margined by a single or double row of prickles which by confluence frequently form a winglike or cupulate border.

Type species: *Myosotis lappula* L. (*Lappula echinata* Gilib.)

1. Nutlets with marginal prickles in at least 2 rows
1. *L. echinata*

1. Nutlets with the marginal prickles definitely in a single row (2).

2. Marginal prickles distinct to the base or nearly so, not confluent to form a cupulate structure 2A. *L. occidentalis* var. *occidentalis*
2. Marginal prickles confluent, forming a conspicuous smooth cupulate structure on the back of some or all the nutlets ... 2B. *L. occidentalis* var. *cupulata*

1. *Lappula echinata* Gilib. Fl. Lith. 1:25. 1781.
Type: Europe.

Myosotis lappula L. Sp. Pl. 131. 1753.

Lappula myosotis Moench Meth. 417. 1794.

Lappula lappula Karst. Deutsch. Fl. 979. 1880-83.

Echinosperrum lappula Lehm. Asperif. 121. 1818.

Annual, with erect, simple to freely branched stems 1.5-8 dm tall, villous-hirsute with upwardly more or less appressed hairs; lower leaves linear to linear-lanceolate or oblong, acute to obtuse, narrowed to a sessile base, closely ascending, 2-5 cm long, roughly pubescent like the stem, passing above into the linear or lanceolate bracts of the usually numerous racemes; pedicels 1-3 mm long; calyx-lobes broadly linear, appressed bristly, in fruit spreading, 2.5-3 mm long; corolla bright blue, the limb 2-4 mm broad, the tube surpassing the calyx; nutlets 3-4 mm long, sharply verrucose or muricate dorsally, with 2 marginal rows of long slender bristles not confluent at the base, these sometimes irregularly distributed over the back. Dry plains, hillsides, and waste places, also cultivated ground. Native of Eurasia. Widespread as a weed in the United States and Canada. June-August. Fig. 81.

Summit Co., John Lambert Ranch, P.B. Lister 12 (UT).

2. *Lappula occidentalis* (Wats.) Greene, Pittonia 4:97. 1899. Not *Lappula redowskii* of European authors.

Echinosperrum redowskii var. *occidentalis*
S. Wats. Bot. King Expl. 246. 1871.

Lappula redowskii occidentalis Rydb. Contr. U. S. Natl. Herb. 3:170. 1895.

Annual, the stems simple or few branched at base and erect or sometimes diffuse, 15-35 cm tall, herbage more or less canescent with a strigose and also a villous pubescence; leaves narrowly linear to narrowly lanceolate or the lower narrowly oblanceolate, 1-3 cm long; flowers in the axils of the small foliaceous bracts forming open and at length elongated terminal racemes; pedicels 1-2 mm long; calyx-segments narrowly

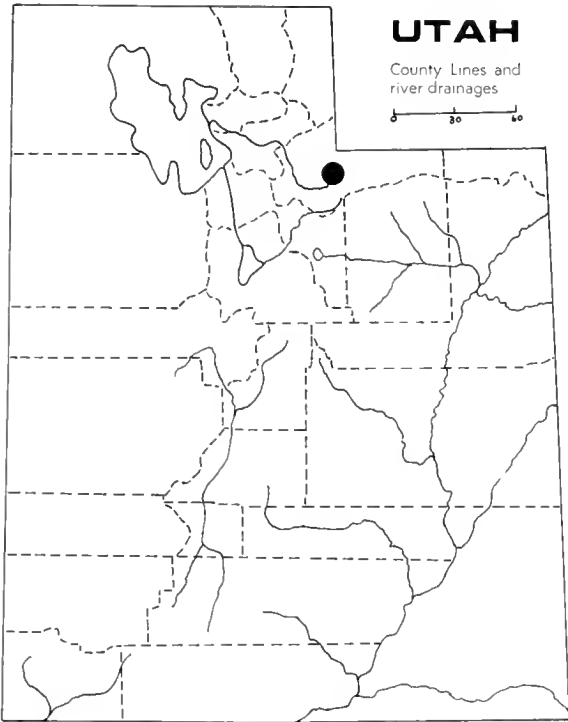


Fig. 81. *Lappula echinata*

lanceolate, erect, or but little spreading in fruit, a little shorter than the corolla-tube, corolla blue, 3-4 mm long, conspicuously crested on the throat; nutlets 2-2.5 mm long, bordered by a single row of barbed prickles, the prickles distinct at base or joined to form a cupulate margin, the dorsal area of nutlets distinctly tuberculate.

2A. *Lappula occidentalis* (Wats.) Greene, var. *occidentalis*

Distinguished by the marginal prickles which are not united at the base, or do not form a cupulate structure of any kind. Dry hillsides and valleys. British Columbia southward to Mexico and eastward to the Dakotas and Texas. April-July. Fig. 82.

Box Elder Co., Hardup, G.F. Knowlton 332 (UTC); Bear River Canyon, C.P. Smith 1678a (UTC); Cottonwood Grove, M. Burke 3104 (UTC); Raft River Mountains S.J. Preece 732 (UT); Beaver Co., Wah Wah Range, Stahmann & Hutchings 40 (UT); Little Reservoir, Beaver Canyon, R.G. Warnock s.n. (UT); Wah Wah Mountains, F. Coles 22 (BRY); Cache Co., Pine Canyon, B. Maguire 3105 (UTC); Logan, Muencher & Maguire 2421 (UTC); intervalle, Logan Canyon, B. Maguire 3713 (UTC); above Pelican Pond, J. Thieret 17 (UTC); Carbon Co., 4 miles north of Price, B. Maguire 18348 (UTC); Price Canyon, S. Flowers 6422 (UT); 5 miles east of Price, B.F. Harrison 10262 (BRY); road to Mounds, D. Atwood 1265 (BRY); Daggett Co.,

vicinity of Flaming Gorge, L. Williams 478 (UTC); 12 miles south of Manila, B.F. Harrison 7901 (BRY); Duchesne Co., Indian Canyon, A.O. Garrett 8329 (UT); 15 miles southwest of Myton, J. Brotherson 1074 (BRY); 5 miles north of Fruitland, J. Brotherson 503 (BRY); 6 miles south of Duchesne, B.F. Harrison 3981 (BRY); 3.5 miles southwest of Duchesne, N.H. Holmgren 1771 (BRY); west of Fruitland, B.F. Harrison 8750b (BRY); Emery Co., 20 miles north of Green River, B. Maguire 18234 (UTC); San Raphael Swell, B. Maguire 18284 (UTC); Huntington Canyon, A.O. Garrett 7018 (UT); Horse Canyon Junction, J.L. Pederson 8 (BRY); 5 miles south of the San Raphael River, B.F. Harrison 9613 (BRY); 5 miles southwest of Temple Mountain, L.C. Higgins 1328 (BRY); Temple Mountain, V.P. Allman s.n. (BRY); Garfield Co., 5 miles south of Hatch, B. Maguire 18270 (UTC); Bromide Peak, Henry Mountains, B.F. Harrison 7450 (UTC); Bryce Canyon Natl. Park, H. Buchanan 70 (UT); Cannonville, J. Reveal 752 (BRY); Mt. Ellen, Henry Mountains, W.D. Stanton 4863 (BRY); Grand Co., near Moab, B.F. Harrison 5957 (BRY); Hill Creek Ranger Station, Vickery & Wiens 1634 (UT); 4 miles east of Green River, J.L. Pederson 10 (BRY); 2 miles north of Thompson, S.L. Welsh 6898 (BRY); Iron Co., Modena, L.N. Goding 1010 (UT); Juab Co., Deep Creek Mountains, Maguire & Beerft 2783 (UTC); Mt. Nebo Ranger Station, R.K. Gierisch 274 (UTC); Trout Creek, Maguire & Beerft 2782 (TC); north of Fumarole, Cottam & MacMillan 9646 (UT); Kane Co., vicinity of Glendale, F.B. Wann 37 (UTC); 2 miles southeast of Kanab, McClain s.n. (UTC); Buckskin Gulch, S.L. Welsh 5312 (BRY); Millard Co., 37 miles west of Delta, Maguire & Beerft 2781 (UTC); 5 miles southwest of Desert Range Exp. Station, B. Maguire 20808 (UTC); 27 miles west of Delta, Maguire & Beerft 2780 (UTC); Desert Range Exp. Station, P. Plummer 30

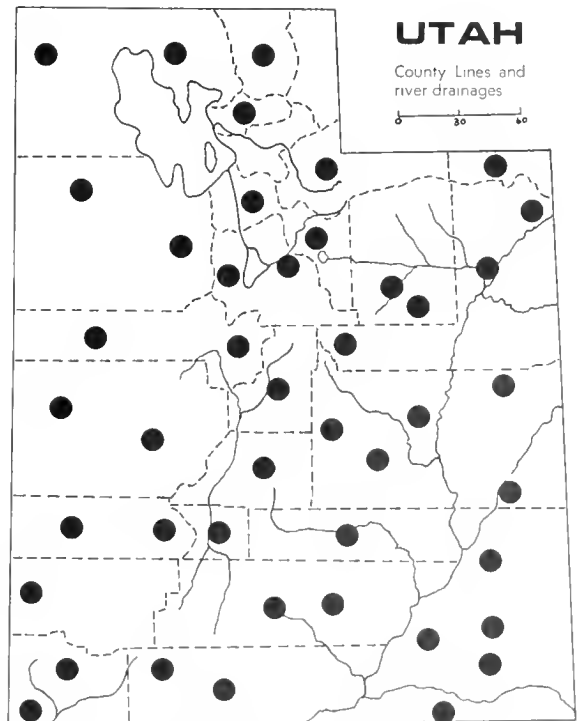


Fig. 82. *Lappula occidentalis* var. *occidentalis*

(UT); Confusion Range, J. Gentry 2033 (BRY); north end of Pine Valley, S. Brewster 18 (BRY); 33 miles north of Millford, Welsh & Moore 6800 (BRY); Piute Co., Monroe Mountain, L.C. Higgins 1158 (BRY); 7 miles south of Puffer Lake, M.L. Morris s.n. (BRY); Highway 22 near milepost 3, D. Atwood 1376 (BRY); Salt Lake Co., Murdock Peak, R.K. Vickery 2360 (UT); City Creek Canyon, K. Brizzee 7783 (UT); San Juan Co., 2 miles east of Mexican Hat, B. Maguire 16258 (UTC); 2 miles northwest of Bluff, B. Maguire 16253 (UTC); 2 miles west of Bluff, B. Maguire 13512 (UTC); 5 miles southwest of Blanding, L.C. Higgins 519 (BRY); Abajo Mountains, Rydberg & Garrett 9663 (UT); Canyonlands Natl. Park, Virginia Park, G. Moore 319 (BRY); Chesler Park, Welsh, Moore & Canter 2905 (BRY); Natural Bridges Natl. Monument, G. Moore 134 (BRY); Sanpete Co., Sanpete-Juab County line, T. Jensen 504 (UTC); Fountain Green, T.R. Stutz 9 (BRY); Tooele Co., Black Rock Canyon, J.L. Reveal 215 (UTC); Benmore Exp. Station, W.H. Blackburn 40 (BRY); near Stockton, L. Amow 278 (UT); Hapah, W.P. Cottam 3149 (BRY); Uintah Co., Dinosaur Natl. Monument, S.L. Welsh 1966 (BRY); 5 miles northwest of Whiterocks, J. Brotherson 559 (BRY); 5 miles south of Ouray, A.D. Youngberg 1106 (BRY); Two Waters Creek drainage, N.H. Holmgren 1870 (BRY); Utah Co., Spanish Fork Canyon, L. Mason s.n. (BRY); 7 miles north of Elberta, R. Coombs 8 (BRY); Diamond Fork Canyon, P.A. Replogle 101 (BRY); west of Utah Lake, W.W. Patton 117 (BRY); Sevier Co., Willow Creek, Duane & Jeffery s.n. (UTC); 5 miles southeast of Sigurd, B. Maguire 18096 (UTC); Fish Lake, B. Markham s.n. (BBY); Fish Lake, L.C. Higgins 1119 (BRY); Fish Creek Canyon, A.O. Garrett 2591 (UT); 2 miles north of Elsinore, J.L. Reveal 734 (BRY); Summit Co., Burnt Fork Creek, E.E. Jensen s.n. (UTC); Browns Meadow, E.M. Christensen s.n. (BRY); Wayne Co., 3 miles from Pace Ranch, B. Maguire 18180 (UTC); Fremont Canyon north of Fruita, B. Maguire 18114 (UTC); Parker Mountain, D.M. Beale 112 (UTC); 6 miles east of Torrey, B. Maguire 18109 (UTC); Fruita, DE. Beck s.n. (BRY); Box Canyon, V. Alexson 47 (BRY); near Torrey W.P. Cottam 9281 (UT); edge of Bicknell Bottoms, R.K. Vickery 593 (UT); Washington Co., Pine Valley Mountains, Gentry & Jensen 2206 (UTC); 10 miles east of Hurricane, Welsh & Moore 6866 (BRY); 5 miles southwest of St. George, L.C. Higgins 1239 (BRY); Pine Valley Mountains, W.P. Cottam 8917 (BRY); 2 miles east of Pinto P. Plummer 7407 (UT); Wasatch Co., east rim of Strawberry Valley, J. Brotherson 694 (BRY); Daniels Canyon, A.O. Garrett 2843 (UT); Weber Co., Snow Basin, A. Collotzi 79 (UTC).

2B. *Lappula occidentalis* (Wats.) Greene var. *cupulata* (Gray) Higgins, comb. nov. (based upon *Echinosperrum redowskii* var. *cupulatum* Gray, Bot. Calif. 1:530, 1876).

Echinosperrum redowskii var. *cupulatum*
A. Gray, Bot. Calif. 1:530, 1876.

Lappula cupulata (Gray) Rydb. Bull. Torrey Club 28:31, 1901.

Lappula texana var. *columbiana* (A. Nels.)
Johnst. Contr. Gray Herb. 70:50, 1924.

Lappula redowskii var. *desertorum*

(Greene) Johnst. Contr. Arn. Arb. 3:93, 1932.

Distinguished from the typical species by having the marginal prickles confluent to about the middle, forming a definite cupulate margin. Southeastern Washington, southward east of the Cascade-Sierra Divide to southern California, eastward to Montana, Wyoming, and New Mexico. April-August. Fig. 83.

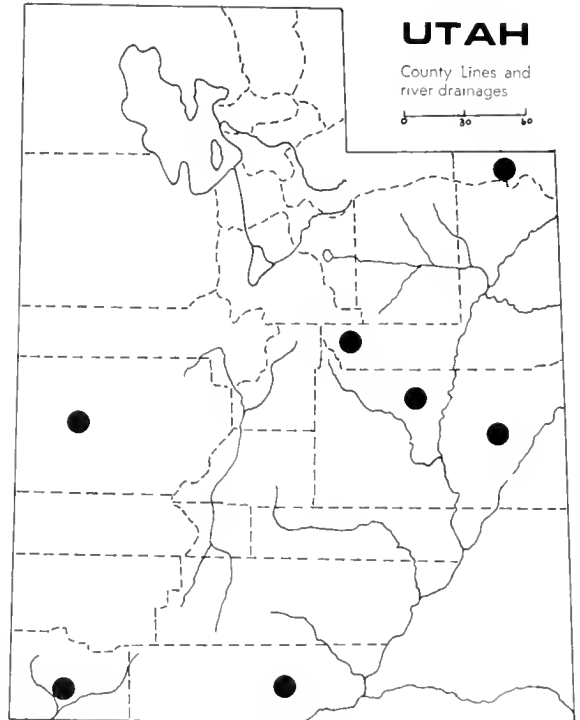


Fig. 83. *Lappula occidentalis* var. *cupulata*

Carbon Co., 3 miles north of Price, R. Hardy s.n. (UT); 1 mile east of Roadside Geyser, R.K. Vickery 718 (UT); Daggett Co., 1 mile south of Manila, B. Maguire 12373 (UTC); Emery Co., 10 miles west of Green River, B. Maguire 2056 (UTC); Grand Co., 3 miles north of Dewey, R.K. Vickery 238 (UT); Kane Co., 47 miles east of Kanab, A. Cronquist 10203 (BRY, UTC); Millard Co., Confusion Range, J. Gentry 2033 (UTC); Washington Co., St. George, W.P. Cottam s.n. (UT).

13. *Lithospermum* L.

Lithospermum L. Sp. Pl. 1:132, 1753, and Gen. Pl. 64, 1754.

Annual or perennial, herbaceous or fruticose plants with alternate leaves; flowers white, yellow, or violet, in bracted racemes; calyx usually undivided; corolla tubular or salverform, the tube cylindrical, lobes spreading and imbricate, the throat with intruded appendages or with pubescent or glandular areas; stamens affixed in

the tube, included; filaments short, anthers oblong, usually with apiculate connectives; style filiform; stigmas geminate; ovules 4; nutlets 4 or rarely fewer, erect, ovoid or angular, smooth or verrucose, affixed by a broad horizontal or slightly oblique basal areola; gynobase flat or very broadly pyramidal.

Type Species: *Lithospermum officinale* L.

- 1. Annual; flowers white; nutlets densely tuberculate and dull 1. *L. arvense*
- 1. Perennial; flowers greenish to yellow, nutlets white, smooth (2).
- 2. Corolla 10 mm long or more, tube definitely exceeding the calyx, green or pale yellow, nutlets 4-6 mm long 4. *L. ruderalis*
- 2. Corolla 10 mm long or more, tube definitely exceeding the calyx, yellow (3).
- 3. Styles of all flowers about the same length; stamens all borne near the top of corolla tube; corolla bright yellow, usually over 20 mm long, its lobes toothed or with a fringe of hairs; later flowers cleistogamous, much smaller, in fruit with recurved pedicels 2. *L. incisum*
- 3. Styles of flowers of 2 lengths (heterostyled); stamens borne either about at the middle or near the top of the corolla tube; corolla deep yellow or orange, not over 20 mm long, its lobes entire or nearly so; smaller cleistogamous flowers absent; root thick, containing a purple dye 3. *L. multiflorum*

1. *Lithospermum arvense* L. Sp. Pl. 132. 1753.
Type: Europe.

Annual; stems erect, 2-7 dm tall, one to several simple or sparsely branched above, hoary strigose; leaves 2-5 cm long, 2-8 mm broad, closely appressed-hispid, firm, veinless, with prominent midrib, pale beneath, basal leaves rosulate, oblanceolate, or spatulate, those of the stem acute and lanceolate or linear; racemes bracted, becoming loosely flowered; calyx parted into linear-subulate lobes, hispid, mature calyx with the erect or ascending lobes becoming 8-13 mm long, the very short tube oblique, pale and chartaceous, pedicels short and stout, about 1 mm long, corolla white or yellowish or even purplish, 5-7 mm long, tubular-funnelform, the tube glabrous within and scarcely if at all surpassing the calyx; corolla-throat gradually expanded, without protuberances, merely pubescent; corolla-lobes ascending ovate, obtuse; nutlets brown, dull, roughened, tuberculate, or rough-wrinkled or pitted, about 3 mm long, ovate. Grassy hillside and grain fields. Naturalized from Europe, widely introduced in the United States. June-August. Fig. 84.

Cache Co., ½ mile south of Providence, B. Maguire 21658 (UTC); just east of Millville, G. Davidse 1026

(UTC); Providence Canyon, B. Maguire 12989 (UTC); Davis Co., above Bountiful, R.K. Vickery 1910 (UT); Tooele Co., south of Tooele, A.F. Heaps 3907 (UT); about 12 miles southeast of Tooele, L.C. Higgins 3345 (BRV); Salt Lake Co., Dry Creek Canyon, J. Ludwig 233 (UT); 5 miles east of Salt Lake City, L. Arnow 291 (UT); Fort Douglas, R.K. Vickery 561 (UT); Utah Co., mouth of Hobble Creek Canyon, B.F. Harrison 12216 (BRV).

2. *Lithospermum incisum* Lehm. Asperif. 2:303. 1818.

Lithospermum angustifolium Michx. Fl. Bor. Amer. 1:130. 1903. not Forsk 1775.

Lithospermum linearifolium Goldie, Edinb. Phil. Journ. 6:322. 1822.

Batschia longiflora Nutt. in Pursh, Fl. Sept. Amer. 1:132. 1814.

Lithospermum longiflorum (Pursh) Spreng. Syst. 1:544. 1825.

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

Lithospermum decumbens (Nutt.) Torr. Ann. Lyc. N.Y. 2:225. 1826.

Lithospermum cryptanthiflorum Brand in Fedde, Report 28:13. 1930.

Lithospermum boreale Brand in Fedde, Report 28:13. 1930.

Lithospermum breviflorum Engelm. & Gray, Journ. Bost. Soc. N.H. 5:252. 1845.

Perennial plants from a thick woody root, stems 1-5 dm tall, usually several, erect or as-

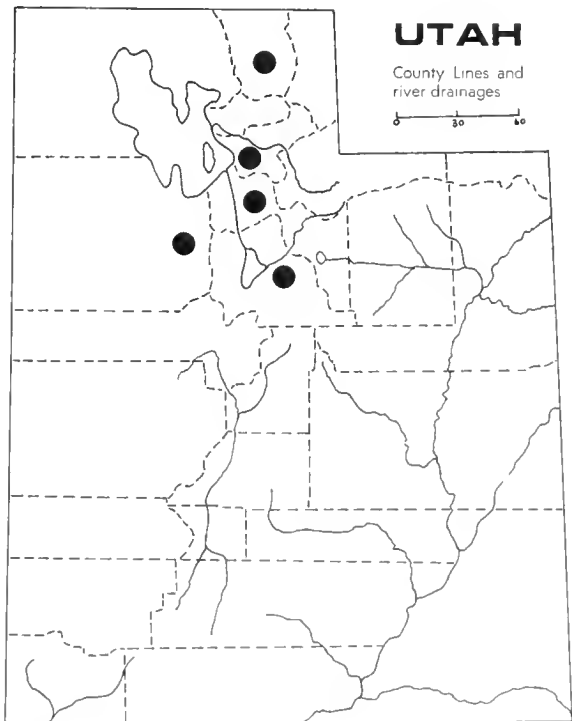


Fig. 84. *Lithospermum arvense*

ending, strigose to somewhat hirsute; leaves 10-50 mm long, linear to linear-oblong, strigose; inflorescence of terminal leafy racemes; calyx 6-10 mm long; corolla 10-30 mm long, yellow, the tube seldom over 2.5 mm wide when pressed, salverform, limb 9-18 mm wide, lobes fimbriate to toothed; nutlets 3-4 mm long, white and shining; cleistogamous flowers present, in fruit usually with recurved pedicels; flowers monomorphic. Dry plains and slopes. Ontario to British Columbia, south to Illinois, Texas, Mexico, and Arizona. April-July. Fig. 85.

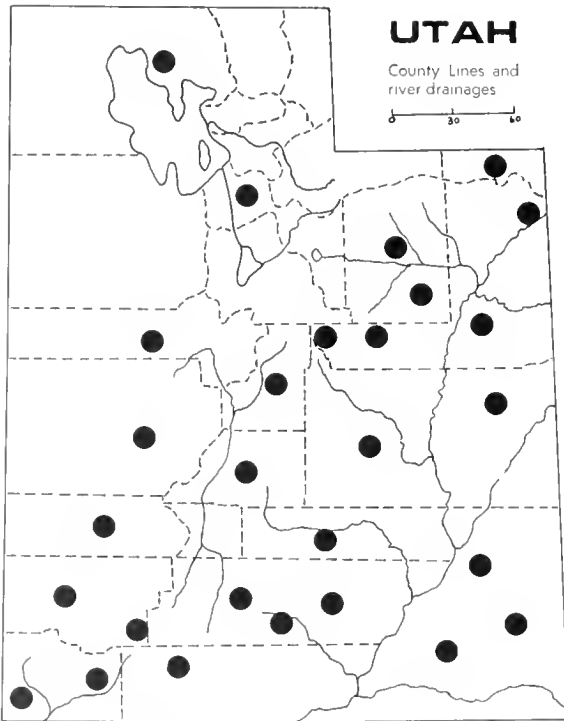


Fig. 85. *Lithospermum incisum*

Beaver Co., Wah Wah Mountains, 4.5 miles up Pine Canyon, B. Maguire 20942 (UTC); Pine Grove, Wah Wah Mountains, W.P. Cottam 8055 (UT); Box Elder Co., 3 miles south of Deweyville, A.H. Holmgren 7002 (UTC); Carbon Co., 10 miles north of Wellington on the Myton highway, B. Maguire 18573 (UTC); Price, S. Flowers 911 (UT); road to Mounds, D. Atwood 1263 (BRY); Daguerre Co., 1 mile below Hole in the Rock Grazing Station, A.H. Holmgren & Tillett 9519 (UTC); north slope of the Uintah Mountains, V.B. Richens s.n. (UTC); Duchesne Co., north rim of Nine Mile Creek, N.H. Holmgren 1951 (BRY, UTC); 6 miles west of Mt. Home, J. Brotherson 875 (BRY); Emery Co., San Raphael Swell B. Maguire 18430 (UTC); head of Cottonwood Wash, D. Atwood 1303 (BRY); head of Buckhorn Wash, B.F. Harrison 8138 (BRY); Garfield Co., 17 miles southwest of Escalante, A. Cronquist 9158 (UTC); 5 miles northeast of Ruby's Inn, Holmgren & Nielsen 7756 (UTC); southeast of Escalante, D. Atwood 301 (UTC); Henry Mountains, W.P. Cottam 5510 (UT); Bryce Canyon Natl. Park, L. Ar-

now 4 (UT); south of Circleville, D. Atwood 1378 (BRY); north side of Boulder Mountain, B.F. Harrison 9164 (BRY); west of Mt. Ellen near Kings Ranch, B.F. Harrison 5540 (BRY); Bryce Canyon Natl. Park, W.S. Boyle 1112 (BRY); Grand Co., near Thompson, S.L. Welsh 6922 (BRY); Iron Co., Iron Mountain, P. Plummer 7425 (UT); Cedar Canyon, W.P. Cottam 3931 (BRY); above Orderville, W.P. Cottam 4270 (BRY); Kane Co., 2.5 miles north of Cottonwood Wash Spring, Reveal, Gentry & Davidse 814 (BRY, UTC); $\frac{1}{2}$ mile north of Mt. Carmel Junction, Maguire & Piranian 12293 (UTC); 10 miles north of Glendale, B. Maguire 18948 (UTC); 15 miles north of Orderville, B. Maguire 18873 (UTC); Juab Co., south base of Topaz Mountain near Thomas, Welsh & Atwood 9675 (BRY); Millard Co., Pavant Butte, W.P. Cottam s.n. (UT); San Juan Co., 1 mile west of Monticello, Holmgren & Anderson s.n. (UTC); Kigalia Ranger Station, D.E. Henriques s.n. (UT); 20 miles west of Blanding, B.F. Harrison 5896 (BRY); 10 miles south of Monticello, B.F. Harrison 11910 (BRY); Natural Bridges Natl. Monument, G. Moore 44 (BRY); Salt Canyon, Welsh, Moore & Canter 2991 (BRY); Canyonlands Natl. Park, Virginia Park, G. Moore 334 (BRY); 5 miles west of Blanding, L.C. Higgins 518 (BRY); Salt Lake Co., point of mountain, E.M. Christensen s.n. (BRY); Sanpete Co., 11 miles west of Fayette, T. Jensen 573 (UTC); Sevier Co., Salina Canyon, W.P. Cottam 9194 (UT); 40 miles north of Fremont, B.F. Harrison 7340 (BRY); Uintah Co., Willow Creek drainage, Holmgren & Reveal 1853a (BRY, UTC); Book Cliffs, L.C. Higgins 1593 (BRY); Dinosaur Natl. Monument, S.L. Welsh 86 (BRY); Washington Co., Zion Natl. Park, Holmgren, Reveal & LaFrance 1985 (BRY, UTC); Zion Natl. Park, W.P. Cottam 6987 (UT); Beaverdam Mountains, L.C. Higgins 909 (BRY); Pine Valley, W.P. Cottam 4053 (BRY); Wayne Co., $\frac{3}{4}$ mile southwest of Teasdale, G. Davidse 1080 (UTC); north trail into Elaterrite Basin, Bryan s.n. (UTC); Standing Rock area, W.P. Cottam 17774 (UT).

3. *Lithospermum multiflorum* Torr. ex Gray, Proc. Amer. Acad. 10:51. 1874. Type: Probably New Mexico.

Lithospermum cognatum Greene ex Spengler, Oesterr. Bot. Zeit. 68:118. 1919.

Perennial plants from a thick woody root containing a purple dye; stem 3-6 dm tall, more or less tufted, often virgately branched above, strigose-hispid; leaves 2-6 cm long, linear or linear-lanceolate, appressed-strigose above, hirsute beneath, becoming smaller and bractlike near the flowers, scarcely if at all longer than the calyx lobes and simulating them; flowers racemose, short-pedicel, often on several ascending corymblike branches; calyx lobes about 4-6 mm long; corolla yellow or orange-yellow, tubular funnellform, the tube about 8-13 mm long, the lobes short, about 2 mm long, rounded, not fimbriate; nutlets about 3 mm long, white and shining; cleistogamous flowers absent; flowers heterostyled and dimorphic. Hills, canyons and mountain slopes, Wyoming to Mexico. May-July. Fig. 86.

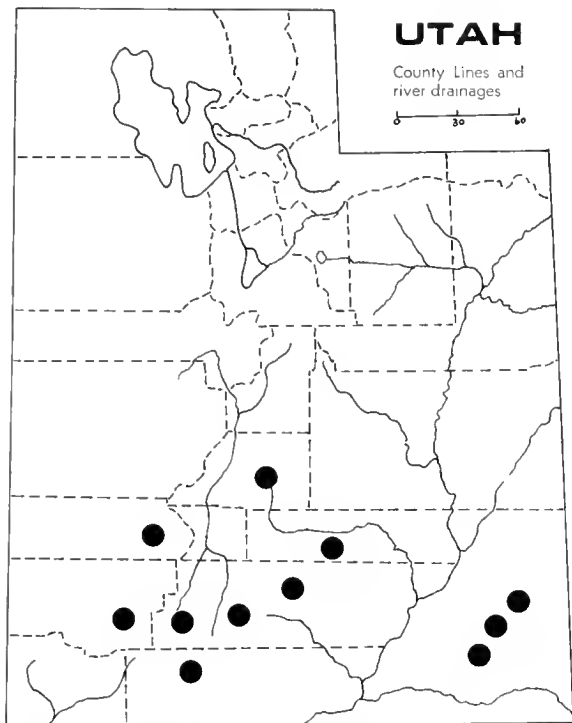


Fig. 86. *Lithospermum multiflorum*

Beaver Co., 8 miles east of Beaver, B. Maguire 19666 (UTC); Garfield Co., 15 miles north of Escalante, N.H. Holmgren 2438 (BRY, UTC); Bryce Canyon Natl Park, Sunrise Point, W.S. Boyle 1114 (BRY); 4 miles east of Widtsoe Junction, Welsh, Isley & Moore 6496 (BRY); Red Canyon, B. Maguire 19082 (BRY); north of Red Canyon Campground, D. Atwood 1889 (BRY); Bryce Canyon Natl. Park, W.P. Cottam 11454 (UT); 15 miles southwest of Escalante, H. Hall s.n. (UT); Iron Co., 10 miles east of Cedar City, Rethke & Raadshoven 4628 (UTC); highway 14, 7.8 miles east of Junction highway 55, L. Arnou 101 (UT); Kane Co., 10 miles north of Orderville, B. Maguire 18767 (UTC); 15 miles northwest of Orderville, B. Maguire 18809 (UTC); San Juan Co., Arch Canyon, W.P. Cottam 2433 (BRY); Church Rock, W.P. Cottam 2316 (BRY); Devils Canyon between Blanding and Monticello, A.H. Holmgren 3492 (BRY, UTC); Elk Ridge, Maguire & Redd 2063 (UTC); 8 miles north of Blanding, Holmgren & Hansen 3381 (UTC); Abajo Mountains, W.C. Twiss s.n. (UT); Sevier Co., Fish Lake, D.W. Lindsay s.n. (BRY); Wayne Co., 16 miles southeast of Torrey, Cronquist & Holmgren 9357 (UTC).

- 4. *Lithospermum rudicale* Dougl. ex. Lehm. Stirp. Pug. 2:28. 1830. Type: Gravelly banks of the Columbia and Willamette rivers.
- Lithospermum pilosum* Nutt. Journ. Acad. Phila. 7:43. 1834.
- Lithospermum torreyi* Nutt. op. cit. 44.
- Lithospermum laxum* Greene, Pittonia 3:263. 189S.
- Lithospermum rudicale* var. *lancoelatum* A. Nels. Bot. Gaz. 52:272. 1911.

Stems usually several from a large root, erect or decumbent, rather stout, 2-5 dm high, simple or branched, hirsute and somewhat hispid to densely villous; leaves numerous, usually crowded above, mostly ascending or sometimes reflexed, linear-lanceolate to lanceolate, 3-8 cm long, 2-12 mm wide, softly to rather harshly pubescent on both sides, scabrous on the margins, flowers in the axils of the upper leaves; pedicels stout, 1-3 mm long; calyx lobes in fruit subulate, 7-10 mm long; corolla pale, often greenish-yellow, 9-12 mm long, tube broad, scarcely dilated at the throat, lobes about 3 mm long; nutlets broadly ovoid, 5-6 mm long, usually abruptly attenuate at the apex into a stout beak, whitish, smooth and highly polished. Dry plains and hillsides. British Columbia, south in the Pacific States east of the Cascade and Sierra Ranges, east to Alberta, Montana, Wyoming, Colorado, and Utah. April-July. Fig. 87.

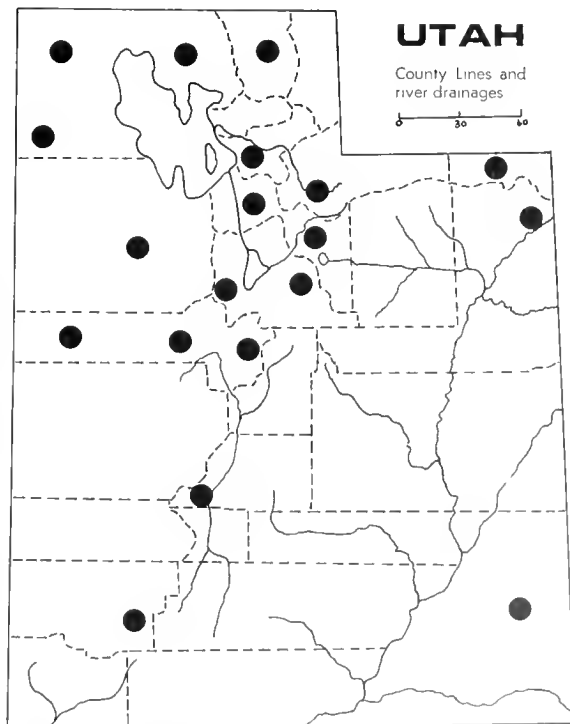


Fig. 87. *Lithospermum rudicale*

Box Elder Co., Copper Mountain, W.P. Cottam 3120 (UT); Cottonwood Canyon, M. Burke 3115 (UTC); south of Staurod, Raft River Mountains, K.S. Erdman 1530 (BRY); Grouse Creek, K.S. Erdman 1629 (BRY); Cache Co., Logan, S. M. Lewis 7 (UTC); top of Sardine Canyon, N.H. Holmgren s.n. (UTC); 3.5 miles south of Hlyrum turnoff, R. Eastmond 245 (BRY); Daggett Co., Green Lakes, L. Williams 601 (UTC); Davis Co., Mueller Park K. Brizzee 7771 (UTC); near Bountiful Reservoir, B.A. Anderson 52 (UTC); Iron Co., Dixie Natl. Forest, G.S. Grew s.n. (UTC); Juab

Co., Johnsons Canyon, Deep Creek Mountains, W.P. Cottam 7184 (UT); Mt. Nebo Ranger Station, R.K. Gierisch 286 (UTC); Robinson, I.E. Diehl D1 (BRY); Salt Lake Co., Dry Creek Canyon, J. Ludwig 20 (UT); San Juan Co., 1 mile west of Monticello, Holmgren & Hansen 3384 (UTC); 3.5 miles south of Monticello, J. Christensen s.n. (UTC); Sevier Co., summit east of Cove Fort, D. Atwood 1516 (BRY); Summit Co., Peoa Cemetery, S.L. Welsh 541 (BRY); Tooele Co., Sheeprock Mountains, E.M. Christensen s.n. (BRY); Uintah Co., 5 miles north of White Rocks, A.D. Youngberg 1017 (BRY); Dinosaur Natl. Monument, S.L. Welsh 489 (BRY); Utah Co., right fork of Hobbie Creek Canyon, L.C. Higgins 3504 (BRY); mouth of Hobbie Creek Canyon, Condom s.n. (UT); 3 miles south of Thistle, B. Maguire 18645 (UTC); Diamond Fork, J.W. Thomas 141 (BRY); east of Provo, B.F. Harrison 6582 (BRY); southeast of Spanish Fork, E. Nixon 64 (BRY); east Tintic Mountains, R. Coombs 132 (BRY); 10 miles east of Springville, W.M. Tingey 148 (BRY); Wasatch Co., southeast slope of Bear Canyon, A.C. Blauer 59 (BRY).

14. *Mertensia* Roth.

Mertensia Roth, Cat. Bot. 1:34. 1797.

Glabrous or pubescent caulescent perennial herbs with fleshy, fusiform, rhizomelike or corm-like roots; leaves entire, linear to cordate, sessile or petiolate, alternate; stems 1-many from each root, decumbent to erect, usually branched below the inflorescence, 0.3-17 dm tall; inflorescence a lax or congested, ebracteate, unilateral, modified scorpioid cyme, or with the lowest flowers often single and subtended by leaves, often becoming panicle in age; calyx 5-parted, occasionally campanulate, the expanded limb exceeding or exceeded by the tube, with or without fornicies in the throat, blue, occasionally white or pink; filaments attached below the throat, the anthers exerted or included; style shorter or longer than the corolla, in some di- or trimorphic; stigma entire or slightly lobed; ovary 2-celled, each cell 2-lobed; nutlets 4, attached laterally to the gynobase, usually rugose or pectinately rugose, coriaceous or smooth and shining, utriclelike.

Type species: *Mertensia virginica* (L.) Pers.

1. Plants usually with prominent lateral veins in the cauline leaves; stems usually 4 dm or more tall (1-17); normally flowering in late spring and in the summer; mostly occurring in moist, shaded situations (2).
1. Plants usually without lateral veins in the cauline leaves, some specimens of *M. oblongifolia* var. *nevadensis* excepted; stems usually less than 4 dm tall, normally flowering in early spring, later when growing in the mountains, but commonly as soon as the snow and temperatures permit; mostly in fairly open habits (7).
2. Limb of the corolla longer than the tube; leaves usually acuminate (3).
2. Limb of the corolla shorter than the tube, or the

- two about subequal; leaves usually not acuminate (6).
3. Leaves pubescent at least on one surface (4).
3. Leaves glabrous on both surfaces (5).
4. Calyx not accrescent, margins densely ciliate, backs pubescent or glabrous 5. *M. franciscana*
4. Calyx accrescent, margins not densely ciliate, backs glabrous 1C. *M. arizonica* var. *subnudata*
5. Calyx campanulate, lobes shorter than the tube 1A. *M. arizonica* var. *arizonica*
5. Calyx not campanulate, the lobes longer than the tube 1B. *M. arizonica* var. *leonardii*
6. Leaves pubescent at least on one surface 5. *M. franciscana*
6. Leaves glabrous on both surfaces, sometimes the upper surface papillate 4. *M. ciliata*
7. Filaments attached in the corolla tube, the anthers not projecting beyond the throat, contained within the tube 3. *M. brevistyla*
7. Filaments attached near the throat of the corolla tube, anthers projecting beyond the throat, not contained within the tube (8).
8. Limb of the corolla longer than or subequal to the tube (8).
8. Limb of the corolla shorter than the tube (11).
9. Leaves pubescent on both surfaces, usually unilateral 8B. *M. viridis* var. *cana*
9. Leaves strigose only above or glabrous on both surfaces (10).
10. Filaments shorter than the anthers; calyx divided nearly to the base; style usually not reaching the anthers; anthers straight; plants alpine 8A. *M. viridis* var. *viridis*
10. Filaments longer than the anthers; calyx not divided to near the base; style usually reaching or surpassing the anthers; anthers usually curved; plants usually not alpine or subalpine 6. *M. fusiformis*
11. Tube of the mature corolla only slightly longer than the limb; plants of the high mountains (12).
11. Tube of the mature corolla usually much longer than the limb; plains and low hills (15).
12. Leaves pubescent only above, or glabrous on both surfaces (13).
12. Leaves pubescent on both surfaces (14).
13. Leaves glabrous on both surfaces, Uinta Mountains 8C. *M. viridis* var. *dilatata*
13. Leaves strigose above 8A. *M. viridis* var. *viridis*
14. Leaves usually unilateral, 1.5-3 cm long, stems ascending 8B. *M. viridis* var. *cana*
14. Leaves not unilateral, usually larger than above; stems more erect; Uinta Mountains 2. *M. bakeri*
15. Leaves glabrous on both surfaces 7C. *M. oblongifolia* var. *nevadensis*
15. Leaves pubescent, at least on one surface (16).
16. Leaves pubescent above, glabrous below 7A. *M. oblongifolia* var. *oblongifolia*
16. Leaves pubescent on both surfaces 7B. *M. oblongifolia* var. *amoena*

1A. *Mertensia arizonica* Greene, Pittonia 3:197. 1897.

Plants erect or ascending, 3-8 dm tall or more; stems 1-several from each root stock, basal leaves narrowly to broadly ovate or oblong-lanceolate, 7.5-15 cm long, 2-6 cm broad, slightly decurrent on the petiole, petiole as long as the blade, glabrous but slightly papillate, margin ciliate; lower cauline leaves spatulate to elliptical, usually petiolate, the petiole winged, upper cauline leaves usually sessile, elliptical to narrowly ovate, acute, 3-12 cm long, 1-5 cm broad, base attenuate, apex acute; inflorescence of axillary peduncles with branches elongating in age; calyx 4-8 mm long, campanulate, glabrous on the back, hairy within, the lobes $\frac{1}{2}$ or less the entire length of the calyx, 2-4 mm long, acute or obtuse, ciliate; pedicels 2-30 mm long, glabrous, papillose or sometimes the papillae developing short hairs; corolla tube 6-9 mm long, with a definite ring of hairs at the base within; corolla-limb 7-11 mm long, always longer than tube, moderately expanded; anthers 2.5-3.5 mm long, as long as or shorter and narrower than the filaments, filaments 3-4 mm long, fornicies conspicuous, pubescent; style 10-15 mm long, usually shorter than the corolla; nutlets rugose, shorter than the calyx. Central to southwestern Utah. Moist stream banks and shaded areas. May-August. Fig. 88.

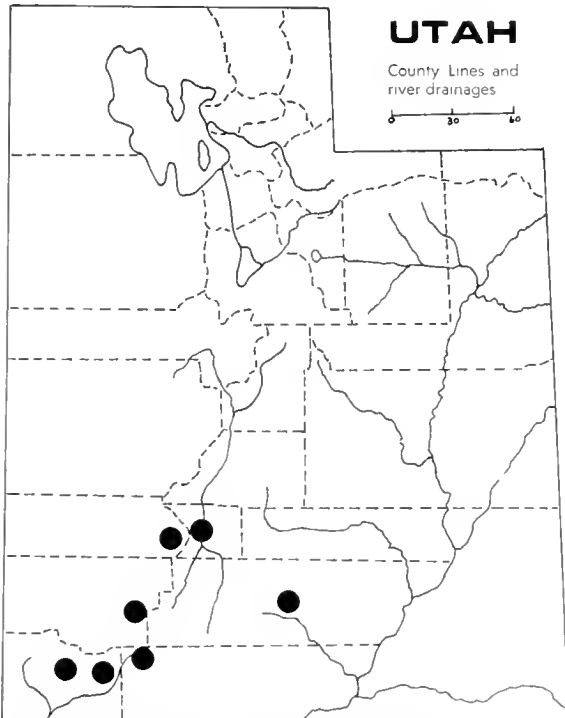


Fig. 88. *Mertensia arizonica* var. *arizonica*

Beaver Co., Big Flat, 5 miles south of Puffer Lake, F.H. Coles 88 (BRY); Tushar Mountains, vicinity of Puffer Lake, M.I. Morris 147 (BRY); Garfield Co., 16 miles south of Escalante, N.H. Holmgren 2519 (UTC); Iron Co., Cedar Breaks Natl. Monument, A. Bruhn 43 (UT); Cedar Breaks Natl. Monument, near Point Supreme, W.S. Boyle 731 (BRY); Cedar Mountain, Duck Creek, A.M. Woodbury s.n. (BRY); Cedar Breaks, W.P. Cottam 3960 (BRY); Cedar Breaks, C.L. Hitchcock 4553, 4572 (UTC); 10.5 miles east of Cedar City, B. Maguire 19469 (UTC); Cedar Breaks, Brian Head Peak, B. Maguire 18995, 17577 (UTC); Kane Co., south side of Navajo Lake, R.K. Gierisch 491 (UTC); Piute Co., Tushar Mountains, Bullion Creek, N.H. Holmgren 2147 (BRY, UTC); Washington Co., Pine Valley Campground, L.C. Higgins 1438 (BRY); Pine Valley Mountains, along middle fork of the Santa Clara River, J.L. Gentry 2231 (BRY, UTC); Zion Natl. Park, N.H. Holmgren 1994 (BRY, UTC); Pine Valley, W.P. Cottam 8874 (UT).

1B. *Mertensia arizonica* var. *leonardii* (Rydb.) Johnston. Contr. Am. Arb. 3:83. 1932.

Mertensia leonardii Rydb. Bull. Torrey Club 36:680. 1909.

Mertensia sampsonii Tidest. Proc. Biol. Soc. Wash. 26:122. 1913.

Mertensia arizonica var. *umbrotalis* Macbr. acc. to Macbride Contr. Gray Herb. n.s. 48:9. 1916.

Plants similar to the species; calyx 4-8 mm long, divided almost to the base, lobes 3-7 mm long, lanceolate, acute, ciliate; anthers and filaments averaging slightly shorter than in the species. Central and north central Utah and southwestern Wyoming. Moist slopes and bottoms and shaded areas. May-August. Fig. 89.

Beaver Co., Puffer Lake, W.P. Cottam 3490 (BRY, UT); headwaters of the Beaver River, B. Maguire 19793 (UTC); Cache Co., Spring Hollow, B. Maguire 12996 (UTC); Logan Canyon, C.P. Smith 2216 (UTC); 1 mile above Tony Grove, B. Maguire 16711 (UTC); Duchesne Co., head of Blind Stream Canyon, B.F. Harrison 8839 (BRY); Emery Co., Huntington Canyon, W.P. Cottam 7452 (UT); Garfield Co., Aquarius Plateau, N.H. Holmgren 2112 (BRY, UTC); 15 miles north of Escalante, N.H. Holmgren 2439 (UTC); Posey Lake, Escalante Road, I. McArthur 173 (BRY); Aquarius Plateau, B. Maguire 19175 (UTC); Iron Co., Cedar Breaks, A. Eastwood & J.T. Howell 7277 (UTC); Juab Co., north of Mt. Nebo, W.P. Cottam 15648 (UT); Millard Co., 2 miles above Adelaide Park, P. Plummer 178 (UT); Robins Valley 20 miles west of Salina, F.H. Coles 42 (BRY); Piute Co., Tushar Mountains, Bullion Creek, N.H. Holmgren 2141 (BRY, UTC); Salt Lake Co., Big Cottonwood Canyon, E.B. Robinson s.n. (UT); above Alta, L. Arnow 458 (UT); Parleys Canyon, G. Davidse 402 (UTC); Emigration Canyon, C.P. Smith 1846 (UTC); Brighton Guard Station, L. Eyre 12 (BRY); Sanpete Co., 15 miles east of Ephraim, R.D. Jorgensen 44 (UT); vicinity of Ephraim, R. Olsen s.n. (UTC); head of Mayfield Canyon, B. Maguire 19992 (UTC); Manti Canyon, N.H. Holmgren 230 (UTC); Horseshoe Flats, I.L. Johnson s.n. (BRY); 10 miles up Ephraim Canyon, J.D. Walker s.n. (BRY); Sevier Co.,

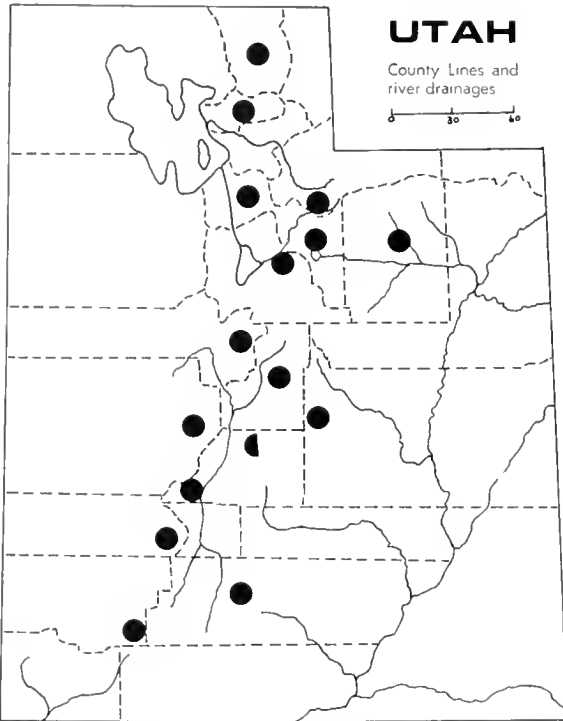


Fig. 89. *Mertensia arizonica* var. *leonardii*

Tushar Mountains, R.G. Warnock s.n. (UT); Musunia Ranger Station, D. Jeffery s.n. (UTC); summit 7 miles east of Cove Fort, L.C. Higgins 1473 (BRY); Summit Co., Soapstone Creek border, W.P. Cottam 3754 (BRY, UT); about 3 miles west of Holiday Park, near head of Weber River, Welsh, Murdock & Stocks 6307 (BRY); north slope of Big Mountain, D.H. Galway 2381 (BRY); Utah Co., Aspen Grove, A.O. Garrett 6187 (UT); Mount Timpanogos, Aspen Grove, H.C. Stutz 5 (BRY); Hobbie Creek Canyon, W. Patrick 111 (BRY); Mount Timpanogos, T.E. Northstrom 112 (BRY); summit of right fork of Hobbie Creek Canyon, R.D. Day 40 (BRY); Aspen Grove, B.F. Harrison 5805 (BRY); Wasatch Co., Provo River near Wolf Creek, W.P. Cottam 9000 (UT); 16 miles southeast of Heber, Cronquist & Holmgren 9228 (UTC); 2 miles east of Soldier Summit, B. Maguire 18396 (UTC); Alpine, at first bridge of Timp. Trail, L.D. Williams 32 (BRY); Cascade Springs, S.W. Sanderson x13 (BRY); Bryants Fork, Strawberry Valley, B.F. Harrison 8739 (BRY); Strawberry Valley, V.B. Matthews 76 (BRY); Weber Co., base of Ben Lomond, W. Call 18 (UT) 6 miles southeast of monastery in Huntsville, L. Huffaker 51 (BRY); Huntsville, J. McNeely 47 (BRY); 5 miles south of Huntsville, A.R. Muir 57 (BRY).

- 1C. *Mertensia arizonica* var. *subnuda* (Macbr.)
Williams, Ann. Mo. Bot. Gard. 24:66. 1937.
Mertensia toyabensis var. *subnuda* Macbr.
Contr. Gray Herb. 48:7. 1916.

Differs from the typical plant in that the leaves are short-strigose on the upper surface, glabrous or sparingly hairy on the lower surface; calyx lobes divided almost to the base, glabrous

on the back or sparingly pubescent, ciliate; anthers 2-2.5 mm long. Sevier County, Utah, to White Pine County, Nevada. May-August. Fig. 89.

Sevier Co., head of Nioteche Creek, M.I. Morris 139 (BRY); Fish Lake Plateau, 8 miles up Goose Creek road from highway 10, Salina Canyon, N.H. Holmgren 1970 (BRY).

2. *Mertensia bakeri* Greene, Pittonia 4:90. 1899.
Mertensia paniculata var. *nivalis* S. Wats.
U. S. Geol. Expl. 40th Par. (Bot. Kings Exped.) 5:239. 1871.
Mertensia nivalis Rydb. Mem. N. Y. Bot. Gard. 1:336. 1900.
Mertensia lateriflora Greene, Pl. Baker. 3:18. 1901.
Mertensia myosotifolia (Heller) Rydb. Colo. Agr. Exp. Sta. Bull. 100:292. 1906.
Mertensia refracta A. Nels. Bot. Gaz. 56:69. 1913.
Mertensia lanceolata var. *myosotifolia*
Macbr. Contr. Gray Herb. 48:15. 1916.

Plants with erect or ascending stems, 1-several, 0.8-4 dm tall, simple or rarely branched, pubescent with soft hairs; basal leaves linear-lanceolate to ovate elliptic, more or less densely canescent on both surfaces, 2-11 (4-6) cm long, 0.5-3.5 (1-1.5) cm broad, petiole longer or shorter than the blade; cauline leaves linear-lanceolate to ovate, usually more or less densely canescent on both surfaces, some plants from the Uinta Mountains sparsely so, sessile or nearly so, semiamplexicaule, 1.5-8 cm long (mostly 3-4) cm, 0.5-2.5 cm broad; inflorescence congested to loosely panicle; pedicels usually canescent, often reflexed in fruit, 1.5 cm or less long; calyx 2.5-5 mm long, divided almost to the base, sparsely to usually densely pubescent on the back and margins of lobes, lobes linear-lanceolate to lanceolate, acute, about 0.5 mm shorter than the entire calyx; flowers dimorphic, the tube typically longer than the limb; corolla-tube with more or less definite ring of hairs toward the base within, 3.5-9 mm long; corolla-limb moderately expanded, 4-6 mm long; anthers 1.2-2 mm long, shorter and narrower than the normal phase, longer and broader in dimorphic phases; fornicies usually prominent, glabrous, papillose, or pubescent; style reaching or surpassing the anthers; nutlets rugose, 2.5-3.5 mm long. Mountains of Colorado, and the Uinta Mountains, Utah to northern New Mexico. June-September. Fig. 90.

Daggett Co., north slope of the Uinta Mountains, V. Richens 52 (UTC); Duchesne Co., Mount Emmons,

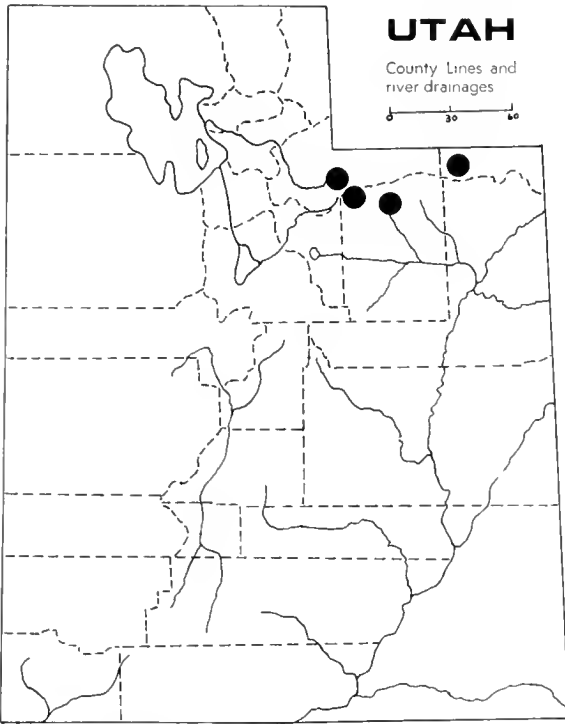


Fig. 90. *Mertensia bakeri*

west meadow, J.R. Murdock 600 (BRY); Atwood Lake, C.L. Hayward 26 (BRY); divide above Daggett Lake, A.O. Spear 145 (BRY); Mount Agassiz, rocky summit, W.P. Cottam 3713 (BRY, UT); Bald Mountain, A.H. Holmgren 7035 (UTC); Mount Agassiz, B. Maguire 4240 (UTC); Summit Co., Mount Lofty, B. Maguire 4238 (UTC); Red Castle Lake, N.H. Holmgren 318 (UTC); 7 miles south of China Lake, N.H. Holmgren 308 (UTC).

3. *Mertensia brevistyla* S. Wats. U. S. Geol. Expl. 40th Par. (Bot. Kings Exped.) 5:239. 1871. Type: Wasatch Mountains, Watson. *Mertensia alpina* var. *brevistyla* Jones Contr. West. Bot. 12:56. 1908.

Plants with erect or ascending stems, 1-4 dm tall; 1-many from each fusiform rootstalk, more or less pubescent; basal leaves broadly lanceolate to oblong, acute or obtuse, strigillose above, glabrous below, 5-13 cm long, 2-4 cm broad, petioles longer than the blade; cauline leaves obovate-oblong to narrowly elliptic, obtuse to acute, densely strigillose above, glabrous below, 2-6 cm long 0.5-3 cm broad; inflorescence congested at first, becoming paniced in age; pedicels strigose, 1-14 mm long; calyx 2-5 mm long, divided almost to the base, strigose, the lobes narrowly triangular to linear, acute, 1.5-4 mm long, 0.5-1 mm broad at the base; corolla-tube 2-4 mm long, slightly shorter to a little longer than the calyx-lobes, with or without a ring of

scattered hairs toward the base within; corolla-limb rotate, 4-6 mm long; anthers 1-1.3 mm long, longer than the filaments, inserted on the tube and not exceeding the throat; formices more or less prominent; style shorter than the calyx-lobes; nutlets rugose, 2-3.5 mm long. Southern Wyoming, west central Colorado, Utah, and southeastern Idaho. May-July. Fig. 91.

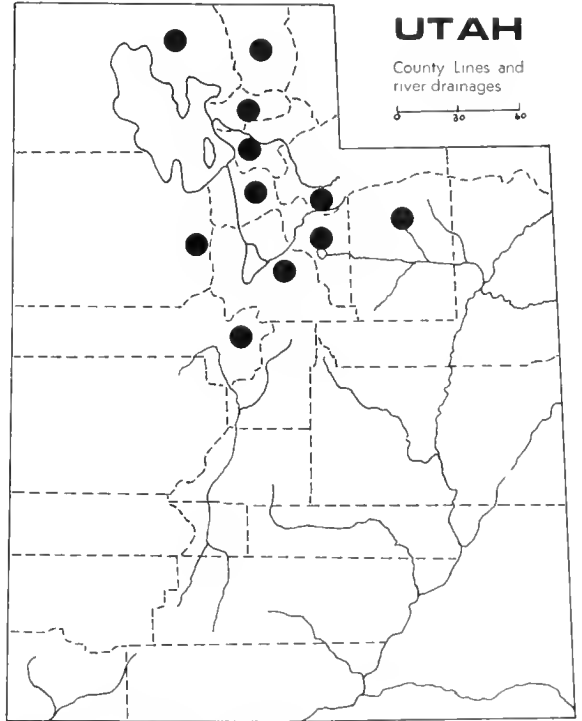


Fig. 91. *Mertensia brevistyla*

Box Elder Co., southeast of Deweyville, G. Piranian s.n. (UTC); Cache Co., Logan Canyon, H. Richardson 2 (UTC); Sardine Canyon, B. Maguire 21662 (UTC); ½ mile west of Mendon, Thomas & Marshall 44 (UT); Davis Co., head of Chicken Creek, S.L. Clark 517 (UTC); Bountiful Peak, W.P. Cottam 15012 (UT); Duchesne Co., head of Blindstream Canyon, Harrison & Nisson 8835 (BRY); Juab Co., north of Mount Nebo Ranger Station, R.K. Gierisch 267 (UTC); Salt Lake Co., Parleys Canyon, G. Davidse 40 (UTC); Lambs Canyon, R.K. Vickery 1934 (UT); south fork of Mill Creek Canyon, W.J. Stubbs 84 (BRY); Summit Co., 3 miles east of Kamas on highway 150, R.J. Eastmond 218 (BRY); Tooele Co., 12 miles southeast of Tooele, L.C. Higgins 3334 (BRY); Utah Co., ridge southwest of Payson, G. Davidse 312.5 (UTC); Payson Canyon, W.P. Cottam s.n. (UT); Rock Canyon, A.O. Garrett 7550 (BRY); 4 miles up Pole Canyon, L.K. Shumway 46A (BRY); Hope Picnic Grounds, Pole Canyon, C.L. Hayward 20 (BRY); Deer Creek Canyon, B.F. Harrison 831J (BRY); 1 mile east of Soldier Summit, B.F. Harrison 7323 (BRY); Pole Canyon Enclosure, R.J. Eastmond 254 (BRY); Hobbie Creek Canyon, B.F. Harrison 2514 (BRY); Squaw Peak, J.B. Karren 63 (BRY); Provo Canyon, C.A. Hanson 14 (BRY); Wasatch Co., Soldier Summit, B. Maguire 18386 (UTC); Cascade

Spring, S. Sanderson 11 (BRY); Hailstone Junction, R.J. Eastmond 232 (BRY); 1 mile west of Deer Creek Reservoir, R.J. Eastmond 235 (BRY); Bryants Fork, Strawberry Valley, B.F. Harrison 8735 (BRY); Weber Co., Snow Basin, A. Collotzi 5 (UTC); base of Ben Lomond Peak, W. Call 38 (UT).

4. *Mertensia ciliata* (James) G. Don, Gen. Hist. 4:372. 1838. Type: "Along streams within the Rocky Mountains," collected by James.

Mertensia polyphylla Greene, Pittonia 4:87. 1899.

Mertensia punctata Greene, loc. cit. 88.

Mertensia ciliata var. *longipedunculata* A. Nels. Bull. Torrey Club 29:402. 1902.

Mertensia picta Rydb. Bull. Torrey Club 31:638. 1904.

Mertensia pallida Rydb. Bull. Torrey Club 36:680. 1909.

Mertensia incongruens (Macbr.) Payson, Contr. Gray Herb. 49:66. 1917.

Pulmonaria ciliata James, Trans. Amer. Phil. Soc. II. 2:176. 1825. Name only; Torr. Ann. Lyc. N. Y. 2:224. 1828.

Plants erect or ascending, 1-12 dm tall, usually with many stems from each rootstock; basal leaves variable, oblong to ovate, or lanceolate, subcordate, 4-15 cm long, 3-10 cm broad, ciliate on the margins, often papillate on the upper surface, petioles longer or shorter than the blades; cauline leaves lanceolate to ovate, acute, acuminate or obtuse at apex, attenuate to subcordate at the base, the lowermost short-petiolate, the uppermost sessile, ciliate on the margins, often papillate on the upper surface, often quite glaucous, thin in texture; pedicels 1-10 mm long, glabrous, papillose or rarely with a few short strigose hairs; inflorescence from the axils of leaves, the peduncles elongated in mature or well-developed plants, in young plants the flowers aggregated at the top of the plant, each peduncle terminated in a modified ebracteate scorpioid cyme, or occasionally subumbellate; calyx-lobes 1.5-3 mm long, glabrous on the back, ciliate to papillate on the margins, more or less strigose within, obtuse or rarely somewhat acute, divided almost or quite to the base, rarely enlarged in fruit; corolla tube 6-8 mm long, glabrous or with crisped hairs within; corolla-limb 4-10 mm long, sometimes longer than the tube, moderately expanded; anthers 1-2.5 mm long, as long as or shorter and narrower than the expanded part of the filament; fornicies prominent, glabrous, papillate or pubescent; style about as long as the corolla or exceeding it; nutlets rugose or mam-

ilate. Foothills and mountains up to 12,000 feet. Montana, Colorado, and Wyoming to eastern Oregon and south to northern New Mexico. May-July. Fig. 92.

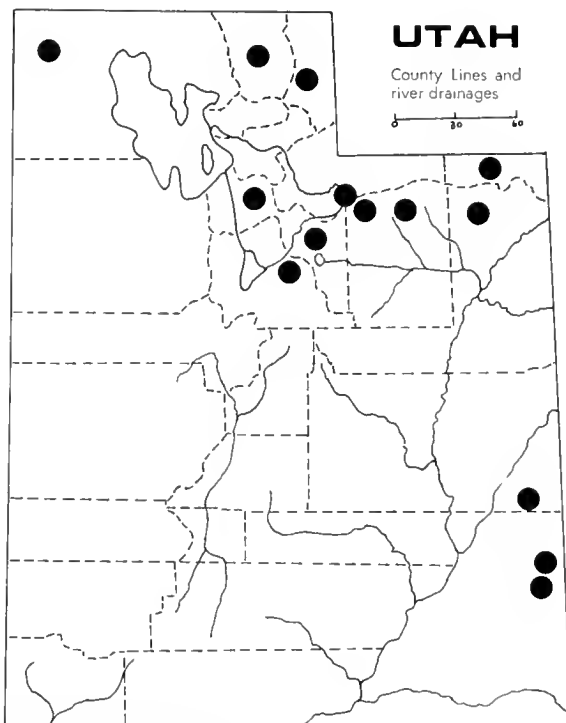


Fig. 92. *Mertensia ciliata*

Box Elder Co., Rosver Canyon, W.P. Cottam 2945 (BRY); Raft River Mountains, W.P. Cottam 7036 (UT); Cache Co., Tony Grove, B. Maguire 3726 (UTC); near Tony Grove, E. Jensen 92 (UTC); White Pine Lake, B. Maguire 14283 (UTC); Daggett Co., Carter Creek, 12 miles south of Manila, B.F. Harrison 7885 (BRY, UTC); Carter Creek, B. Maguire 12387 (UTC); Duchesne Co., Roberts Pass, Uinta Mountains, J.R. Murdock 584 (BRY); Moon Lake, B.F. Harrison 7741 (BRY); Mount Agassiz, W.P. Cottam 3714 (BRY, UT); southeast base of Mount Emmons, C.L. Hayward 145 (BRY); Mount Emmons, J.R. Murdock 53 (BRY); west of Mount Agassiz, B. Maguire 4242 (UTC); Grand Co., north slope of Mineral Peak, La Sal Mountains, B.F. Harrison 12472 (BRY); north side of Gold Mountain, B. Maguire 452 (UTC); north base of Haystack Mountain, B. Maguire 5115 (UTC); Rich Co., 10 miles west of Bear Lake, C. Greenhalgh 93 (UT); Salt Lake Co., Albian Basin, W.P. Cottam 17704 (UT); south of Brighton, R.K. Vickery 1199 (UT); 1 mile southwest of Brighton, B. Maguire 17349 (UTC); San Juan Co., Mount Peal, La Sal Mountains, Rydberg & Garrett 8999 (UT); Canyon east of Mount Tukulnikivat, A. Cronquist 9478 (UTC); between Mount Peal and Mount Tukulnikivat, B. Maguire 2116 (UTC); Summit Co., headwaters of Provo River, Cottam & Biddulph 3642 (BRY, UT); Soapstone, W.P. Cottam 3755 (BRY); Bald Mountain, Cottam & Biddulph 3699 (BRY); Stillwater Fork, Bear River, D. Henriques s.n. (UT); Upper Henrys Fork Basin, B. Maguire 14334 (UTC); above Dollar Lake, B. Maguire 14596 (UTC);

Uintah Co., 29 miles east of Kamas, B. Maguire 12535 (UTC); Utah Co., Hidden Lake, E. Castle 63c (BRY); American Fork Canyon, I.E. Diehl s.n. (BRY); cirque at base of Elk Peak, Mount Timpanogos, E. Castle 9767 (BRY); Silver Lake Area, American Fork Canyon, E. Nixon 25 (BRY); Aspen Grove, B. Decker s.n. (BRY); Aspen Grove, A.O. Garrett 3960 (UT); Mount Timpanogos, B. Maguire 17461 (UTC); Wasatch Co., near Lost Lake, about 2 miles from Trial Lake, E.C. Davenport 36 (BRY); Wolf Creek Pass, A.O. Garrett 7721 (UT).

5. *Mertensia franciscana* Heller Bull. Torrey Club 26:549. 1899. Type: Vicinity of Flagstaff, MacDougal 232.

Mertensia pratensis Heller loc. cit. 550.

Mertensia alba Rydb. Bull. Torrey Club 31:638. 1904.

Mertensia grandis Woot. & Standl. Contr. U.S. Natl. Herb. 16:165. 1913.

Mertensia pratensis f. *alba* Macbride, Contr. Gray Herb. 48:8. 1916.

Plants with erect or ascending stems, 1-10 (17) dm tall, usually with several from each rootstock; basal leaves oblong-elliptic to elliptic, 6-20 cm long, 5-9 cm broad, base subcordate to obtuse, apex acuminate, acute or obtuse, upper surface short strigillose, lower surface glabrous or with spreading pubescence; petioles longer or shorter than the blade; cauline leaves elliptical to narrowly ovate, 4-14 cm long, 1-5 cm broad, obtuse to acuminate, the lowermost petiolate, becoming sessile toward the inflorescence, strigillose on the upper surface, glabrous to densely pubescent with spreading hairs below; flowers of the inflorescence paniculately disposed in an ebracteate modified scorpioid cyme, the branches of the inflorescence elongating in age; pedicels strigose, 1-20 mm long; calyx 2.5-5 mm long, divided almost to the base, the lobes linear to lanceolate, 1-2 mm wide at the base, acute, rarely obtuse, glabrous or pubescent on the back, strongly ciliate; corolla-tube 5-9 mm long, glabrous or pubescent within; corolla limb 4-6 (9) mm long, subequal to or slightly shorter or longer than the corolla-tube, moderately expanded; anthers 2.5-3 mm long, longer than the filaments; filaments 2-2.5 mm long, glabrous or with spreading hairs; fornicies prominent, usually pubescent; style 9-20 mm long, usually shorter than the corolla, sometimes exceeding it; nutlets rugose and papilliferous. Southern Colorado, New Mexico, Arizona, southern Utah, eastern Nevada, and California. June-August. Fig. 93.

Grand Co., Warner Ranger Station, La Sal Mountains, H.K. Sharsmith 4432 (BRY); La Sal Mountains, S. Flowers s.n. (UT); Oowah Lake, La Sal Mountains, Weins & Arnow 4147 (UT, UTC); south base of Gold Hill, B. Maguire 5120 (UTC); north base of Haystack

Mountain, B. Maguire 5119 (UTC); San Juan Co., La Sal, Aspen, W.P. Cottam 2220 (BRY); La Sal Ranger Station, Cottam & Hutchings 2192 (BRY); Kigalia, along creek, W.P. Cottam 2489 (BRY); 10 miles north of Blanding, B. Maguire 2109 (UTC); Abajo Peak, B. Maguire 2115 (UTC); La Sal Pass, Medicine Lake, Cronquist & Holmgren 9469 (UTC); Kigalia Ranger Station, D. Henriques 128 (UT); La Sal Mountains, Rydberg & Garrett 8597 (UT).

6. *Mertensia fusiformis* Greene, Pittonia 4:89. 1899. Type: Open glades, Bob Creek, West La Plata Mountains, Baker, Earle & Tracy 206.

Mertensia congesta Greene, Pl. Baker. 3:17. 1901.

Mertensia papillosa fusiformis A. Nels. Coult. & Nels. Man. Rocky Mt. Bot. 421. 1909.

Plants with erect stems or nearly so, 1-3 dm tall, glabrous or sparingly pubescent, 1-few from each root stalk which is usually rather large and fusiform; basal leaves elliptic to oblong-ovate, 4-12 cm long, 1.5-3 cm broad, usually densely strigose above, glabrous below, petiole 7-12 cm long; cauline leaves linear-oblong to ovate-oblong, 1.5-10 cm long, 0.4-3 cm broad, sessile or the lowermost short-petiolate, more or less densely strigose above, glabrous below, usually quite obtuse, rarely somewhat acute; inflorescence usually congested, sometimes slightly paniced; ped-

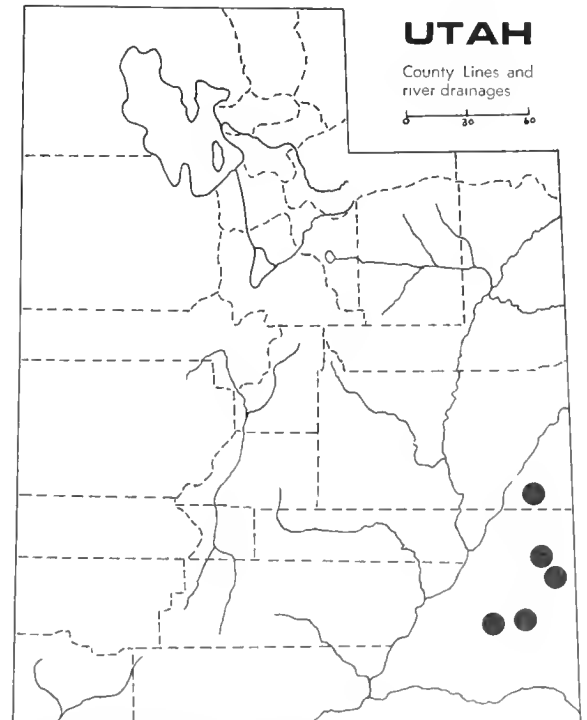


Fig. 93. *Mertensia franciscana*

iceles 1-15 mm long, densely strigose; calyx 3-6 mm long, slightly accrescent, the lobes lanceolate to lanceolate-ovate, 2-5 mm long, acute, ciliate, usually pubescent on the backs, occasionally nearly glabrous, not divided to the base; corolla-tube 4-7 mm long, with a ring of crisp hairs within at the base; corolla-limb 5-7 mm long, moderately expanded, usually subequal to or shorter than the limb, but sometimes longer; anthers 1.5-2.5 mm long; filaments 1-3 mm long; fornicies present but usually not conspicuous, glabrous or nearly so; style usually surpassing the anthers, sometimes shorter; nutlets rugose, about 3 mm long. Wyoming, Utah, and Colorado in the mountains. June-September. Fig. 94.

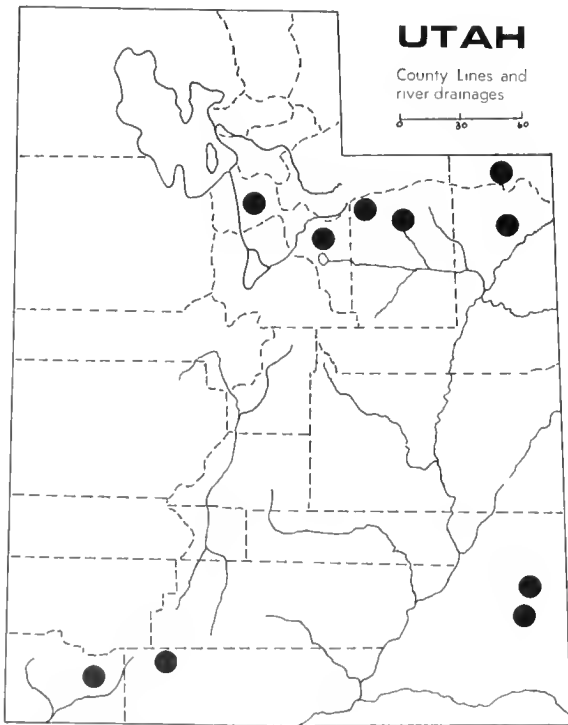


Fig. 94. *Mertensia fusiformis*

Daggett Co., summit along the Vernal-Manila road, W.P. Cottam 6070 (UT); Duchesne Co., shore of Moon Lake, L.M. Hartman 36 (BRY); Rock Creek, J. Brotherson 907 (BRY); 4 miles south of Moon Lake, Harrison & Larsen 7618 (BRY); Kane Co., 15 miles northwest of Orderville, B. Maguire 18802 (UTC); 20 miles northwest of Orderville, B. Maguire 18756 (UTC); Salt Lake Co., Parleys Canyon, R.K. Selander 1502 (UT); San Juan Co., west slope of the La Sal Mountains between Horse and Brunler Creek, Cronquist & Holmgren 9285 (UTC); along La Sal Creek, A. Cronquist 9215 (UTC); Yellow Pine Association, B.F. Harrison, 5895 (BRY); La Sal, along La Sal Creek, Cottam & Hutchings 2270 (BRY); Uintah Co., Diamond Mountain, Laycock & Conrad 137 (BRY); Diamond Mountain, 15 miles north of Vernal, Welsh & Moore 1959 (BRY); Wasatch Co., Wolf Creek Pass, W.P. Cottam

9013 (UT); Washington Co., Zion Natl. Park, Horse Pasture Plateau, Potato Hollow, N.H. Holmgren 1976 (BRY, UTC).

7A. *Mertensia oblongifolia* (Nutt.) G. Don, Gen. Hist. 4:372. 1838. Type: Montana, probably collected by Wyeth.

Mertensia nutans subsp. *subclava* Piper, Contr. U.S. Natl. Herb. 11:479. 1906.

Mertensia foliosa var. *subclava* Macbr. Contr. Gray Herb. 58:18. 1916.

Mertensia nelsonii Macbr. Ic. 19, in part.

Mertensia bakeri var. *subglabra* Macbr. & Payson, Contr. Gray Herb. 49:66. 1917.

Mertensia foliosa var. *subclava* f. *macbridii* Johnst. Contr. Arn. Arb. 3:84. 1932.

Pulmonaria oblongifolia Nutt. Journ. Acad. Nat. Sci. Phila. 7:43. 1834.

Cerinthodes oblongifolium Kuntze, Reo. Gen. Pl. pt. 2:436. 1891.

Plants with erect or ascending stems, 1-3 dm tall, one to many from each elongated rootstalk; blade of basal leaves 3-8 cm long, 0.5-2 cm broad, oblong or spatulate to narrowly oblong-ovate, usually obtuse, strigose on the upper surface, glabrous below, petiole longer or shorter than the blade; cauline leaves sessile or the lowermost short-petiolate, linear to oblong-elliptical, 2-8 cm long, 0.3-1.5 cm broad, pubescent as of basal leaves; inflorescence congested, becoming paniced with age; pedicels strigose to essentially glabrous, 1-10 mm long; calyx 3-7 mm long, divided to within about 1 mm of the base, the lobes linear to lanceolate-triangular, acute, ciliate, glabrous dorsally or rarely with a few hairs; corolla-tube 5-12 mm long, usually quite glabrous within, occasionally with a few scattered hairs; corolla-limb 4-7 mm broad; anthers 1.2-2 mm long, oblong and straight; filaments 2-4 mm long, usually longer and broader than the anthers; style exceeding the anthers; fornicies prominent, glabrous or occasionally sparsely hairy; immature nutlets 3-4 mm long, rugose. Western Montana, Wyoming, and Utah to Washington and northern California. June-July. Fig. 95.

Salt Lake Co., Little Cottonwood Canyon, W.P. Cottam 3532 (BRY); Uintah Co., Split Mountain Gorge, S.L. Welsh 244 (RRY); Utah Co., Silver Lake, American Fork Canyon, I.E. Diehl s.n. (BRY).

7B. *Mertensia oblongifolia* var. *amoena* (A. Nels.) Williams, Ann. Mo. Bot. Gard. 24:130. 1937. Type: Monida, Madison Co., Nelson & Nelson 5413.

Mertensia amoena A. Nels. Bot. Gaz. 30:195. 1900.

Mertensia cusickii Piper, Bull. Torrey Club 29:643. 1902.

Mertensia pubescens Piper, Contr. U.S. Natl. Herb. 11:479. 1906.

Mertensia bakeri amoena A. Nels. Coult. & Nels. Man. Rocky Mt. Bot. 422. 1909.

Mertensia foliosa var. *pubescens* Macbr. Contr. Gray Herb. 48:19. 1916.

Mertensia oblongifolia var. *nimbata* Macbr. Contr. Gray Herb. 53:18. 1918.

Mertensia cooperae Peck, Torreya 32:151. 1932.

Mertensia foliosa var. *amoena* Johnst. Contr. Arn. Arb. 3:85. 1932.

Similar to the species, often more robust; leaves more or less densely pubescent on both surfaces. Sporadic with the species and variety *nevadensis*. Fig. 95.

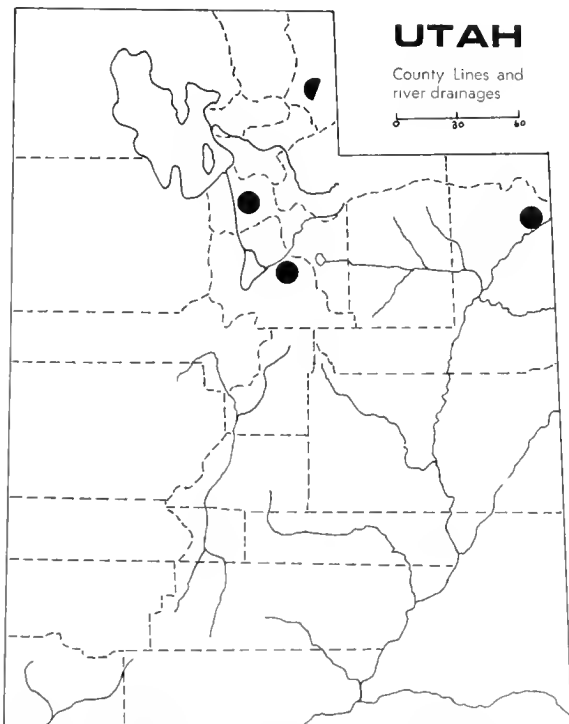


Fig. 95. *Mertensia oblongifolia* var. *oblongifolia*

Rich Co., among sagebrush, north slope of a small canyon about 3 miles east of Laketown, 28 May 1935 Williams & Williams 2152 (NY).

7C. *Mertensia oblongifolia* var. *nevadensis* (A. Nels.) Williams, Ann. Mo. Bot. Gard. 24:125. 1937. Type: 5 miles west of Reno, Kennedy & True 711.

Mertensia foliosa A. Nels. Bull. Torrey Club 26:243. 1899.

Mertensia tubiflora Rydb. Bull. Torrey Club 26:544. 1899.

Mertensia intermedia Rydb. Mem. N.Y. Bot. Gard. 1:335. 1900.

Mertensia nutans Howell, Fl. N.W. Amer. 491. 1901.

Mertensia stenoloba Greene, Pl. Baker. 3:20. 1901.

Mertensia symphytoides Greene, Ic. non Fisch. 1872.

Mertensia coronata A. Nels. Bull. Torrey Club 29:403. 1902.

Mertensia nevadensis A. Nels. Proc. Biol. Soc. Wash. 17:96. 1904.

Mertensia praecox Smiley ex Macbr. Contr. Gray Herb. 48:10. 1916.

Mertensia foliosa var. *nevadensis* Macbr. Ic. 19.

Mertensia nelsonii Macbr. Ic. in part as to type specimen.

Similar to the species but often more robust; cauline leaves 2-10 cm long, 0.8-6 cm broad, lanceolate-oblong to ovate, glabrous or the upper surface pustulate, sometimes the pustules toward the apex of the leaves developing mucros, some specimens, particularly from northeastern Utah; with lateral veins in the well-developed cauline leaves; corolla extremely variable as to size in different localities. Western Montana, Wyoming, and Utah west to Washington and northern California. April-July. Fig. 96.

Box Elder Co., Goose Creek Mountains, 3 miles northwest of Divide, K.S. Erdman 1644 (BRY); Rosvere, top of mesa, W.P. Cottam 2847 (BRY); Raft River Mountains, at summit, N.H. Holmgren 2850 (BRY); above Cottonwood Grove, M. Burke 3118 (UTC); Raft River Mountains, C. McMillan 1503 (UT); Cache Co., Logan Canyon, B. Maguire s.n. (UTC); Providence Canyon, B. Maguire 3719 (UTC); Logan Canyon, M. Burke 3725 (UTC); 11 miles up Smithfield Canyon, B. Maguire 13776 (UTC); Juab Co., Deep Creek Range, Maguire & Holmgren 22050 (UTC); Sheba Mine, Deep Creek Mountains, W.P. Cottam 3176 (BRY, UT); Deep Creek Mountains, Maguire & Beecraft 2784 (UTC); Deep Creek Range, A.H. Holmgren 3746 (UTC); Salt Lake Co., Big Cottonwood Canyon, R.J. Eastmond 186 (BRY); Big Cottonwood Canyon, B. Fowler s.n. (UT); Summit Co., Henrys Fork, A. Collotzi 45 (UTC); Weber Co., Snow Basin, A. Collotzi 50 (UTC); Pine View Dam, J. McNeley 40 (BRY); Tooele Co., 3 miles south of Tooele, L. Arnow 266 (UT); trail to Mount Deseret, B. Maguire 21767 (BRY); Bennion Canyon, N.C. Frischknecht 81 (BRY); Muir Trail, Oquirrh Mountains, Cottam, Allen & Rowland 16867 (BRY); Black Bunch, 1 mile north of Miner Fork Road, M.E. Lewis 1115 (BRY); Utah Co., Springville, B. Dougall 97 (UT); Provo Canyon, M.E. Jones s.n. (UTC); Hobbie Creek Canyon, L.C. Pack 7 (BRY); along Timp. Creek, L.K. Shumway 92 (BRY); Bridal Veil Falls, S.L. Welsh 3053 (BRY); north end of Lake Mountain, Welsh & Moore 1927 (BRY); Hobbie Creek Canyon, B.F. Harrison 264 (BRY); just east of

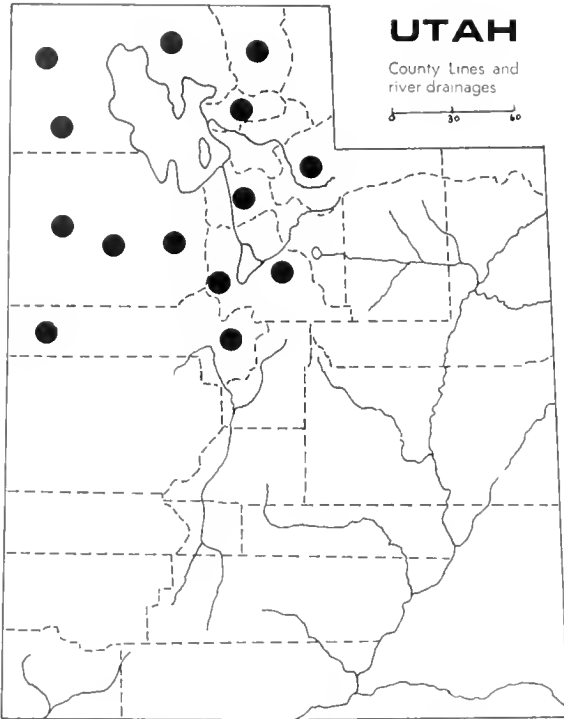


Fig. 96. *Mertensia oblongifolia* var. *nevadensis*

Eureka, J.B. Karren 79 (BRY); Hobbie Creek Canyon, F.J. Camenzind s.n. (BRY); Hobbie Creek Canyon, T.E. Northstrom 13 (BRY); Hobbie Creek Canyon, L.C. Higgins 3500 (BRY).

8A. *Mertensia viridis* A. Nels. Bull. Torrey Club 26:244. 1899. Type: Wyoming, Laramie Peak, Nelson 1608.

Mertensia lanceolata var. *viridis* A. Nels. First Rept. Fl. Wyo. 158. 1896.

Mertensia ovata Rydb. Bull. Torrey Club 28:32. 1901.

Mertensia lineariloba Rydb. l.c.

Mertensia parrisi Rydb. Bull. Torrey Club 31:639. 1904.

Mertensia perplexa Rydb. l.c.

Mertensia viridula Rydb. l.c.

Mertensia papillosa lineariloba A. Nels. Coult & Nels. Man. Rocky Mt. Bot. 421. 1909.

Mertensia lanceolata var. *lineariloba* Macbr. Contr. Gray Herb. 48:15. 1916.

Mertensia alpina var. *perplexa* Macbr. l.c. 20.

Stems erect or ascending, 5-35 cm tall, 1-several from each rootstalk; basal leaves lanceolate to ovate, 2-10 cm long, 1-4 cm broad, strigillose above, glabrous below, lateral veins sometimes apparent, petioles longer or shorter than the blade; cauline leaves sessile or nearly

so, lanceolate to broadly ovate, 2-7 cm long, 0.7-2.5 cm broad, strigillose above, glabrous below, lateral veins rarely visible; inflorescence a crowded, modified, scorpioid cyme; pedicels strigose or glabrous, 1-10 mm long; calyx 2-6 mm long; the lobes divided almost to the base, linear-lanceolate to narrowly ovate-lanceolate, acute or obtuse, glabrous on the backs, ciliate, somewhat accrescent in fruit; corolla-tube 3-9 mm long, usually with a ring of crisped hairs near the base within, occasionally also with scattered hairs; corolla-limb 4-9 mm long, moderately expanded, usually a little shorter than the tube in flowers having a long style and filaments longer than the anthers, in flowers having a short style and filaments about the same length as or shorter than the anthers, the tube may be much shorter than the limb; anthers 1-2.5 mm long; filaments 1-3.5 mm long, longer to shorter than the anthers; fornicies conspicuous, glabrous to densely pubescent; style various, exceeding the anthers and about as long as the corolla to shorter than the tube of the corolla; nutlets 2-3 mm long, rugose. Montana, south through Utah and Colorado. July-September. Fig. 97.

Garfield Co., 25 miles south of Hanksville, Henry Mountains, Cronquist & Holmgren 9435 (UTC); south rim of Bull Creek Basin, Henry Mountains, B. Maguire 19362 (UTC); Grand Co., north side of Gold Mountain, B. Maguire 5113 (UTC); saddle between Castle and Waas mountains, B. Maguire 5112 (UTC); west

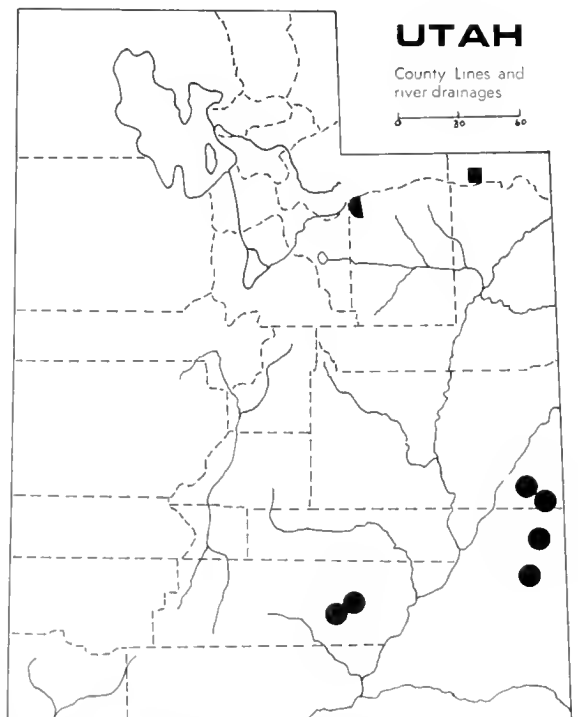


Fig. 97. *Mertensia viridis* var. *viridis*

slope of Mount Hobbs, B. Maguire 5111 (UTC); San Juan Co., west slope of Mount Peal, B. Maguire 2117 (UTC); saddle south of Mellenthin, B. Maguire 5109 (UTC); La Sal Mountains, Mount Peal, N.H. Holmgren 3003 (BRY).

8B. *Mertensia viridis* var. *cana* (Rydb.) Williams, Ann. Mo. Bot. Gard. 24:115. 1937. Type: Colorado, Grand Co., Berthoud Pass, Tweedy 5664.

Mertensia canescens Rydb. Bull. Torrey Club 31:640. 1904.

Mertensia cana Rydb. Bull. Torrey Club 36:698. 1909.

Cauline leaves linear to narrowly ovate, more or less densely canescent on both surfaces; calyx lobes usually glabrous on the backs but sometimes slightly pubescent. Bald Mountain, Utah. Fig. 97.

Bald Mountain, 11 August 1911. Clemons s.n. (POM).

8C. *Mertensia viridis* var. *dilatata* (A. Nels.) Williams, Ann. Mo. Bot. Gard. 24:113. 1937. Type: Wyoming, Albany Co., Medicine Bow Mts., Nelson 7844.

Mertensia coriacea A. Nels. Bull. Torrey Club 29:402. 1902.

Mertensia coriacea var. *dilatata* A. Nels. l. 403.

Similar to the species but the leaves glabrous on both sides. Uinta Mountains, Utah. Fig. 97.

Daggett Co., Uinta Mountains, 10,000 feet, 11 June 1932, L. Williams 599 (UTC).

15. *Myosotis* (Dill.) L.

Myosotis (Dill.) L. Sp. Pl. 1:131. 1753, and Gen. Pl. 63. 1754.

Annual or perennial herbs; leaves alternate; racemose, bractless or bracted, calyx cut to beyond the middle into lanceolate or triangular lobes; corolla blue, white or rarely rose, with a short tube; lobes contorted, rounded, spreading; throat with intruded appendages; stamens affixed on the tube, included or exerted, the filaments filiform; anthers oblong or ovate, obtuse; ovules 4; nutlets 4, erect, ellipsoid, smooth and shiny, with a basal areola; gynobase flat or high convex; style filiform; a stigma disciform.

Type species: *Myosotis scorpioides* L.

- 1. *Myosotis scorpioides* L. Sp. Pl. 131. 1753.
- Myosotis scorpioides* var. *palustris* L. l.
- Myosotis palustris* Lem. Fl. Fr. 2:283. 1778.

Perennial, with slender rootstocks or stolons, herbage appressed-pubescent with straight pointed hairs; stems slender, 1.5-4 dm long, decumbent or ascending, rooting at the lower nodes; leaves oblanceolate to oblong-lanceolate, 2.5-8 cm long, 4-12 mm wide, upper stem leaves sessile, the lower narrowed to a winged petiole; racemes loosely many flowered; fruiting pedicels longer than the calyx; calyx with straight appressed hairs, the lobes equal, ovate triangular, acute, shorter than the tube, more or less spreading in fruit; corolla blue with a yellow eye, the limb flat, 6-8 mm broad; nutlets angled and keeled on the inside. Wet meadows and margins of streams. Native of Europe and Asia, well established in the United States. June-August. Fig. 98.

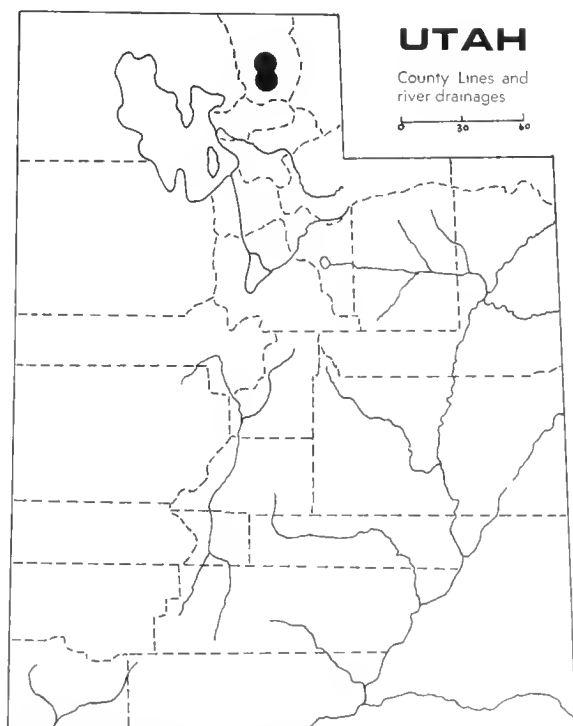


Fig. 98. *Myosotis scorpioides*

Cache Co., ½ mile west of Logan, B. Maguire 20100 (UTC); 1 mile west of Logan along canal, B. Maguire 21579 (UTC); Logan, ditch bank, W.S.F. 544 (UT).

16. *Pectocarya* DC. ex Meisn.

Pectocarya DC. ex Meisn. Gen. 279. 1840.

Low, often spreading annual herbs, with slender stems and narrowly linear leaves, canescent with a close-appressed pubescence; flowers scattered along the stems or branches, on short pedicels, solitary in the axils; calyx 5-parted, the

lobes narrow, spreading or reflexed in fruit; corolla white, the tube shorter than the calyx, lobes broadly oval, the throat nearly closed by prominent crests; stamens included; style very short; nutlets flattened, thin, widely divergent either radiately or in pairs, their margins, at least toward the apex, with a row of hooked bristles.

Type species: *Cynoglossum lateriflorum* Lan.

1. Nutlets orbicular or nearly so, both the body and the very thin conspicuous wing beset with slender uncinuate bristles 4. *P. setosa*
1. Nutlets oblong or linear, the body without uncinuate bristles (2).
2. Nutlets heteromorphic, 1 of each divergent pair wingless, or merely margined, the other with a broad somewhat incurved uncinuate-toothed wing 1. *P. heterocarpa*
2. Nutlets not heteromorphic, all 4 winged-margined or toothed (3).
3. Margin of nutlet conspicuous, the teeth confluent at base 2. *P. platycarpa*
3. Margin of the nutlet very narrow or wanting, the teeth being nearly or quite distinct, subulate, nutlets strongly recurved 3. *P. recurvata*

1. *Pectocarya heterocarpa* Johnst. Journ. Arn. Arb. 20:399. 1939. Type: Corn Springs, Chuckwalla Valley, Riverside County, California.

Pectocarya penicillata var. *heterocarpa*
Johnst. Contr. Gray Herb. 70:37. 1924.

Diffusely branched from the base; stems slender, ascending or spreading, 3-15 cm long, strigose and canescent throughout; leaves narrowly linear, 1-3 cm long, 1-2 mm wide, the hairs on the basal ones often pustulate at base; corolla minute, its limb about 1.5 mm broad; fruiting nutlets widely divergent, dissimilar, 2 narrower and with or without a narrow margin, and 2 prominently winged-margined, the wings pectinately bristly at the apex, irregular, few toothed and with or without scattered bristles on the sides. Sandy or gravelly slopes and plains. Southwestern Utah, southern Nevada south through Arizona and southern California to Sonora, Mexico. January-May. Fig. 99.

Washington Co., 1 mile east of Hurricane, B. Maguire 1522 (UTC); volcanic hills west of Hurricane, B. Maguire 1525 (UTC); St. George, M.E. Jones s.n. (UTC); Dixie State Park, L.C. Higgins 918 (BRY); Beaverdam Mountains, L.C. Higgins 284-352 (BRY); Black Hills west of St. George, C.W. Cottam s.n. (DIX).

2. *Pectocarya platycarpa* Munz & Johnst. Contr. Gray Herb. 81:81. 1928. Type: Mesa near Camp Lowell, Arizona.

Pectocarya gracilis var. *platycarpa* Munz

& Johnst. Contr. Gray Herb. 70:36. 1924.

Stems slender, diffusely branched from the base, prostrate or widely ascending, 5-20 cm long, cinereous-strigillose throughout; leaves narrowly linear to linear-oblongate, 0.5-1.5 mm wide, 1-3.5 cm long; calyx-lobes nearly as long as the nutlets; corolla 2 mm long; nutlets divergent in pairs, sometimes heteromorphic, linear-oblong or spatulate-oblong, 2.5-3 mm long, with a wide conspicuous stramineous margin bearing irregular uncinuate-tipped teeth, the odd nutlet when differentiated, with more deeply dissected wing and with more pubescent body. Dry gravelly slopes and benches. Southwestern Utah, south and west through Arizona, southern Nevada and California. February-May. Fig. 100.

Washington Co., Watercress Springs, D.H. Galway s.n. (DIX); north of St. George, D. Hall s.n. (DIX); Beaverdam Mountains, L.C. Higgins 350 (BRY); St. George, D.H. Galway 6286 (BRY); Black Hill west of St. George, D. Hall s.n. (BRY).

3. *Pectocarya recurvata* Johnst. Contr. Arn. Arb. 3:97. 1932. Type: near Chandler, Maricopa County, Arizona.

Stems slender, simple below, with 2 to several erect or ascending branches above, or sometimes diffusely branched throughout and more

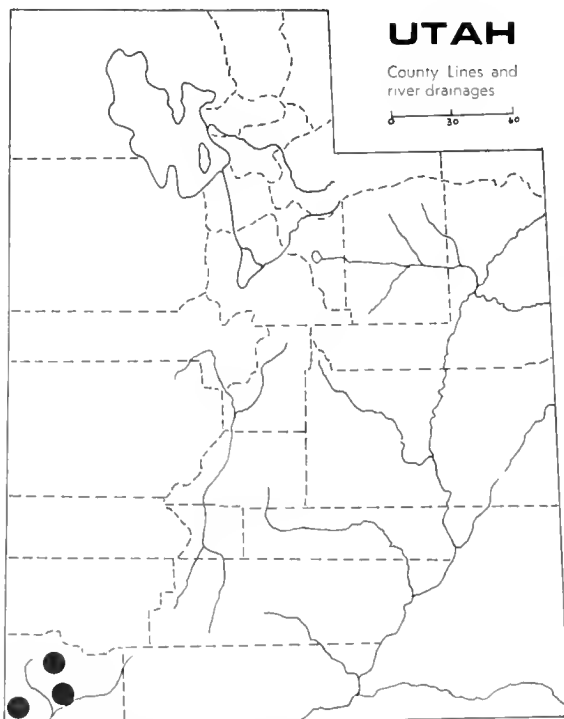


Fig. 99. *Pectocarya heterocarpa*

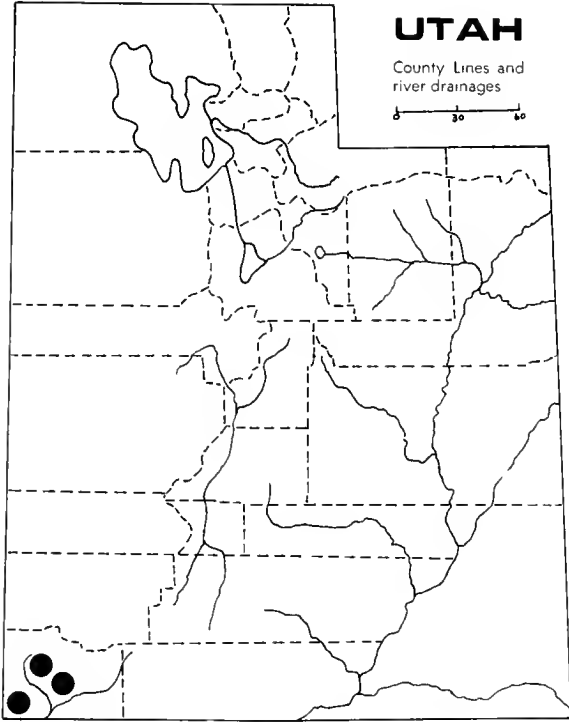


Fig. 100. *Pectocarya platycarpa*

spreading. 5-25 cm long; herbage cinereous-strigose; leaves narrowly linear, acute, 1-3.5 cm long, 0.5-2 mm broad; calyx-lobes barely 2 mm long in fruit, acute; nutlets divergent in pairs, linear, strongly recurved, the wing divided to or almost to the body into prominent subulate straw-colored uncinuate bristles, at the apex the wing prolonged into a short scarious tip, uncinuate bristly on the margin. Sandy or gravelly slopes and ridges, Lower Sonoran Zone. Southern Nevada, western Utah, Arizona, and southern California. March-May. Fig. 101 (semi-circle).

I have seen no Utah specimens of *P. recurvata*, but the species has been collected a few miles from the Utah border in Mohave County, Arizona.

- 4. *Pectocarya setosa* A. Gray, Proc. Amer. Acad. 12:81. 1876. Type: desert plains of the Upper Mohave River.
- Pectocarya setosa* var. *aperta* Johnst. Contr. Gray Herb. 70:38. 1924.
- Pectocarya setosa* var. *holoptera* Johnst. op cit. 39.
- Gruvelia setosa* Rydb. Bull. Torrey Club 40:479. 1913.

Stems usually diffusely branched from the base, ascending, slender to rather stout, 5-20 cm

tall, herbage rather thinly strigose and setose with spreading bristle-like hairs; leaves linear to linear-oblongate, 5-20 mm long; calyx-lobes narrowly linear, 3-4 mm long in fruit, armed with 3 to 6 straight divergent bristles; nutlets divergent in pairs, broadly obovate to orbicular, 2 borders all around with a thin scarious wing, 2 wingless, the body of the nutlets and usually the wing bearing slender uncinuate bristles, the wing usually slightly undulate and slightly curved upward saucerlike. Usually fine sandy areas. Eastern Washington and central Idaho, southward to Utah, Arizona, Nevada, and Baja California. April-June. Fig. 101. (circles).

Washington Co., Diamond Valley, F.W. Gould 1557 (DIX); 10 miles north of St. George, F.W. Gould 1557 (UTC); Diamond Valley, L.N. Goodding 815 (UTC); Welcome Springs, Beaverdam Mountains, B. Maguire 20521 (UTC); Beaverdam Mountains, B. Maguire 4952 (UTC); Diamond Valley, 10 miles north of St. George, L.C. Higgins 4203 (BRY,WTSU).

17. *Plagiobothrys* Fisch. & Mey.

Plagiobothrys Fisch. & Mey. Ind. Sem. Hort. Petrop. 2:46. 1835.

Slender, glabrate or mostly soft-pubescent, annual or perennial herbs; leaves mostly linear or linear-lanceolate, alternate above and either opposite at base or forming a rosette; flowers

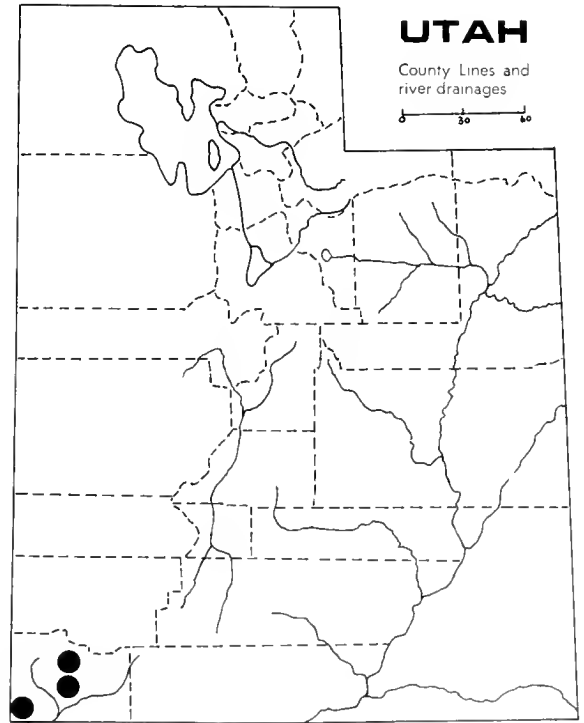


Fig. 101. *Pectocarya recurvata*

in bractless or bracteate spikelike racemes, the racemes more or less scorpioid and usually elongated in fruit; corolla white, small, salverform, with crests at the mouth of the throat; nutlets rugose, erect or incurved, attached at or below the middle to a depressed gynobase through a caruncular scar, this decurrent on the lower part of the ventral keel or situated at the lower end of the keel and sunken below its crest.

Type species: *Plagiobothrys rufescens* Fisch. & Mey.

1. Plants glabrous or nearly so; nutlets attached basally or nearly so 3. *P. leptocladus*
1. Plants strigose or bristly hairy; nutlets attached laterally or obliquely basal (2).
2. Nutlets checkered with broad flattened, contiguous, pavementlike raised areas; plants erect, hispid, with terminal bractless scorpioid cymes 2. *P. jonesii*
2. Nutlets not checkered, the back rugose, the raised areas scattered or none (3).
3. Leaves charged with purple dye, particularly at midrib and margins; calyx with a weakened ring which allows it to break loose, lobes short, strongly pressed together at maturity 1. *P. arizonicus*
3. Leaves lacking conspicuous purple dye, green; calyx without weakened ring (4).
4. Basal leaves crowded into a rosette, none opposite, plants slender, erect, loosely branched, not producing flowers near the base; nutlets incurved, contracted at both ends, somewhat cruciform, transverse ridges very broad 5. *P. tenellus*
4. Basal leaves distinct, at least not in well-developed rosettes, lower leaves opposite; nutlets not incurved, but highly variable 4. *P. scouleri*

1. *Plagiobothrys arizonicus* (A. Gray) Greene, Proc. Amer. Acad. 20:284. 1885. Type: Arizona.

Eritrichium canescens var. *arizonicum* A. Gray, Proc. Amer. Acad. 17:227. 1882.

Stems slender, several from the base, ascending, simple or few branched, 1-4 dm high, hirsute-hispid with spreading hairs and also rather sparingly villous pubescent; leaves hirsute-hispid with more or less appressed hairs, pustulate at base, without shorter pubescence, the lower linear-lanceolate, 1.5-5 cm long, upper linear-oblong to lanceolate; roots, lower parts of stems and veins of the leaves, or sometimes the whole plant purplish; spikes at length elongated, remotely flowered and bractless or with a few foliaceous bracts; calyx about 3 mm long, cleft to about the middle, lobes narrow-attenuate, connivent, hirsute-hispid, the tube at length usually circumscissile near the base; corolla 2-2.5 mm broad; nutlets 1-4 commonly 2, ovoid and abruptly acute at apex, median and lateral keels

often tuberculate, and with connecting transverse rugae, the areolae between smooth or minutely papillate; scar median, seated in a sunken area at the base of the keel. Sandy to gravelly slopes and plains. Southwestern Utah, south to southern California, Sonora, and New Mexico. March-June. Fig. 102.

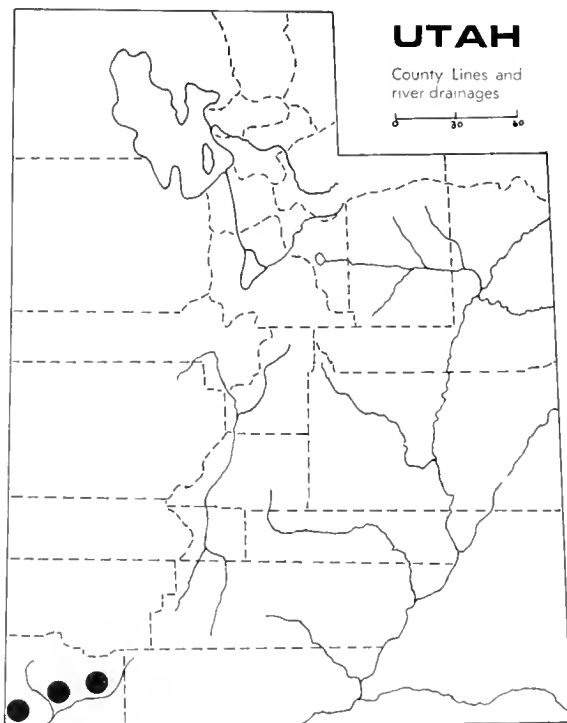


Fig. 102. *Plagiobothrys arizonicus*

Washington Co., west slope of the Beaverdam Mountains, W.P. Cottam 7545 (UT); east of Laverkin, W.P. Cottam 5165 (UT); west slope of the Beaverdam Mountains, D. Nish 68 (UTC); Beaverdam Mountains, B. Maguire 20508 (UTC); St. George, D.H. Galway 8451 (BRY); Black Hill west of St. George, F.W. Gould 1481 (BRY); Beaverdam Wash at Terry's Ranch, L.C. Higgins 300 (BRY); Dixie State Park, L.C. Higgins 850 (BRY).

2. *Plagiobothrys jonesii* A. Gray, Syn. Fl. N. Amer. 2:430. 1886. Type: Needles, California.

Sonnea jonesii Greene, Pittonia 1:23. 1887.

Stems erect, 1-several from the base, divergently branched, 1-3 dm high, hispid with spreading bristly hairs pustulate at base, and also retrorsely-pubescent; basal leaves linear or narrowly oblanceolate, cauline mostly lanceolate with pubescence similar to the stem but thinner; racemes terminating the branches, mostly conspicuously leafy-bracted at base, 1.5-3 cm long, the lower leaves of the branches often

bearing one or few axillary flowers, calyx lobes subulate-linear, 6-8 mm long, corolla 1-2 mm broad; nutlets 3 mm long, incurved and 4-angled by the dorsal and ventral keels and the 2 lateral ridges, abruptly pointed at apex, the keel and lateral angles tuberculate, the concave surface between densely tessellate; scar narrow or medial-narrow merging into the keel above, and with a diverging lateral ridge extending to either side. Washes and rocky desert slopes. Southwestern Utah, south to southern California, and Arizona to Sonora. April-May. Fig. 103.

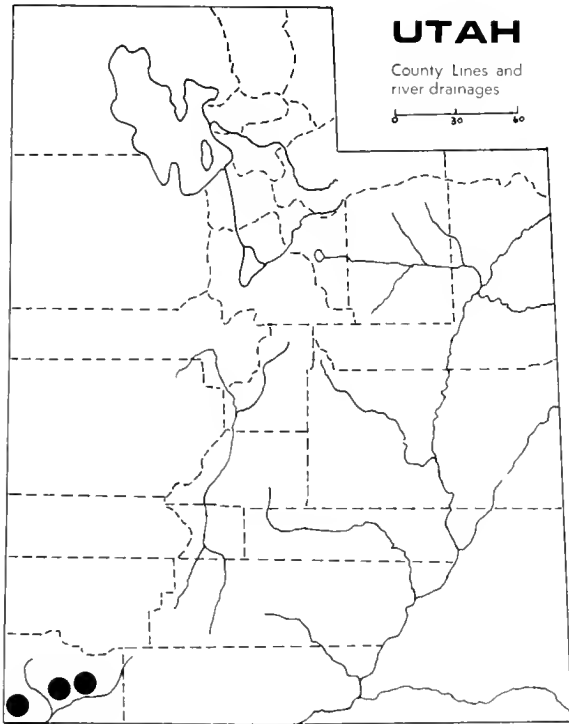


Fig. 103. *Plagiobothrys jonesii*

Washington Co., 5 miles west of Leeds, B. Maguire 1536 (UTC); Black Hill west of St. George, D.H. Galway 8532 (BRY); Beaverdam Mountains, L.C. Higgins 454 (BRY).

3. *Plagiobothrys leptocladus* (Greene) Johnston. Contr. Arn. Arb. 3:38. 1932. Type: Pine Creek, Eureka County, Nevada.

Eritrichium californicum var. *subglochidiatum* A. Gray, Bot. Calif. 1:526. 1876.

Allocarya leptoclada Greene, Pittonia 3:109. 1896.

Allocarya orthocarpa Greene, op. cit. 4:235. 1901.

Allocarya versicolor Brand, Rep. Spec. Nov. 19:71. 1923.

Stems branched from the base, the branches prostrate, 1-3 dm long, straight, slender, and somewhat wiry, thinly strigose or glabrate, often floriferous nearly to the base; leaves narrowly linear, the lower 3-10 cm long, glabrous or nearly so above, thinly strigose beneath, the hairs mostly pustulate at base; racemes simple, becoming loosely flowered; mature calyx-lobes usually accrescent, 3-8 mm long, about 1 mm wide, connivent or sometimes spreading, more or less definitely curved toward one side; corolla 1-2 mm broad; nutlets narrowly to broadly lanceolate, acute; dorsal side keeled only above the middle, more or less obliquely or transversely rugose, smooth, granulate or penicillate-hairy; ventral side keeled down to the basal scar, this horizontal or slightly oblique, not surrounded by a ridge, but frequently with a downwardly directed dorsal flange. In heavy, usually alkaline soils. Eastern Oregon to southern Idaho and northern Utah, south to southern California. March-July. Fig. 104.

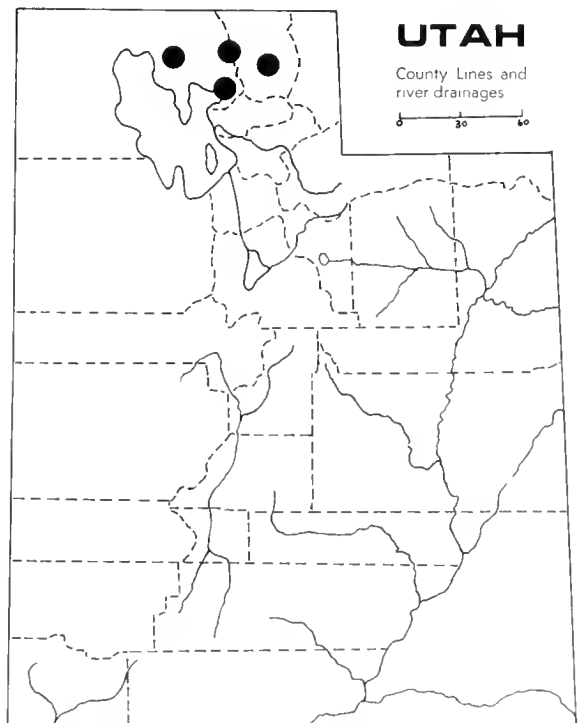


Fig. 104. *Plagiobothrys leptocladus*

Box Elder Co., 10 miles east of Bear River Refuge, B. Maguire 13989 (BRY, UTC); alkaline flats west of Perry, B. Maguire 3727 (UTC); 7 miles west of Brigham City, H. Jensen s.n. (UTC); 9 miles east of Bear River Refuge, Maguire & Piranian 13985 (UTC); 4 miles northwest of Logan, B. Maguire 12966 (UTC); 4 miles west of Smithfield, B. Maguire 13782 (UTC); 4.5 miles west of Logan, B. Maguire 13781 (UTC); 3 miles northwest of Logan, B. Maguire 12965 (UTC).

4. *Plagiobothrys scouleri* (Hook & Arn.)
Johnst. Journ. Arn. Arb. 16:192. 1935. Type:
Northwest Coast, Dr. Scouler.

Myosotis scouleri Hook & Arn. Bot. Beechey
370. 1840.

Allocarya scouleri Greene, Pittonia 1:18.
1887.

Allocarya cusickii Greene, Pittonia 1:17.
1887.

Allocarya hispidula Greene, op. cit.

Allocarya penicillata Greene, op. cit.

Allocarya nitens Greene, Pittonia 3:108.
1896.

Allocarya cognata Greene, Pittonia 4:235.
1901.

Plagiobothrys scopulorum Johnst. Contr.
Gray Herb. 68:79. 1923.

Plagiobothrys nelsonii Johnst. Contr. Gray
Herb. 68:77. 1923.

Plagiobothrys nitens Johnst. Contr. Gray
Herb. 68:78. 1923.

Plagiobothrys hispidulus Johnst. Contr. Arn.
Arb. 3:71. 1932.

Plagiobothrys cusickii Johnst. op. cit. 3:63.
1932.

Plagiobothrys cognatus Johnst. op. cit. 3:59.
1932.

Plants more or less densely branched from
the base; stems 5-25 cm tall, ascending or

spreading, with stiff appressed hairs; leaves 1-8
cm long, linear to oblanceolate, strigose to some-
what setose; racemes rather lax, the bracts re-
sembling the leaves; calyx 1-1.5 (2) mm long
in flower, in fruit becoming 1.5-2.5 mm long;
corolla about 1.5 mm long, inconspicuous; nut-
lets 1.5-2 mm long, variously roughened, with or
without setose projections. Moist soils in sandy
to clayey areas. Widely scattered over the west-
ern United States. May-July. Fig. 105.

Box Elder Co., Raft River Mountains, W.P. Cot-
tam 3051 (BRY); Raft River Mountains, S.J. Preece 752
(UT); Cache Co., $\frac{3}{4}$ mile west of Logan Airport, B.
Maguire 2412 (UTC); Davis Co., Farmington Water-
fowl Refuge, B. Maguire 13905 (UT); Centerville, S.
Flowers 1193 (UT); Garfield Co., Panguitch Lake, B.
Maguire 12958 (UTC); Aquarius Plateau, 19 miles
north of Escalante, N.H. Holmgren 2442 (BRY); Salt
Lake Co., Big Cottonwood Canyon, A.O. Garrett 1629a
(UT); Sanpete Co., 2 miles south of Indianola, B.F.
Harrison 10422 (BRY); Ephraim, W.P. Cottam 2783
(UT); Sevier Co., Fish Lake, mud flats, B. Maguire
12957 (UTC); Koosharem Reservoir, W.P. Cottam
9472 (UT); Summit Co., north slope of Big Mountain,
D.H. Galway 2375 (BRY); north slope of the Uinta
Mountains, Welsh, Moore & Matthews 9171 (BRY);
Gorgoza, A.O. Garrett 2291 (UT); Snyderville, A.O.
Garrett 7758 (UT); Tooele Co., Pilot Mountain, W.P.
Cottam 13812 (UT); Uintah Co., Upper Bear River,
B.F. Harrison 10968 (BRY); Utah Co., east slope of
Mount Timpanogos, B.F. Harrison 11447 (BRY); Ameri-
can Fork Canyon, A.O. Garrett 3800a (UT); Wasatch
Co., summit of Daniels Canyon, A.O. Garrett 8050
(UT); Washington Co., Pine Valley Mountains, B. Ma-

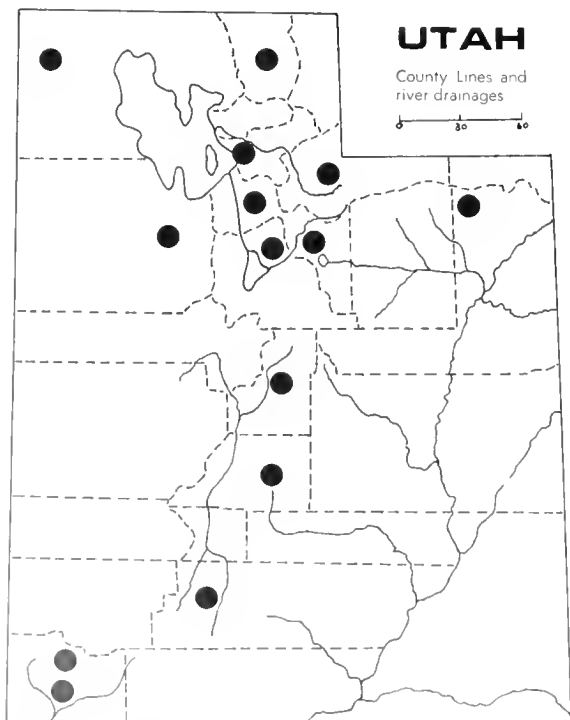


Fig. 105. *Plagiobothrys scouleri*

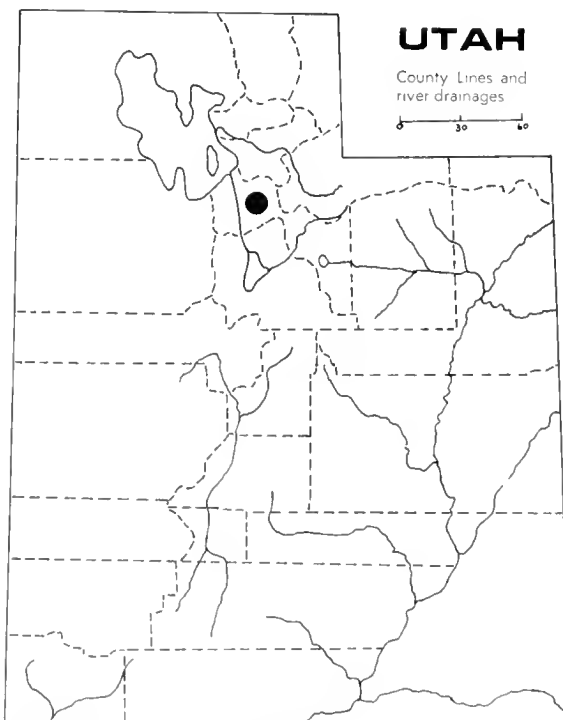


Fig. 106. *Plagiobothrys tenellus*

quire 12956 (UTC); Rock Spring, Pine Valley Mountains. R. Hardy s.n. (DIX).

5. *Plagiobothrys tenellus* (Nutt.) Gray, Proc. Amer. Acad. 20:283. 1885. Type: Sunny rocky slopes of the mountains along the valley of Coeur d'Alene River, Idaho.

Myosotis tenella Nutt. Kew Journ. Bot. 3:295. 1851.

Plagiobothrys parvulus Greene, Pittonia 3:261. 1898.

Plagiobothrys asper Greene, op. cit. 262.

Plagiobothrys humifusus M. E. Jones, Contr. West. Bot. 13:7. 1910.

Plagiobothrys tenellus var. *parvulus* subvar. *humifusus* Brand, Pflanzenreich 4, 252:108. 1931.

Stems slender, erect, freely branched from

the base or sometimes simple, 5-25 cm high, soft villous with spreading and reflexed hairs; leaves of the basal rosette oblong-lanceolate or oblong-oblancheolate, obtuse or acutish, villous, 1-2.5 cm long, cauline distinct, the lower ones linear-oblong, the upper becoming lanceolate or ovate-lanceolate, gradually reduced in size; spikes elongated in age and loosely flowered, only the lowest flowers bracteate; calyx densely short-villous with whitish or more often rufous hairs, about 3 mm long in age; corolla limb about 2-3 mm broad; nutlets 1.5-2 mm long, thick cruciform, light colored, sharply ridged dorsally and on the margins, the ridges commonly tuberculate. Grassy slopes and meadows. British Columbia and Idaho, south to Arizona, Utah, and northern lower California. March-June. Fig. 106.

Salt Lake Co., near mouth of Big Cottonwood Canyon, A.O. Garrett 2233 (UT).

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The help of the curators of the following her-

baria which have so graciously provided me with assistance and the use of their facilities is greatly appreciated.

BRY	Brigham Young University, Provo, Utah
DIX	Dixie Junior College, St. George, Utah
UTC	Intermountain Herbarium, Utah State University, Logan, Utah
UT	Garrett Herbarium, University of Utah, Salt Lake City, Utah
WTSU	West Texas State University, Canyon, Texas

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**CONTRIBUTIONS TO THE STUDY
OF THE GENUS *ERIASTRUM***

II. Notes concerning the type specimens and
descriptions of the species

by

H. Keith Harrison



BIOLOGICAL SERIES — VOLUME 16, NUMBER 4

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TABLE OF CONTENTS

INTRODUCTION	1
TAXONOMY	1
ACKNOWLEDGMENTS	25
LITERATURE CITED	26

CONTRIBUTIONS TO THE STUDY OF THE GENUS *ERIASTRUM*

II. Notes concerning the type specimens and descriptions of the species

by

H. Keith Harrison¹

ABSTRACT

The species of the genus *Eriastrum* are described. Keys to the species and subspecies and the geographic ranges are provided. Discussions with regard to the type specimens or lectotypes and interspecific relationships are presented.

INTRODUCTION

The species of the genus *Eriastrum* are closely related; and the range of variation found in one species in branching, the lobing of the leaves, vesture, etc., overlaps that found in other species to a considerable degree. The species as they are now generally known were described by Mason (1945). At that time, it was noted that the proportions and size of the corolla and stamens were important in identification of the plants. Further study (Harrison 1959, 1968) introduced new methods, emphasized the importance of the relative size and proportions of the corolla and androecium, and elucidated the nature of these characteristics.

During the investigation of the species of *Eriastrum* (Harrison 1959), it was found that the type specimen for one of the species had not been published and that other problems concerning types and lectotypes require some discussion. Inasmuch as nearly three decades have passed since the first major paper on the species of *Eriastrum* was published (Mason

1945), and as a later work (Harrison 1959) is not generally available, it seems desirable to include the information as to the type specimens and synonymy for all the species, together with the additions and discussions by the author.

It is understood that the first elements to be found of a new species may represent either the norm or one extreme in the variation of the species. At a later time, other plants may be collected which cause the investigator to create a name for a subspecies, thereby segregating certain specimens as being closely related to (but still distinct from) the type upon which the species is based. The formation of a subspecific category for the new element then necessitates, according to the International Code of Botanical Nomenclature (Article 25) and logic, the establishment of another subspecies to include only those plants most representative of the type—one could otherwise make no distinction between the type subspecies and specimens identified only to the species level.

TAXONOMY

Eriastrum Wooton and Standley

Hugel Bentham, Bot. Reg. 19: under pl. 1622, 1833, not *Huegelia* Reichenbach, Consp. 144, 1828. *Welwitschia* Reichenbach, Handb. 194, 1837, not *Welwitschia* Hooker, Gard. Chron.

22:71, nom. cons. *Eriastrum* Wooton and Standley, Contr. U.S. Nat. Herb. 16:160, 1913, *Gilia* and *Navarretia* of authors, in part.

Erect, or spreading and erect, annuals or perennials, virgately, racemosely, corymbosely,

¹Weber State College, Ogden, Utah

diffusely, or paniculately branched; herbage subglabrate to densely floccose; leaves linear, entire or pinnately lobed; bracteate floral heads, few or numerous, few- to many-flowered, rarely solitary, lightly floccose to densely so with arachnoid wool; calyx lobes unequal, joined along the lower two-thirds of their length by a hyaline margin; corollas blue, yellow or white, sometimes cream, rarely pink, funnellform to sal-

verform, regular or irregular; stamens equally inserted at the base of the throat, on the throat or just below the sinuses, equal, subequal, or distinctly unequal; anthers sagittate, versatile; capsule ellipsoid, three-lobed, few-seeded; seeds mucilaginous.

Type species: *E. filifolium* (Nutt.) Woot. & Standl.

Range: Western North America.

Key to the Species

- A. Plants perennial, woody, branching from the base; stamens inserted at the sinus 1. *E. densifolium*
- AA. Plants annual, herbaceous, branching from the base or above; stamens inserted at the sinus or below.
- B. Corolla 15.0 to 23.0 mm long.
- C. Stamens inserted at the sinus; corolla salverform, or very narrowly funnellform 2. *E. pluriflorum*
- CC. Stamens inserted at the base of the throat; corolla funnellform.
- D. Corolla bilabiate, or irregular to obscurely so; stamens distinctly unequal, filaments often oriented toward lower lip, and anthers turned toward upper lip, lavender blue; desert areas 6. *E. eremicum*
- DD. Corolla regular, or very nearly so; stamens usually equal, filaments not oriented toward one side of corolla, bright blue; Monterey County 3. *E. virgatum*
- BB. Corolla 5.0 to 15.0 mm long.
- C. Stamens 5.0 to 10.0 mm long, nearly equalling or exceeding tips of the corolla lobes; anthers (restored)* 2.0 to 3.0 mm long.
- D. Corolla bright golden yellow, 8.0 mm long, regular to very slightly irregular; Monterey, San Luis Obispo counties 4. *E. luteum*
- DD. Corolla bright sapphire blue, ca. 1.0 to 1.5 cm long, distinctly irregular to obscurely so; southern California to Baja, 1000 ft to 9000 ft 5. *E. sapphirinum*
- CC. Stamens less than 5.0 mm long, not equalling or exceeding tips of corolla lobes; anthers (restored) not more than 2.0 mm long.
- D. Stamens equal; corolla lobes 1.0 mm broad, or less; corolla narrowly funnellform; throat expanding slightly or not at all.
- E. Filaments 2.5 to 3.0 mm long; floral heads distinctly "brushy" with tips of bracts and calyx lobes conspicuous; ovary cylindric, three-times longer than wide 7. *E. filifolium*
- EE. Filaments 1.5 mm or less; tips of bracts and calyx lobes not conspicuously prominent; ovary 1 to 1.5 times longer than wide.
- F. Corolla 7.0 to 11.0 mm long; plants 15.0 to 35.0 cm high.
- G. Leaves mostly 1.0 to 1.5 cm long and entire, or to 3.0 cm and with one pair of lateral lobes; foliage often remaining somewhat soft; throat expanding slightly 8. *E. sparsiflorum*
- GG. Leaves mostly 1.5 to 2.5 cm long with one pair of lateral lobes, less commonly entire; foliage becoming rigid and brittle; throat not expanding.
- H. Corolla lobes 3.0 to 3.5 mm long and 1.0 mm broad 11. *E. brandegeae*

*The addition of a drop of 10 percent liquid detergent restores dried anthers to the size at the time of dehiscence

HH. Corolla lobes 2.5 mm long and 1.5 mm broad 12 *E. trayci*

FF. Corolla 5.0 to 8.0 mm long; plants to 15.0 cm high.

G. Leaves, when present, 2.0 to 4.5 cm long, with one to three pair of lateral lobes to 1.0 cm or longer; floral heads many-flowered, very densely floccose, often found under *Adenostoma* chaparral or on obsidian rubble 13. *E. abramsii*

GG. Leaves filiform, 0.5 to 2.5 cm long, entire or with one pair of lateral lobes 2.0 to 5.0 mm long; floral heads few-flowered, somewhat floccose, occurring in dry stream beds and on alkaline flats 14. *E. hooveri*

DD. Stamens unequal, corolla lobes 1.25 to 2.25 mm broad, corolla funnellform.

E. Plants robust to 30.0 cm high, racemose, corymbose, or branched from the base; herbage floccose, often densely so; leaves 1.5 to 3.0 cm long, usually with one or two pair of lateral lobes; floral heads several-flowered 9. *E. wilcoxii*

EE. Plants to 15.0 cm high, diffusely branched from the base; stem and leaves slender; herbage lightly floccose; leaves 1.0 to 2.5 cm, usually with one pair of lateral lobes; floral heads few-flowered 10 *E. diffusum*

1. *Eriastrum densifolium* (Benth.) H. L. Mason, Madroño 8:73, 1945.

Perennial, woody subshrub to 75.0 cm high, branching from the base, erect, or spreading, then erect; secondary branches erect, appearing below the dead persistent heads; herbage light green and lightly floccose or subglabrate to dull grey green and grey-canescens; stems leafy with short inconspicuous internodes or sparingly leaved with internodes to 4.0 cm long; leaves sessile, 1.0 to 5.0 cm long, pinnately parted with one to five pair of lateral lobes or entire; leaf rachis 1.0 to 3.5 mm wide; axils naked or with a spur shoot or a canescent bud; heads terminal or in a compact group; bracts as long as or far exceeding heads, with one to four pair of lateral pinnae, less commonly entire; calyces 0.5 to 1.0 cm long, densely floccose to canescent; lobes unequal, joined by a hyaline membrane; corolla funnellform, regular, 1.5 to 3.0 cm long; lobes blue to lavender blue, elliptic to elliptic-spatulate, 0.5 to 1.5 cm long and to 5.0 mm broad; stamens adnate to sinus, equal, 4.0 to 8.0 mm long; filaments 2.5 to 6.0 mm long; anthers sagittate, versatile, 2.5 to 4.0 mm long; stigma 1.0 to 1.75 mm long; ovary three-loculed, few-seeded.

Key to the Subspecies

- A. Herbage lightly floccose, subglabrous, or glabrous; leaves light green.
 - B. Leaves entire or with one to two pair of lateral lobes; internodes very short; spur-shoot in axils often 1.0 to 2.0 cm

long; corolla broadly funnellform; found at elevations below 1000 ft, San Luis Obispo to Santa Barbara County
 1a. *E. densifolium* subsp. *densifolium*

BB. Leaves with three to four pair of lateral lobes, rarely entire; internodes 1.0 to 1.5 cm; axils most commonly naked or spur-shoot *ca.* 1.0 cm long; corolla narrowly funnellform; found from 1500 ft to 8000 ft, Monterey to Baja California, Inyo County to Baja California 1b. *E. densifolium* subsp. *austromontanum*

AA. Herbage floccose, lanate, or canescent; leaves grey green.

B. Well-developed spur-shoot often present in the axils; corolla *ca.* 30.0 mm long; San Bernardino and Orange County region
 le. *E. densifolium* subsp. *sanctorum*

BB. Short canescent buds often present in axils; corolla *ca.* 16.0 to 18.0 mm long.

C. Plants to 50.0 cm high; leaves 1.5 to 4.0 cm long; leaf rachis to 1.5 mm broad; Monterey to Baja California, Inyo County to Baja California
 1c. *E. densifolium* subsp. *elongatum*

CC. Plants 20.0 to 30.0 cm high; leaves 1.0 to 2.0 cm long; leaf rachis 1.5 to 3.5 mm broad; Kern, San Bernardino, Los Angeles County region 1d. *E. densifolium* subsp. *mohavensis*



Fig. 1. *Eriastrum densifolium* subsp. *densifolium*. a. Habit, K. Harrison 250 UC M141468, X 1.1. b. Habit, K. Harrison 250 US M141469, X .6.

1a. *Eriastrum densifolium* (Benth.) H. L. Mason subsp. *densifolium*.

Hugelia densifolia Benth. Bot. Reg. 19: under Pl. 1622. 1833.

Gilia huegelia Steud., Nom. ed. 2, 1:683. 1840.

G. densifolia Benth. in D.C. Prod. 9:311. 1845.

Navarretia densifolia Kuntze, Rev. Gen. Pl. 2:433. 1891.

N. densifolia Brand in Engler, Pflanzenreich IV, 250:165. 1907.

Wehwitschia densifolia Tidestrom, Contr. U.S. Herb. 25:429. 1925.

Hugelia densifolia Benth. in Jepson, Man. Fl. Pl. Calif. 792. 1925 in part.

Gilia densifolia var. *typica* (Benth.) Craig, Bull. Torrey Club 61:390. 1934.

H. densifolia Benth. in Jepson, Fl. Calif. 3:161-162. 1943 in part.

Perennial, woody subshrub to 50 cm high; major branching from the base, erect or spreading, then ascending; secondary branches erect, appearing at various distances below the dead, persistent heads from the previous year; herbage subglabrous or glabrate; stems leafy, stems may be nearly hidden by the close-set leaves; internodes very short; leaves light green, 2.0 to 4.0 cm long, ascending, commonly entire or with one or two (rarely more) pair of short, lateral pinnae 2.0 to 8.0 mm long, usually set toward the basal portion of the leaf; the terminal lobe thus long (rarely, the outer pair of pinnae may branch from the midpoint of the leaf), subulate, awn-tipped; spur-shoots in the axils often well developed, 1.0 to 2.0 cm long or longer, green; the floral heads are terminal, or a compact group of heads may be formed; the terminal heads themselves are composed of a few smaller heads in a very compressed inflorescence appearing as one structure; heads large, 2.0 to 4.0 cm in diameter and 1.5 to 2.5 cm in length, excluding flowers; in full flower, the tight cluster of heads may make a mass of flowers 6.0 cm across; bracts distinct to 2.0 cm long, exceeding the calyces, with one or two pair of lateral pinnae set on the lower portion; the terminal lobe long, subulate, awn-tipped, lightly lanate to subglabrous, light green contrasting with the white wool surrounding the calyces; calyx 1.0 cm long, covered with a mass of persistent, tangled, white trichomes, calyx cleft in subequal lobes; lobes united two-thirds of their length by a hyaline membrane, which margins the lobes nearly to their tips; corolla bright blue; throat and tube

white or yellow; corolla to 2.5 cm long, broadly funnelform; lobes to 1.1 cm long, elliptic to elliptic-spatulate, to 5 mm broad; throat plus tube to 1.25 cm long; tube puberulent; stamens adnate to sinus, 8.0 mm long; filaments 6.0 mm; anthers versatile sagittate, white, 3.5 mm long; stigma 1.25 mm long; style 1.5 cm long; ovary three-loculed; locules approximately six-seeded.

Type: David Douglas in 1833. KEW. Photograph of type POM^o188266; probable isotype UC 163785. "California." Probably San Luis Obispo County.

Range: San Luis Obispo and Santa Barbara counties, California.

Eriastrum densifolium subsp. *densifolium* is a very distinct subspecies and is limited in its geographic range to the coastal region, centering about San Luis Obispo. The large, broadly-spreading, funnelform corolla, the large heads, and the nearly glabrous, green, closely-set leaves mark it as distinct. The closest affinities are with *E. densifolium* subsp. *austromontanum*.

1b. *Eriastrum densifolium* subsp. *austromontanum* (Craig) H. L. Mason, Madroño 8:74. 1945.

Gilia densifolia var. *austromontana* Craig, Bull. Torrey Club 61:391. 1934.

Huegelia densifolia subsp. *austromontana* Ewan, Bull. Torrey Club 64:520. 1937.

Huegelia densifolia var. *austromontana* Jepson, Fl. Calif. 3:162. 1943.

Woody-based perennial to 30 cm high, erect, or spreading, then erect; secondary branches erect, axillary branches may be present; herbage slightly floccose to subglabrous; stems leafy; internodes 1.0 to 1.5 cm long, rarely to 2.5 cm; leaves light green, 1.5 cm long to 3.5 cm, ascending usually with three to four pair of lateral pinnae, rarely entire, subulate-tipped; outer two to three pair of pinnae, sometimes nearly equally spaced; the terminal lobe thus short; axils without canescent buds, short spur shoots sometimes present in the axil, or axil naked; floral heads commonly terminal, heads small to medium, 1.0 to 1.5 cm long (excluding flowers and tips of bracts), to 3.0 cm long (including tips), 1.0 to 3.0 mm across (excluding tips of bracts), to 4.0 cm across (including tips), moderately woolly; bracts numerous, well developed, 1.5 to 3.0 cm long, exceeding the calyces by 1.0 to 2.0 cm in length, with one to four pair of lateral pinnae; pinnae sometimes short or exceeding 1.0

*Abbreviations are in accordance with Lanjouw and Stafleu, Index Herbariorum (1964).

cm in length; calyx 6.0 to 8.0 mm long, cleft into subequal lobes, hyaline margin joining the lobes into a tube nearly the length of calyx, calyx lobes narrow; corolla blue, narrowly funnelform, 16 to 18 mm, rarely to 23 mm long; lobes 5.0 to 7.0 mm long, elliptic to elliptic-spatulate, 2.5 to 3.25 mm broad; tube plus throat 9 to 12 mm long, tube puberulent; stamens adnate to sinus (or to 0.5 mm below sinus), 5.0 to 6.0 mm long; filaments 3.0 to 4.0 mm long; anthers versatile, sagittate, white, 3.0 to 3.5 mm long; stigma 1.0 mm long; ovary few-seeded.

Type: P. A. Munz 8341 POM 48414. Palomar Mountains near Nellie, San Diego County, California.

Range: Monterey County south to Baja California and north to Inyo County, California, occurring from 1500 ft to over 8000 ft, and generally over 4000 ft.

Eriastrum densifolium subsp. *austromontanum* is closely related to the type subspecies. Similarities may be noted in the branching habits, the light green, lightly floccose or subglabrate leaves, in the short internodes, in the absence of canescent buds in the axils, and in the size of the heads. It differs in having more elaborately lobed leaves and bracts and in the slightly smaller and more narrowly funnelform flowers.

1c. *Eriastrum densifolium* subsp. *elongatum* (Benth.) H. L. Mason, Madroño 8:73. 1945.

Hugelia elongata Benth. Bot. Reg. 19: under Pl. 1622. 1833.

Gilia elongata Steud., Nom. ed. 2, 1:683. 1840.

Navarretia densifolia subsp. *elongata* Brand in Engler, Pflanzenreich IV, 250: 165. 1907.

G. densifolia var. *elongata* (Benth.) Gray ex. Brand, loc. cit.

H. densifolia Benth. in Jepson, Fl. Calif. 3:161-162. 1943 in part.

Perennial to 50 cm high, branching from the woody base, erect or spreading, secondary branches erect; herbage canescent (particularly in the upper younger region), usually remaining canescent in age, occasionally subglabrous; internodes 1.0 to 4.0 cm long; leaves grey green ascending, 1.5 to 3.0 cm long, rarely to 4.0 cm long, entire or pinnate, with one pair near the base of the leaf to four pairs of short lateral pinnae; pinnae commonly less than 5.0 mm long,

occasionally to 1.0 cm long when three to four pair of pinnae are present, the outer two to three pair may be nearly equally spaced, making the terminal lobe short and comparable to the spacing between the outer pinnae; often many axils show weak development of short canescent buds; short axillary branches with small heads are often present in the upper portion; the numerous heads may be terminal, or the terminal branching may be racemose or corymbose; heads small, 0.75 to 1.5 cm long, 1.0 to 2.0 cm across (excluding tips of bracts), white-canescent; bracts 0.75 to 1.5 cm long, occasionally to 2.0 cm long, merely equalling to exceeding the calyces; bracts not always distinct, as they may be half-hidden by dense, canescent wool; calyces completely hidden by dense wool, cleft into subequal lobes, 5.0 to 7.5 mm long; lobes margined by a hyaline membrane uniting the lower two-thirds of the calyx, subulate-tipped; corolla bright blue or lavender blue; veins may be marked by dark lavender blue, throat and tube white or yellow, 14 to 18 mm long, narrowly funnelform to salverform; lobes to 7.0 mm long, elliptic to elliptic-spatulate, 2.0 to 3.0 mm broad; throat plus tube 8.0 mm to 1.25 cm long, tube puberulent; stamens adnate to sinus, 5.0 to 7.0 mm long; filaments 3.0 to 4.0 mm long; anthers versatile, sagittate, white, 3.0 to 3.5 mm long; stigma 1.0 mm long, style 1.25 cm long; ovary three-loculed, locules few-seeded.

Type: David Douglas in 1833, "California." KEW. Probably Monterey, San Benito, or San Luis Obispo County.

Range: San Benito County south to Baja California and north to Inyo County, California.

Eriastrum densifolium subsp. *elongatum* differs from the type subspecies in having weakly developed white-canescent buds in the axils instead of well-developed spur-shoots, and in having lanate-canescant, grey-green herbage, particularly in the younger parts.

1d. *Eriastrum densifolium* subsp. *mohavensis* (Craig) H. L. Mason, Madroño 8:74. 1945.

Gilia densifolia var. *mohavensis* Craig, Bull. Torrey Club 61:392. 1934.

Hugelia densifolia var. *mohavensis* Jepson, Fl. Calif. 3:162. 1943.

Perennial to 20 or 30 cm high, much branched, dead heads persisting from the previous year, new branches arising below; stem in older portions scaly and light cream-tan in color as outer layers flake off; herbage, except the old

stem, canescent-lanate; stem somewhat leafy, internodes 1.0 cm long; leaves dull grey green, 1.0 to 1.5 cm long, occasionally to 2.0 cm long, ascending or reflexed; leaf rachis 1.5 to 3.5 mm broad, with one to four pair of very short lobes 2.0 to 3.0 mm long; lower axils usually with short canescent buds; heads few to numerous, to 200 in a plant 20.0 cm high, each branch producing several; heads small, ca. 1.0 cm long and 1.5 cm broad, excluding flowers; bracts with one to three pair of very short spinescent lobes or teeth or entire, canescent, often only the tip is visible; calyces hidden by the dense mat of white wool; calyx cleft into unequal lobes; lobes with a hyaline margin forming a tube and covered with a dense mat of long trichomes; corolla light or lavender blue, 16 mm long, narrowly funnellform; lobes to 5.0 mm long, elliptic-spatulate and 2.0 mm broad, throat 2.0 mm long, tube 9.0 mm long, tube puberulent; stamens 4.0 mm long, filaments 2.5 mm long; anthers versatile, sagittate, 2.75 mm long; stigma 1.25 mm long, style 12 mm long, locules few-seeded.

Type: T. Craig 1630. POM 182123. Between Rosamond and Mojave, Kern County, California.

Range: Mohave Desert; Kern, San Bernardino, and Los Angeles counties, California.

Eriastrum densifolium subsp. *mohavensis* is most closely related to *E. densifolium* subsp. *elongatum*. The relationship may be noted by the dull, grey-green leaves, the small canescent heads and the short bracts. The former subspecies differs in its shorter stature, shorter internodes and in the broader, shorter leaves which may also be recurved.

1c. *Eriastrum densifolium* subsp. *sanctorum* (Milliken) H. L. Mason, Madroño 8:75. 1945.

Gilia densifolia var. *sanctora* (Milliken) Univ. Calif. Pub. Bot. 2:39. 1904.

Hugelia densifolia var. *sanctorum* (Milliken) Jepson, Man. Fl. Pl. Calif. 792. 1925.

H. densifolia var. *sanctorum* (Milliken) Jepson, Fl. Calif. 3:162. 1943.

Woody subshrub to 75 cm high; stems leafy; herbage canescent, usually remaining so; leaves dull grey green, ascending, to 5.0 cm long, entire or with one to three pair of lateral pinnae on the lower portion of the leaf; spur-shoots in the axils well developed and short branches common; heads terminal or upper branches racemose-corymbose; heads woolly; bracts to

2.5 cm long equalling or exceeding the heads; calyces 1.0 cm long, cleft into unequal lobes; corolla lavender blue; throat and tube yellow; veins may be marked by deep lavender blue, to 33.0 mm long, funnellform; lobes to 9.0 mm long, elliptic to elliptic-spatulate, to 5.0 mm broad; throat plus tube to 25.0 mm in length, tube slightly puberulent; stamens adnate to sinus or to 0.5 mm below, 6.5 to 8.0 mm long; filaments 4.5 to 5.5 mm long; anthers versatile, sagittate, white, 4.0 mm long and to 2.0 mm broad; stigma to 1.75 mm long, style 25 to 30 mm long, ovary three-loculed, each approximately five-seeded.

Type: H. M. Hall 683 and 173, UC 52454 and UC 23521. Santa Ana River, Spanishtown Crossing above Riverside, California.

Range: Santa Ana River, San Bernardino and Orange counties, California.

Eriastrum densifolium subsp. *sanctorum* may be recognized as a distinct subspecies by its long corolla. The large spur-shoots in the axils and the leafy stems suggest aspects of the type subspecies. The grey-green, densely woolly herbage, the occasional heads with short bracts and the woolly axillary buds suggest a relationship with *E. densifolium* subsp. *elongatum*.

2. *Eriastrum pluriflorum* (Heller) H. L. Mason, Madroño 8:75. 1945.

Annual, 2.0 to 30.0 cm high or more, simple to densely-branched; herbage floccose to subglabrous; leaves light green, to 5.0 cm long, entire or pinnately divided with one to five pair of lateral lobes; heads bracteate, lanate; bracts 1.0 to 3.0 cm long, pinnately divided with one to four pair of lobes; calyx 0.5 to 1.0 cm long; corolla regular, 16.0 to 23.0 mm long, blue, or throat yellow, or tube and throat yellow; stamens adnate to the sinus, equal or subequal; anthers sagittate, versatile; stigma 0.75 to 1.0 mm long, style 11.0 to 16.0 mm long; ovary three-loculed, locules few-seeded.

Key to the Subspecies

- A. Plants 2.0 to 30.0 cm high, lobes of the leaves to 2.0 cm long, corolla salverform or very narrowly funnellform, lobes elliptic 2.0 to 2.5 mm or occasionally to 3.0 mm broad; hills bordering the San Joaquin Valley
 2a. *E. pluriflorum* subsp. *pluriflorum*
 AA. Plants 2.0 to 15.0 cm high, lobes of the leaves to 8.0 mm long, corolla narrowly

funnelform, throat expanding, corolla lobes broadly elliptic to 4.0 mm broad; Antelope Valley, Los Angeles and San Bernardino counties

2b. *E. pluriflorum* subsp. *sherman-hoytate*

2a. *Eriastrum pluriflorum* (Heller) H. L. Mason subsp. *pluriflorum*.

Gilia virgata var. *floribunda* Gray, Proc. Amer. Acad. 8:272. 1870. Not *G. floribunda* Gray.

G. pluriflora Heller, Muhlenbergia 2:113. 1906.

Navarretia virgata var. *floribunda* Brand in Engler, Pflanzenreich IV, 250:168. 1907.

G. brauntonii Jepson and Mason, Fl. Econ. Pl. Calif. 130. 1924.

Hugelia brauntonii Jepson, Man. Fl. Pl. Calif. 793. 1925.

H. pluriflora Ewan, Bull. Torrey Club 64:520. 1937.

H. pluriflora (Heller) Ewan in Jepson, Fl. Calif. 3:163. 1943 in part.

Annual, 2.0 to 30.0 cm or more high, and to 50.0 cm in breadth; erect, unbranched, or virgate, racemose, or corymbose; branching above or from the base; internodes 1.0 to 5.0 cm long; herbage floccose to subglabrous; leaves light green, to 5.0 cm long, subulate-tipped, pinnately divided with three to five pair of lateral lobes, rarely entire; lateral lobes to 2.0 cm long, spreading; floral heads variable from 1.0 to 4.0 cm long, broad, lanate, conspicuously bracteate; bracts 2.0 cm to 3.0 cm long (exceeding the heads), with three to four pair of lateral lobes, lobes spreading slender, often to 1.0 cm long or to 1.5 cm long, subulate-tipped; calyx 0.5 to 1.0 cm long, cleft into unequal lobes, joined by the hyaline membrane; flowers numerous; corolla regular 16.0 to 23.0 mm long, salverform or very narrowly funnelform, far exceeding the heads; tube long and slender, ca. 1.0 to 1.25 mm in diameter; corolla blue to lavender blue, or throat yellow, or throat and tube yellow; veins of the lobes often marked by darker lines, tube puberulent; lobes 5.0 to 6.0 mm long and 2.0 to 2.5 mm broad, occasionally to 3.0 mm broad; tube plus throat 10.0 to 18.0 mm long; stamens adnate just below the sinus, 3.0 to 5.0 mm long, equal or subequal, the longest equalling the tip of the corolla lobe or nearly so; the anther base of the shortest stamen occasionally may be only 0.5 mm above the sinus, filaments 1.5 to 4.0 mm long; anthers sagittate, versatile, white or yellow or purple, 2.5 mm long, 1.0 mm broad; stigma 0.75 to 1.0 mm long; style ca. 11.0 to 16.0 mm

long; ovary three-loculed, approximately three-seeded.

Lectotype: W. H. Brewer 1212. GH. Corral Hollow, Alameda County, California.

Range: West Central California, hills bordering the San Joaquin Valley from Contra Costa County south to Santa Barbara County, east to Fresno, Tulare and San Bernardino counties, California.

The plants described by Gray as *Gilia virgata* var. *floribunda* were based upon California collections by Fitch, Wallace, and Brewer (Gray 1870). Jepson (1943) felt that the collection by Fitch, being the first cited by Gray, could well be taken as the type, and so indicated it. In the *Synoptical Flora* (1878, 1886), Gray listed the collection as Wallace, Brewer, and Palmer, omitting the Fitch collection. In the herbarium of the University of California, there is a collection by W. H. Brewer 1212, June 3, 1862, taken while he was engaged on the state survey, from Camp 72, Corral Hollow, Alameda County, California, that is inscribed by Jepson as the type. In 1905, A. A. Heller found *Gilia virgata* var. *floribunda* abundant on the dry hillsides near Sunset, Kern County, California, and listed two collections: 7734 from Sunset and 7742 from Oil City. He noted that the variety was sufficiently distinct from the species with which it had been associated to warrant raising it to specific level. Since *Gilia floribunda*, Gray was already occupied; he chose another name descriptive of the numerous flowers, that of *Gilia pluriflora*. The Heller collection 7734 was subsequently taken to be the type, and Sunset, Kern County, as the type locality (Craig 1934). Heller based his species on *Gilia virgata* var. *floribunda*; and it is evident that he did not intend his collection to be construed as the type, for he was explicit whenever he referred to a type (Heller 1906, Ewan 1937).

An isotype of Heller 7734 at UC is adequate, and the Heller 7742 (not mentioned in connection with the type) is an excellent specimen. However, in accordance with custom, it is appropriate to refer to the Fitch, Wallace, or Brewer collection for the type. The Fitch collection has no information as to where or when it was collected other than "Calif. Fitch." The specimen is a fragment with very few flowers, which could be regarded as adequate were there no other selections available. The Wallace collection is much better, with many flowers; and the location is given as Tejon. The Brewer collection is satisfactory; adequate information is given with respect to location; and specimens of

the collection are known at Gray, University of California, and Jepson Herbaria. Of these, the best is one of those at the University of California. This is the specimen inscribed by Jepson as being the type and is annotated by Craig as "*Gilia pluriflorum* Heller, type of *Gilia virgata* var. *floribunda* Gray"; still, Gray did not cite this specimen as type. It seems appropriate to select the Brewer collection 1212 (Gray Herbarium) from Corral Hollow, Alameda County, California, and which is annotated by Gray as "*Gilia (Hugelia) virgata* var. *floribunda*," as a lectotype.

Eriastrum pluriflorum is a very variable species with regard to size and branching habit. Plants may flower when only 2.0 cm high. They may grow strictly virgate to 15.0 or 30.0 cm or more with one stem only and one terminal head. Branching may be virgate, racemose, corymbose, or paniculate. The plants often possess one stem below that becomes branched in the upper portion; or branching occurs from the base, producing a small plant with a cluster of branches or a very densely branched shrubby plant to 50.0 cm or more in diameter.

Probably the closest connection between the perennial and the annual species lies between *E. densifolium* subsp. *austromontanum*, and *E. pluriflorum*. Characters which link these entities are the light green, lightly floccose or subglabrous herbage, the leaves and bracts with 2-5 pair of lobes, the bracteate-lanate heads, the long, slender corollas and the stamens inserted at the sinus. The more elaborately lobed leaves and bracts, the long salverform corolla and the insertion of the stamens at the sinus, distinguish *E. pluriflorum* from all of the other annual species of *Eriastrum*; it is perhaps the most easily recognized of the annual species. Another close relationship exists between this species and *E. eremicum*. This relationship will be discussed in connection with the latter species.

2b. *Eriastrum pluriflorum* subsp. *sherman-hoytae* (Craig) H. L. Mason, Madroño 8:75. 1945.

Gilia sherman-hoytae Craig, Bull. Torrey Club 61:415. 1934.

Hugelia pluriflora (Heller) Ewan in Jepson, Fl. Calif. 3:163. 1943 in part.

Annual, 3.0 to 15.0 cm high, simple to corymbosely branched; herbage floccose to subglabrous; leaves green 1.0 to 4.0 cm long, entire or pinnately divided with one to four pair of lateral lobes; lobes to 8.0 mm long, often reduced to teeth; floral heads approximately 1.0 cm broad,

lanate; bracts 1.0 to 2.0, occasionally to 3.0 cm long, pinnately divided with one to three pair of lobes, exceeding the heads; calyx 5.0 to 7.5 mm long, cleft into unequal lobes; corolla regular, to 20.0 mm long, narrowly funnelform; tube long and slender; throat expanding, blue or yellow, or throat and tube yellow, lobes broadly elliptic to 6.0 mm long and to 4.0 mm broad; stamens adnate just below the sinus or as much as 0.75 mm below, equal or subequal, 2.0 to 4.0 mm long; filaments 1.0 to 3.0 mm long; anthers sagittate, versatile, 1.5 mm long; stigma 1.0 mm long, style ca. 14.0 mm long, ovary three-lobed.

Type: P. A. Munz and T. Craig 12925. POM 185022. Ten miles south of Muroc, Los Angeles County, California.

Range: Antelope Valley, Los Angeles and San Bernardino counties, California.

This subspecies differs from the type subspecies in the short stature of the plants and the small heads. The corolla lobes are broader and the corolla more funnelform. The stamens are shorter and are sometimes inserted 0.25 to 0.75 mm below the sinus. The leaves have fewer and shorter lobes. This subspecies is known from Antelope Valley near Lancaster and Muroc, which is near the southern limits of the species.

3. *Eriastrum virgatum* (Benth.) H. L. Mason, Madroño 8:84. 1945.

Hugelia virgata Benth. Bot. Reg. under Pl. 1622. 1833.

Gilia virgata Steud., Nom. ed. 2, 1:684. 1840.

Navarretia virgata Kuntze, Rev. Gen. Pl. 2:433. 1891.

N. virgata Brand in Engler, Pflanzenreich IV, 250:167. 1907.

N. densifolia var. *lanata* Brand, op. cit. 165.

G. virgata var. *typica* Craig, Bull. Torrey Club 61:394. 1934.

Annual, erect, 3 to 40 cm high, occasionally to 50 cm high, virgate, or racemosely branched above, or branching from the base, then ascending virgately; herbage light green, usually lanate to lightly floccose, sometimes subglabrous, but remaining woolly on the axillary buds and heads; leaves linear, filiform, ascending, often somewhat appressed, 2.0 to 5.0 cm long, entire or with one pair of lateral pinnae near the base of the leaf, rarely with two pair; lateral pinnae slender, to 12 mm long; heads woolly, 1.25 to 2.0 cm long and 1.0 to 3.0 cm broad, including

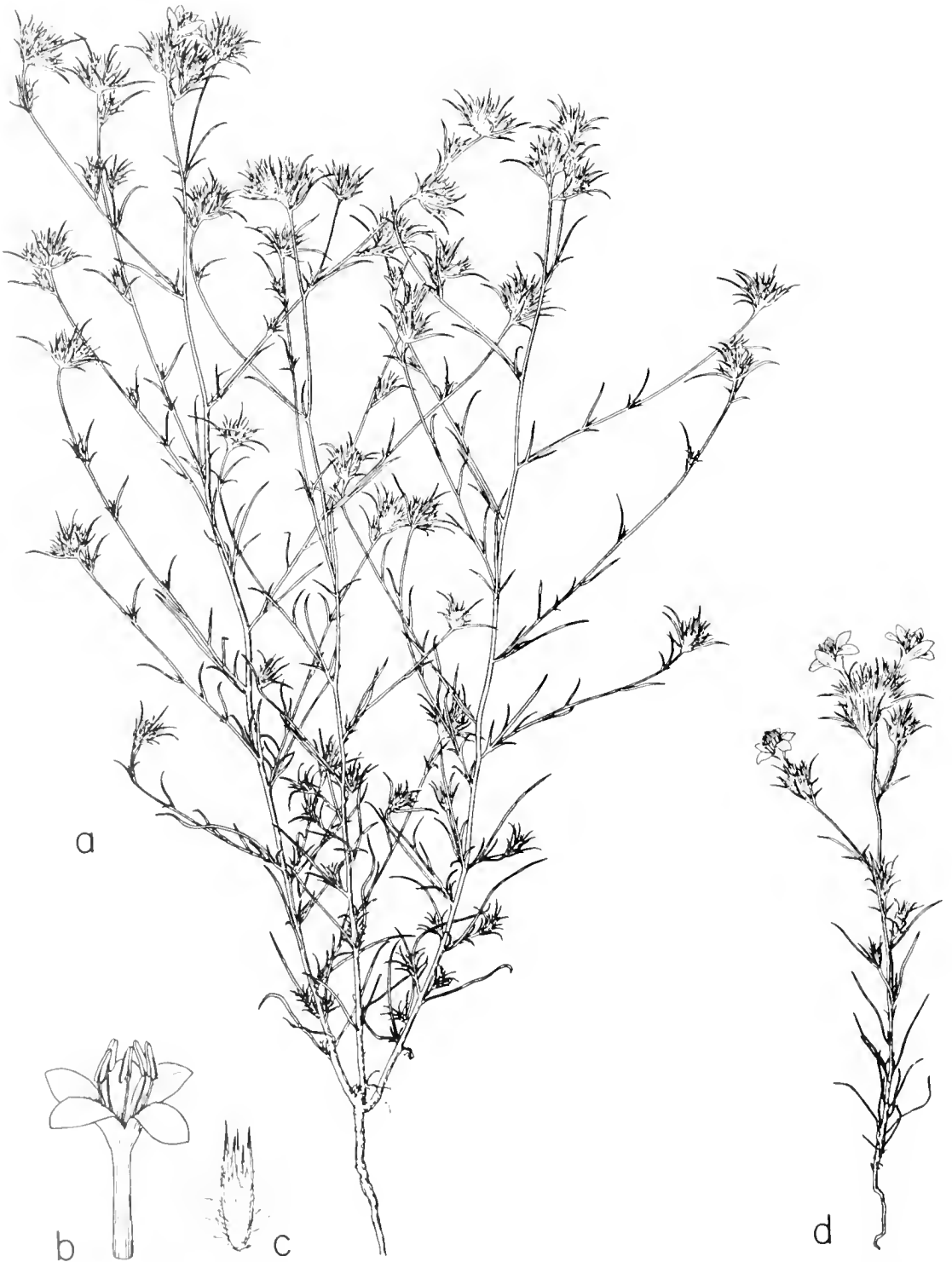


Fig. 2. *Friatum virgatum*. a. Habit, X 1.6. b. Corolla and stamens, X 2.3. c. Calyx, X 2.3. d. Habit, K. Harrison 237 U.C. MH41467, X .6.

the bracts; central mass usually 0.75 cm to 2.0 cm broad, few-flowered; bracts 1.0 to 2.5 cm long exceeding the heads, usually with one pair of lateral lobes; calyx lobes unequal, to 9.0 mm long, joined by a hyaline membrane, subulate-tipped; corolla funnellform, regular or very nearly so, 15.0 to 22.0 mm long, bright blue with yellow throat and tube; lobes 6.5 to 9.5 mm long and to 3.0 mm broad; throat plus tube 8.0 to 13.0 mm long; stamens equal or subequal, inserted 1.0 to 2.0 mm below the sinuses, rarely less, and extending to or nearly to the tip of the corolla lobe, 6.0 to 11.0 mm long, filaments 5.0 to 9.5 mm long, anthers linear-sagittate, versatile 2.5 to 3.0 mm long and 0.5 to 1.0 mm broad; stigma 0.75 to 1.0 mm long, style approximately 15.0 mm, ovary three-loculed, few-seeded.

Type: David Douglas in 1833. Photograph of type POM 188883; probable isotype UC 163784. "California." Probably Monterey County.

Range: Monterey County, California.

The heads are relatively few-flowered; and the individual flowers, with their bright blue lobes and yellow throats, are particularly showy in *E. virgatum* and in *E. sapphirinum*. *Eriastrum virgatum* is limited in its geographic range and is far from being the most common of the annual species. Close relationships are with *E. luteum* and *E. sapphirinum* subsp. *dasyanthum*.

4. *Eriastrum luteum* (Benth.) H. L. Mason, Madroño 8:81. 1945.

Hugelgia lutea Benth. Bot. Reg. 19: under pl. 1622. 1833. Not *Gilia lutea* Steud. *Gilia lutescens* Steud. Nom. ed. 2, 1:684. 1840.

G. floccosa Kuntze, Rev. Gen. Pl. 2:433. 1891 in part.

Navarretia lutescens Kuntze, loc. cit.

N. lutea Brand, Pflanzenreich IV, 250: 168. 1907.

Annual, to 25.0 cm high, erect, virgate or racemose or branched from the base; herbage lightly to densely floccose; stems and lower leaves often red brown, upper leaves and bracts light green; internodes 1.0 to 2.0 cm long; leaves to 4.0 cm long, ascending, entire or with one pair of lateral lobes at the base of the leaf, and that which appears to be a pair of lateral lobes often is a part of the axillary bud; lateral lobes spreading, to 1.0 cm long; floral heads to 1.5 cm broad, densely floccose-lanate; bracts 0.75 to 1.5 cm long, rarely more, with one or two pair of lateral lobes; calyx lobes nearly equal 5.0 mm long, joined by a hyaline membrane; corolla regular or

very slightly irregular, funnellform, 8.0 mm long, bright golden yellow; lobes 3.5 mm long, often obovate, 2.0 to 2.5 mm broad; throat 1.5 mm long, tube 3.0 mm long; stamens equalling or exceeding tips of corolla lobes, 5.0 to 5.5 mm long; filaments 3.5 to 4.5 mm long, anthers 2.0 to 2.25 mm long and 0.75 mm broad; stigma 0.5 mm long, style ca. 7.5 mm long; locules one- to two-seeded.

Type: David Douglas in 1833. KEW. "California." Probably Monterey, San Luis Obispo County.

Range: Santa Lucia Mountains, Monterey and San Luis Obispo counties, California.

The bright, golden-flowered species, *E. luteum*, which is found somewhat infrequently, seems to be most closely related to *E. virgatum*. The corolla form and proportion and stamen size are approximately the same; the obovate lobes of the corolla, the branching, plant-size, leaves and pubescence of *E. luteum* are found in *E. virgatum* and the geographic range overlaps. Cytological studies will probably yield further insight into these relationships.

5. *Eriastrum sapphirinum* (Eastwood) H. L. Mason, Madroño 8:79. 1945.

Annual, erect to 40.0 cm high and to 30.0 cm broad; branching open, paniculate, corymbose, racemose, or simple, frequently branching from nearly every axil; branches usually slender, rarely appearing below dead persistent heads and flowering continuing into a second season; herbage with minute glandular hairs throughout or in part, otherwise glabrous to floccose; stems sparsely leaved; internodes 1.0 to 5.0 cm long; leaves 0.5 to 3.0 or to 5.5 cm long; filiform-linear, entire or with one pair of slender lateral lobes at leaf base, subulate, or awn-tipped; heads few to numerous, pedicelled or sessile, one- to many-flowered, to 1.5 cm broad, glabrous, glandular, to densely floccose; bracts broad and short, 3.0 to 10.0 mm long, more or less equal to the head; lowermost, subtending the head, not apparent or to 2.0 cm long and exceeding head, simple or with one to two pair of short and often broad lateral lobes; hyaline membrane between the lobes frequently apparent; calyx lobes unequal to nearly equal, 6.0 to 8.0 mm long, joined by hyaline membrane; corolla broadly funnellform to narrowly so, to 15.0 mm long, irregular; three lobes occasionally appearing longer than the other two due to unequal sinuses, especially in the broad corollas, less markedly so in narrowly funnellform type; lobes broadly to narrow-

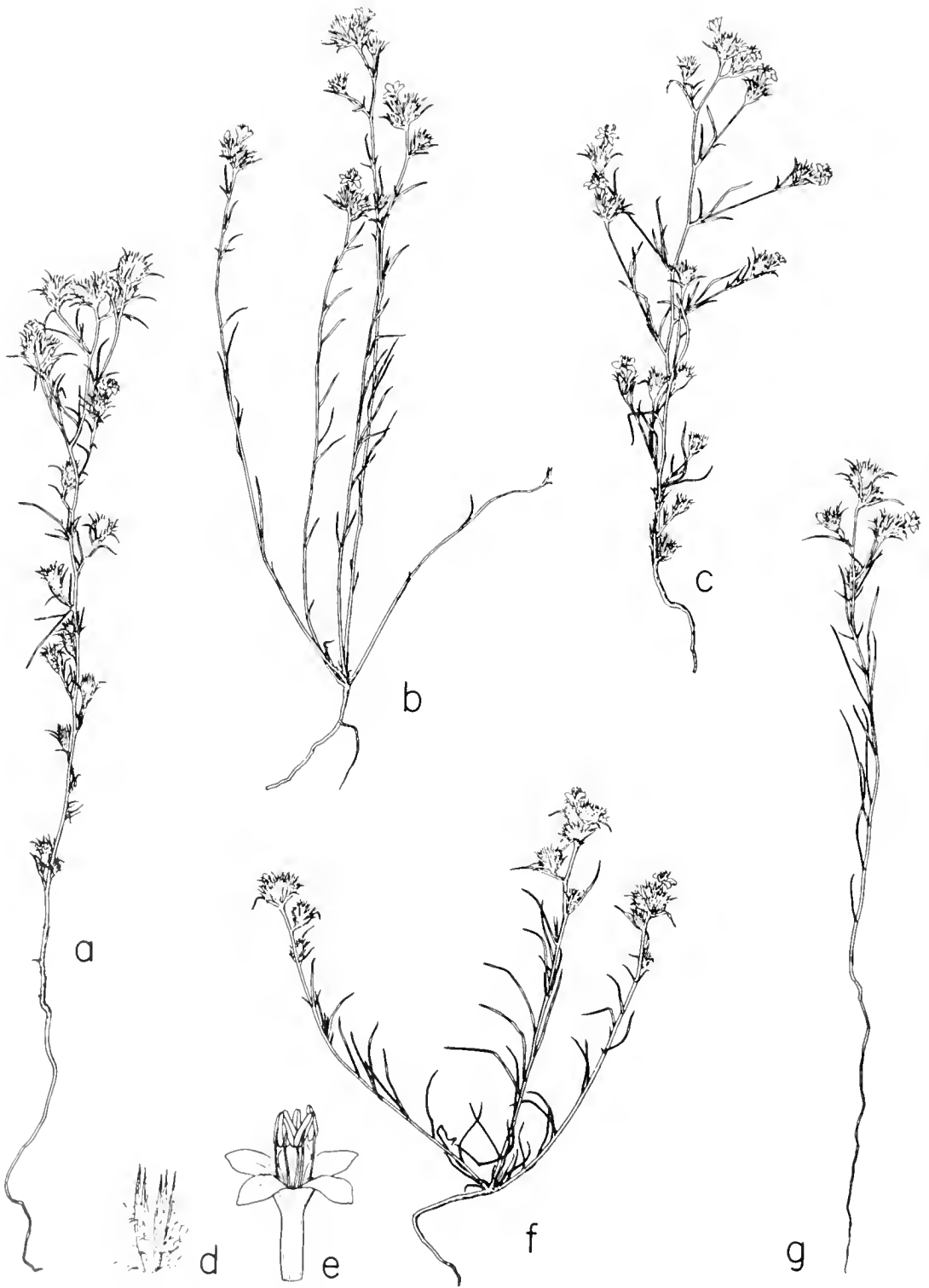


Fig. 3. *Eriastrum luteum*. a. Habit, David Douglas UC 163780, X .6. b. Habit, R. F. Hoover 7125 UC 023830, X .6. c. Habit, Katherine Brandegee 136, 9 VI 09, 130858, X .6. d. Calyx, G. T. Nordstrom 1353 UC 123876, X 3.4. e. Corolla and stamens, G. T. Nordstrom 1353 UC 123876, X 3.4. f. Habit, G. T. Nordstrom 1353 UC 123876, X .6. g. Habit, R. F. Hoover 7192 UC 023829, X .6.

ly elliptic, half the length of corolla or more, to 9.5 mm long and 2.5 to 5.0 mm broad, bright blue; throat 1.0 to 3.0 mm long, yellow; tube to 5.5 mm long or 1/5 to 1/3 length of corolla, blue or yellow; stamens adnate to bottom of throat, usually equal, to 10.0 mm long, extending nearly to tip of corolla lobe, occasionally beyond, anthers sagittate, versatile, 2.5 to 3.0 mm long, 1.0 mm broad; filaments to 8.0 mm long; ovary three-loculed; seeds 2.0 to 2.5 mm long.

Key to the Subspecies

- A. Heads single- to few-flowered, 2.5 to 8.0 mm broad, seldom more; stems slender, bracts subequal to or slightly exceeding the heads; corolla often broadly funnellform, lobes broadly elliptic
 - 5a. *E. sapphirinum* subsp. *sapphirinum*
 - AA. Heads several-flowered, 0.75 to 1.5 cm broad or more; stems slender to somewhat robust; bracts commonly exceeding the heads, often prominent; corolla mostly narrowly funnellform, lobes narrowly elliptic
 - 5b. *E. sapphirinum* subsp. *dasyanthum*
- 5a. *Eriastrum sapphirinum* (Eastwood) H. L. Mason subsp. *sapphirinum*.
- Gilia sapphirina* Eastwood, Bot. Gaz. 38: 71. 1904.
 - Navarretia virgata* subsp. *gymnocephala* Brand in Engler, Pflanzenreich IV, 250: 168. 1907.
 - N. virgata* subsp. *gymnocephala* var. *oligantha* Brand, op. cit.
 - N. virgata* subsp. *gymnocephala* var. *sapphirina* Brand, op. cit.
 - G. floccosa* var. *ambigua* Jones, Contr. West. Bot. No. 13:2. 1910.
 - G. virgata* var. *sapphirina* MacBride, Contr. Gray Herb. No. 49:58. 1917.
 - Hugelia virgata* var. *sapphirina* Jepson, Man. Fl. Pl. Calif. 793. 1925.
 - G. virgata* var. *ambigua* Craig, Bull. Torrey Club 61:412. 1934.
 - H. virgata* var. *ambigua* (Jones) Jepson in Jepson, Fl. Calif. 3:165. 1943.
 - Eriastrum sapphirinum* subsp. *gymnocephalum* Mason, Madroño 8:80. 1945.
 - E. sapphirinum* subsp. *ambiguum* Mason, op. cit.

Branches slender; leaves 0.5 to 2.0 cm long, occasionally to 3.5 cm long, filiform-linear, subterrate, entire or with one pair of lateral lobes at the leaf base; lateral lobes 2.0 to 5.0 mm long; heads small, few to a few hundred, pedicelled or

sessile, single- or few-flowered, 2.5 to 8.0 mm broad, seldom more, glabrous, glandular, to floccose; bracts 3.0 to 10.0 mm long, more or less equal to the head, the lowermost subtending the head often not apparent, occasionally exceeding the head; corolla to 15.0 mm long, broadly funnellform; lobes often broadly elliptic.

Type: Blanche Trask in 1903. CAS 510. San Jacinto Mountain, Riverside County, California.

Range: Southern California from Los Angeles and San Bernardino counties to Baja California, occurring between 1500 and 8700 feet.

Navarretia virgata subsp. *gymnocephalum* was described by Brand (1907) and implied in the name was the naked head. Its variety *oligantha* was characterized as having flowers single or in pairs. The type specimen of *E. sapphirinum* has perhaps 150 to 175 heads which are naked or glandular, pedicellate or sessile and one- to five-flowered. *Eriastrum sapphirinum* subsp. *gymnocephalum* is regarded here as a synonym of the type subspecies.

The degree of pubescence in the heads of *E. sapphirinum* subsp. *sapphirinum* varies from being completely naked to lightly floccose. The type of *E. sapphirinum* subsp. *ambiguum* is not particularly unlike the type subspecies, and the only character by which it might differ is the degree of pubescence. Jones described his specimen as being "floccose-woolly mostly throughout" and the type of *E. sapphirinum* subsp. *ambiguum* (Jones 10011 Victor [now Victorville], California POM 75010) is almost completely glabrous. Except for the minute glandular hairs and the floccose heads, the plant is not at all floccose. In his descriptions, Jones cited both 10011 from Victorville and 9917 from Bear Valley as being typical. The latter specimen was reported by Craig (1934) as being "not at all typical," and Mason (1945) referred the specimen to *E. sapphirinum* subsp. *dasyanthum*. It is this specimen that is floccose-woolly throughout. *Eriastrum sapphirinum* subsp. *ambiguum* is regarded here as insufficiently distinct to warrant recognition and is regarded as a synonym.

With a large representation of *E. sapphirinum*, a continuous series can be observed. The size of the heads varies from 2.5 to 15.0 mm or so with every intergradation. The slender plants with small heads have a tendency to have broadly spreading and broadly-lobed corollas which are distinctly irregular; and those plants with larger heads have a tendency to have more narrowly funnellform, less irregular corollas. The series suggests two entities within the species with complete interbreeding. The subspecies

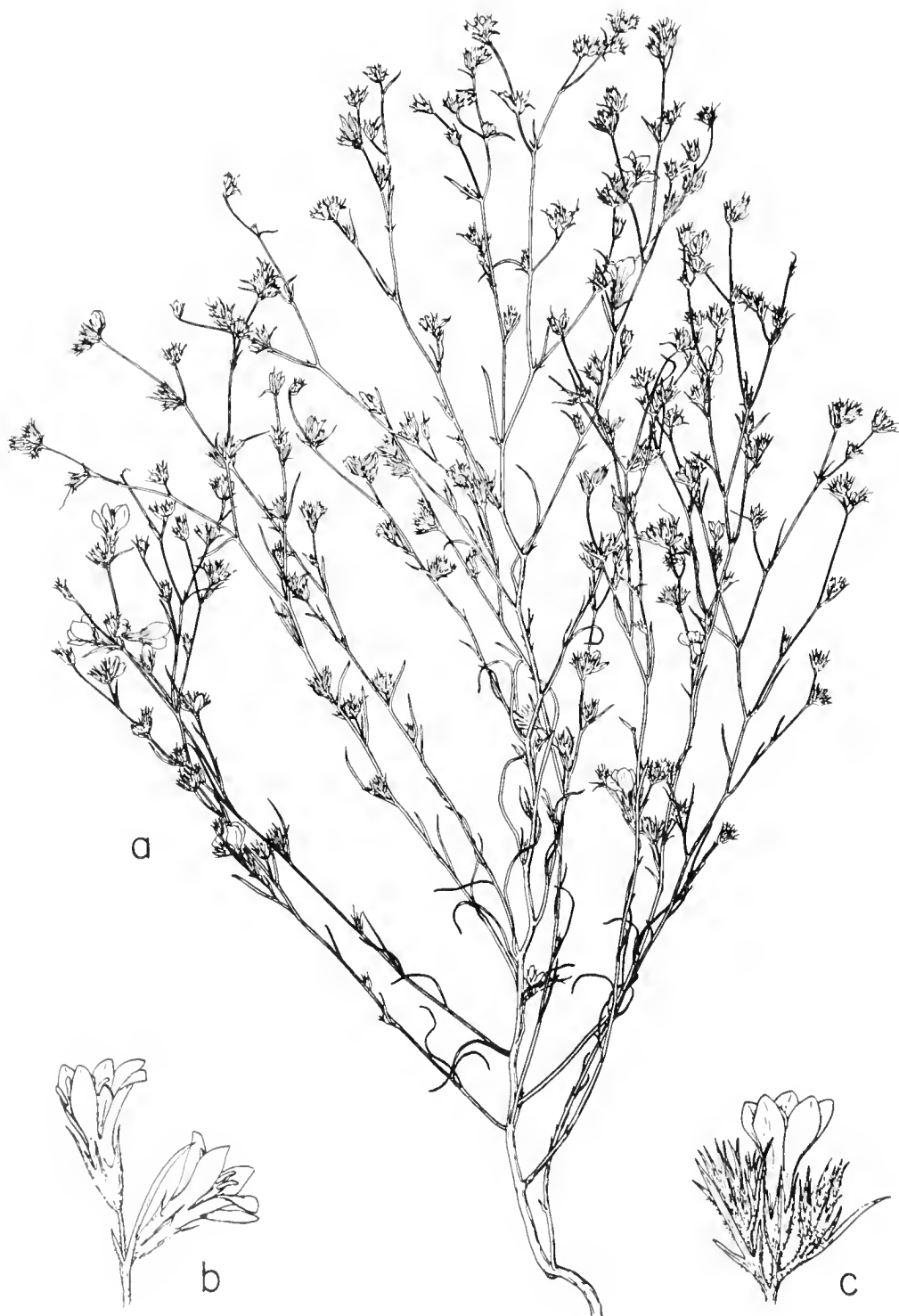


Fig. 4. *Eriastrum sapphirinum* subsp. *sapphirinum*. a. Habit, Blanche Trask in 1903. CAS 510 (type), X .6. b. Two flowers, Katherine Brandegee I6-V1-06, UC 133928, X 2.3. c. Floral head, C. Epling, M. Darsie, c. Knox, William Robison 20 VI 32, UC 519836, X 2.3.

overlap almost completely in geographic distribution. The corollas of the type subspecies have three lobes, which appear longer than the others due to the unequal sinuses. The lobes are broadly elliptic and extend from 1/2 to 2/3 the length of the corolla; the throat is spreading and prominent; and the tube is approximately 3.0 mm in length, or 1/5 of the length of the corolla. Corollas vary from this to the less irregular form of *E. sapphirinum* subsp. *dasyanthum*, in which the slightly expanding throat and narrowly elliptic lobes are usual. Cytological studies are needed to elucidate the nature of the subspecies.

- 5b. *Eriastrum sapphirinum* subsp. *dasyanthum* (Brand) H. L. Mason, Madroño 8:80. 1945.
 - Navarretia virgata* var. *dasyantha* Brand in Engler, Pflanzenreich IV, 250:168. 1907.
 - Hugelia virgata* var. *dasyantha* Jepson, Man. Fl. Pl. Calif. 793. 1925.
 - Gilia virgata* var. *dasyantha* Craig, Bull. Torrey Club 61:395. 1934.

Plants slender to somewhat robust; leaves 1.0 to 3.0 cm long, occasionally to 5.5 cm long, entire or with one pair of lateral lobes; lateral lobes 2.0 to 15.0 mm long; heads 7.5 to 15.0 mm broad, several-flowered, densely floccose; bracts usually exceeding the heads; bracts subtending the heads to 2.0 cm long, often prominent; corolla to 15.0 mm long, more commonly narrowly funnelform; the lobes narrowly elliptic.

Type: H. M. Hall 298 6-VIII-96. Swartout Canyon, San Antonio Mountain, elevation 7000 feet; within the San Gabriel Mountains, Los Angeles County, California. Present repository of the specimen is unknown. Also cited in the original description as representative of the type are: Parry and Lemmon 249 (represented POM), S. B. and W. F. Parish 1478 (represented UC), S. B. Parish 3803 (represented UC). The specimen, H. M. Hall 237, San Antonio Mountain (elevation 7000 feet), Los Angeles County, California (UC), is cited in the H. M. Hall fieldbook (UC) as being "identical" with his 298 collection.

Range: Southwestern California from Ventura County, south to Baja California and northeast to Inyo County, California, occurring from 1000 to 7000 feet.

- 6. *Eriastrum eremicum* (Jepson) H. L. Mason, Madroño 8:78. 1945.

Annual, to 30.0 cm high and to 40.0 cm broad,

erect or spreading, branched from the base or racemose, or virgate; stems floccose to subglabrate, sometimes glandular; leaves light green or grey green, 0.6 to 5.5 cm long, with one to three pair of lateral lobes, subulate, awn-tipped; heads one to many, floccose, 0.5 to 1.5 cm broad, excluding tips of bracts; bracts 1.0 to 2.0 cm long with one to three pair of lateral lobes; calyx 0.5 to 1.0 cm long; lobes unequal, joined by a hyaline membrane; corolla bilabiate or irregular to nearly regular, funnelform, 11.0 to 18.0 mm long; lobes elliptic, 4.0 to 8.0 mm long and 1.75 to 3.5 mm broad, lavender blue to dark blue; throat 1.0 to 4.0 mm long, sinus to stamen insertion 1.0 to 4.0 mm, tube 4.0 to 8.5 mm long; tube and throat light lavender, yellow, or blue; stamens adnate to base of throat, unequal, 2.0 to 9.0 mm long; filaments 1.5 to 8.5 mm long; anthers sagittate, versatile, 1.0 to 2.25 mm long and 1.0 mm broad; stigma ca. 1.0 mm long, style ca. 12.0 mm long, ovary three-loculed.

Key to the Subspecies

- A. Corolla bilabiate to obscurely irregular; lobes narrowly elliptic 1.75 to 2.75 mm broad, lavender blue; desert regions southern California, Nevada, Utah, and Arizona6a. *E. eremicum* subsp. *eremicum*
- AA. Corolla irregular to nearly regular; lobes broadly elliptic, 3.0 to 3.5 mm broad, blue to dark blue; Arizona 6b. *E. eremicum* subsp. *yageri*
- 6a. *Eriastrum eremicum* (Jepson) H. L. Mason subsp. *eremicum*.
 - Navarretia densifolia* var. *jacumbana* Brand, Ann. Conserv. and Jard. Bot. Geneve 15 and 16:340. 1913.
 - Hugelia eremica* Jepson, Man. Fl. Pl. Calif. 793. 1925.
 - Gilia eremica* Craig, Bull. Torrey Club 61:416. 1934.
 - G. eremica* var. *typica* Craig, op. cit. 417.
 - G. eremica* var. *zionis* Craig, op. cit. 418.

Annual, erect or spreading, much-branched, to 30.0 cm high and to 40.0 cm across; stems lightly floccose to nearly glabrate, often wiry or thick, becoming dark red or becoming very light with age as epidermal layers flake off; leaves grey green, 6.0 to 30.0 mm long, pinnatifid with one to three pair of lateral pinnae, commonly with two pair; when three pair occur, the lowermost pinnae are shorter than the adjacent pinnae, lightly floccose to glabrate, subulate-tipped; pinnae 2.0 to 10.0 mm long; heads small, lanate,

numerous (2-250), few-flowered (2-15); bracts 10.0 mm long, with one to two pair lateral lobes, lanate, recurved, subulate-tipped; calyx 6.0 to 7.0 mm long, subequal; calyx lobes connected along two-thirds of the lower margin by a membranous tissue; corolla irregular or obscurely so, from bilabiate to nearly regular, 11.0 to 18.0 mm long, the upper lip may consist of either three or four lobes; lobes 4.0 to 8.0 mm long, differing in length in a particular flower by 0.50 mm to 1.75 mm due to unequal sinuses, sometimes asymmetrical with one margin much more convex than the other, 1.75 to 2.75 mm broad; throat 1.0 to 3.5 mm long; sinus to stamen insertion distance differing in one flower by 0.50 to 2.0 mm, and usually by 1.0 mm or more; tube 4.0 mm to 8.5 mm long, usually less than half the length of the corolla; inner surface of the tube puberulent; corolla light lavender to violet, prominent reddish lines follow veins of lobes; stamens 2.0 to 9.0 mm long, distinctly unequal in length, inserted at base of the throat, 1.0 mm to 3.5 mm below the sinuses; in conjunction with the corolla shape, the stamen filaments are very often inclined toward the lowermost lobe with the anthers turned toward the upper lip; anthers sagittate, 1.5 mm to 2.5 mm long, filaments 1.5 mm to 8.0 mm long; ovary three-loculed, few-seeded.

Type: W. L. Jepson 5414. JEPS. Calico Wash, northeast of Barstow, San Bernardino, California.

Range: Desert regions, Southern California to Baja California, southern Nevada and Utah and northern Arizona.

A few plants of *E. eremicum* approach the growth forms of *E. pluriflorum*. The corolla of the latter is usually regular, and the equal to subequal stamens are adnate throughout the length of the tube to the sinus. Rarely, a stamen will become free as much as 0.75 mm below the sinus. In the irregular to bilabiate flower of *E. eremicum*, all the clefts are unequal and the lobes may be irregularly disposed. The stamens are adnate to 1.0 to 3.5 mm below the sinuses. In many flowers of *E. eremicum*, the filaments diverge toward the lowermost lobe and the anthers turn toward the upper lobes. Within *Eriastrum* this characteristic seems to be unique to this species.

6b. *Eriastrum eremicum* subsp. *yageri* (Jones) H. L. Mason, Madroño 8.78. 1945.

Gilia virgata var. *yageri* Jones, Contr. West. Bot. 13:2. 1910.

G. eremica var. *arizonica* Craig, Bull. Torrey Club 61:419. 1934.

G. eremica var. *yageri* (Jones) Craig, op. cit. 420, as to name, not as to lectotype.

Annual, 5.0 to 25.0 cm high, branched from the base, or racemose, or virgate; herbage floccose to subglabrate, often glandular; internodes 1.0 to 6.0 cm long; leaves light green, 1.0 to 5.5 cm long, 0.5 to 2.0 mm broad, with one or two pair of lateral lobes, or entire, subulate, or awn-tipped; heads 1 to 50, floccose to densely so, 0.5 to 1.5 cm broad, excluding tips of bracts; bracts 1.0 to 2.0 cm exceeding the heads, 1.0 to 2.5 mm broad at base, with one to three pair of lateral lobes, lightly floccose; hyaline membrane between lobes sometimes present; calyx 0.5 to 1.0 cm long; lobes unequal, joined by hyaline membrane; tips not obscured by trichomes; corolla funnellform, to 18.0 mm, irregular to nearly regular; lobes broadly elliptic, 5.5 to 7.0 mm long and 3.0 to 3.5 mm broad, commonly dark blue; throat ca. 2.0 to 4.9 mm long, broadly spreading, yellow; sinus to stamen insertion 2.0 to 4.0 mm; tube 5.0 to 8.0 mm long, yellow or blue; stamens adnate to base of throat, unequal, 5.0 to 9.5 mm long, varying in same flower by 1.0 to 3.0 mm; filaments 5.0 to 8.5 mm long; anthers sagittate, versatile, 1.0 to 1.5 mm long and 1.0 mm broad; stigma ca. 1.0 mm long, style ca. 12.0 mm long, ovary three-loculed.

Type: M. E. Jones 10253 and 10279. POM 74569 and POM 74570. Wickenburg, Maricopa County, and Hillside, Yavapai County, Arizona.

Range: Arizona.

Mason (1945) reviewed and corrected the use of the name "Yageri." It seems necessary, however, to include here a history of its usage in order to treat the lectotype (lectotype only, not the name) of *Gilia eremica* var. *yageri* (not *E. eremicum* subsp. *yageri*), which is also the type specimen of *Eriastrum diffusum* subsp. *jousii*, which is here considered as a synonym of *E. diffusum*.

In describing *G. virgata* var. *yageri*, Jones (1910) cited Jones 10253 and Jones 10279 as the type, and included a list of several specimens as being representative, which, however, included a few different entities. Presumably, the name was derived from that of Yager, Arizona, where one of the specimens had been collected. K. Brandegee regarded Jones 10279 as too fragmentary for identification, and Craig also regarded it as inadequate. Through use of the lactophenol method (Harrison 1968), it was possible to examine a flower of Jones 10279; and it appears

to belong with Jones 10253 as designated by Jones.

Craig evidently thought that because of the geographic distribution, the name "Arizona" would be more appropriate than *yageri* and considered Jones 10253 (type of *G. virgata* var. *yageri*) as the type for his *Gilia eremica* var. *arizonica*. Thus, the name "yageri" was separated from its type. The name "yageri" was perpetuated, however, as Craig selected Jones 9935 from Yager, Arizona, from Jones's list of "representative material" (1910) as a lectotype of *G. eremica* var. *yageri* (Craig, 1934).

As discussed by Mason (1945), the adequacy of Jones 10253 necessitates recognition of Jones's concept of *G. virgata* var. *yageri* and the restoration of the name to its type. *Gilia eremica* var. *arizonica* was therefore referred to synonymy under *Eriastrum eremicum* subsp. *yageri* (Jones) H. L. Mason.

Jones 9935 was then selected by Mason as the type of *E. diffusum* subsp. *jonesii* Mason. This plant was described as having larger corollas, slightly larger anthers and longer filaments than the typical form of the species. The specimen is here considered as being insufficiently distinct to warrant recognition and is considered by the present author as a synonym of *E. diffusum*.

Craig (1934) had placed this plant with *G. eremica* and had stated that he was uncertain whether it should be referred to that species or to *G. filifolium* var. *diffusa*, which should be interpreted as referring to *E. diffusum*, and not *E. filifolium*.

Eriastrum eremicum subsp. *yageri* (Jones) H. L. Mason is described (Kearney & Peebles 1951) as having less irregular corollas and simpler leaves. The leaves of the type are similar to those of *E. eremicum* subsp. *eremicum*, and some depauperate plants have simple, entire leaves. Lack of sufficient specimens has prevented a broad examination of this character, but the leaves appear to have fewer lobes than those of *E. eremicum* subsp. *eremicum*. With respect to the different depths of the sinuses, the corollas are often quite irregular. Corolla lobes of this subspecies are broader, much darker and brighter blue than the usual pale lavender of *E. eremicum* subsp. *eremicum*.

7. *Eriastrum filifolium* (Nutt) Wootton & Standley, Contr. U.S. Nat. Herb. 16:160. 1913.

Gilia filifolia Nutt, Jour. Acad. Phila. 11:156. 1848.

Navarretia filifolia Kuntze, Rev. Gen. Pl. 2:433. 1891.

G. virgata var. *filifolia* Milliken, Univ. Calif. Pub. Bot. 2:39. 1904.

N. filifolia subsp. *enfilifolia* Brand, Pflanzenreich IV, 250:167. 1907.

G. floccosa var. *filifolia* Nels & Macbride, Bot. Gaz. 61:35. 1916.

Welwitschia filifolia Rydberg, Fl. Rocky Mtns. 688. 1917.

Hugelia filifolia Jepson, Man. Fl. Pl. Calif. 792. 1925.

G. filifolia var. *typica* Craig, Bull. Torrey Club 61:422. 1934.

Annual, 4.0 to 40.0 cm high, virgate, racemose, or diffusely branched; herbage subglabrous to lightly floccose; internodes 1.0 to 3.0 cm long, occasionally to 4.0 cm long; leaves filiform, 1.0 to 3.0 cm long, light green becoming red brown, sometimes appressed, ascending subulate-, or awn-tipped; first-formed leaves entire; younger leaves with one pair of filiform lateral lobes to 1.25 cm long, sometimes occurring 5.0 mm above the leaf base, or entire, or with two pair of lobes from the base of the leaf; heads few to several, long-tapered, often narrow and elongate, distinctly brushy; tips of bracts and calyces not obscured by wool, few-flowered; bracts 1.25 to 2.0 cm long, exceeding the heads, with one or two pair of lateral lobes; calyx slender-cylindric, lobes unequal to subequal, 6.0 to 8.0 mm long, joined by a hyaline membrane; corolla regular, salverform, narrowly funnelform, 7.0 to 9.0 mm long; lobes 3.0 mm long and 1.0 mm broad, blue; sinus to stamen insertion 1.0 mm, throat ca. 1.0 mm long; tube 4.0 mm long, throat and tube yellow; stamens 3.5 mm long, equal; anthers sagittate, versatile, 1.0 mm long; filaments 2.5 to 3.0 mm long; stigma 0.75 to 1.0 mm long, style 3.0 to 4.0 mm long; ovary long, cylindric, three-loculed; capsule 5.0 mm long and 1.5 mm broad, each locule approximately four to five-seeded.

Type: T. Nuttall. KEW. Santa Barbara, California.

Range: Southern California from Santa Barbara and Los Angeles counties south to Baja California.

8. *Eriastrum sparsiflorum* (Eastwood) H. L. Mason, Madroño 8:86. 1945.

Annual, to 30.0 cm high, racemose, corymbose, or often branched from the base, more erect than spreading; herbage not disposed to becoming brittle, light green, grey green or yellow green; lightly floccose or subglabrate to conspicuously floccose; internodes 1.0 to 4.0 cm



Fig. 5. *Eriastrum filifolium*. a. Habit, L. Abrams 3724 POM 156092, X .6. b. Calyx, T. Craig & M. Zornes 1856 POM 186740, X 4.6. c. Corolla and stamens, T. Craig & M. Zornes 1856 POM 186740, X 4.6. d. Habit, T. Craig & M. Zornes 1856 POM 186740, X .6. e. Habit, Katherine Brandegee, V-06, UC 133849, X .6. f. Habit, T. Craig & M. Zornes 1856 POM 186708, X .6. g. Habit, Nuttall GH (probable isotype), X .6.

long; leaves 0.5 to 3.5 cm long, most commonly 1.0 to 1.5 cm long, mostly entire, or with one pair of lateral lobes; lobes to 7.0 mm long; heads few to numerous, 0.5 to 1.0 cm broad excluding tips of bracts, floccose to densely so, few-flowered; bracts 0.7 to 2.5 cm long exceeding the heads, entire or with one or two pair of lateral lobes; calyx lobes unequal, 5.0 to 8.0 mm long, joined by a hyaline membrane; corolla regular, salverform to narrowly funnelform, 6.0 to 10.5 mm long; lobes elliptic, 2.0 to 3.0 mm long, rarely more, blue, light pink, dull yellow or cream; throat 0.75 to 1.0 mm long, yellow; sinus to stamen insertion 0.25 to 0.50 mm, tube 4.0 to 5.5 mm long; stamens equal, 1.0 to 2.25 mm long, filaments 0.50 to 1.0 mm long; anthers sagittate, versatile, 0.75 to 1.0 mm long; stigma 0.5 mm long, style 3.5 to 4.5 mm long; ovary three-loculed, few-seeded.

7.0 mm long; heads few to numerous, small, 0.5 to 1.0 cm broad, floccose, few-flowered; bracts 0.7 to 2.7 cm long, entire or with one pair of lobes, exceeding the heads by 0.3 to 1.5 cm; calyx lobes unequal or nearly equal, 5.0 to 8.0 mm long, rarely more, joined by a hyaline membrane; corolla regular, salverform or very narrowly funnelform, 6.5 to 8.5, sometimes to 10.5 mm long; lobes light blue and throat yellow, or corolla light pink or cream; lobes narrowly elliptic 2.0 to 3.0 mm long, less commonly to 4.0 mm; lobes 1.0 mm broad; tube 4.0 to 5.5 mm long, rarely more; stamens adnate to 0.5 mm below sinus, equal, 1.50 to 2.25 mm long; filaments 1.0 mm long; anthers sagittate, versatile, 1.0 mm long; stigma 0.5 mm long, style ca. 4.5 mm long; ovary three-loculed, few-seeded.

Type: Alice Eastwood. CAS 516. July 1-13, Bubbs Creek, South Fork of Kings River, Fresno County, California.

Range: Central Oregon, western Nevada, Sierra Nevada Mountains from Lassen County, California, south to Inyo County, to San Bernardino County, west to Ventura County and south to Baja California.

Key to the Subspecies

- A. Leaves light green or light grey green; corolla 6.5 to 8.5 or to 10.5 mm long, light blue to light pink or cream; central Oregon, Nevada, California along the Sierra Nevada, and south to Baja California
 ... 8a. *E. sparsiflorum* subsp. *sparsiflorum*
- AA. Leaves yellow green; corolla ca. 6.0 to 7.0 mm long, straw yellow; eastern Mohave desert
 ... 8b. *E. sparsiflorum* subsp. *harwoodii*

8a. *Eriastrum sparsiflorum* (Eastwood) H. L. Mason subsp. *sparsiflorum*.

Gilia sparsiflora Eastwood, Proc. Calif. Acad. III, 2:291. 1902.

Navarretia filifolia subsp. *sparsiflora* Brand in Engler, Pflanzenreich IV, 250: 167. 1907.

G. filifolia var. *sparsiflora* Macbride, Contr. Gray Herb. 49:57. 1917.

Hugelia filifolia var. *sparsiflora* Jepson, Man. Fl. Pl. Calif. 792. 1925.

Annual, erect, 10.0 to 30.0 cm high, occasionally to 35.0 cm high, racemose, or often much-branched from the base, paniculate, or corymbose, more erect than spreading; herbage not disposed to becoming rigid and brittle, light green or light grey green, lightly floccose to subglabrate, in part becoming more glabrate with age; stems sometimes red brown; internodes 1.0 to 4.0 cm long; leaves few, 0.5 to 3.0 cm long, most commonly 1.0 to 1.5 cm long, linear or with one pair of lateral lobes, 4.0 to

8b. *Eriastrum sparsiflorum* (Eastwood) H. L. Mason subsp. *harwoodii* (Craig) H. K. Harrison, Phytomorphology 18:401. 1968.

Gilia filifolia var. *Harwoodii* Craig, Bull. Torrey Club 61:424. 1934.

Hugelia diffusa var. *Hardwoodii* Jepson, Fl. Calif. 3:167. 1943.

Eriastrum diffusum subsp. *Hardwoodii* (Craig) H. L. Mason, Madroño 8:77. 1945.

Annual, to 20.0 cm high, racemose or corymbose; herbage floccose to conspicuously so, yellow green to grey green; internodes 1.0 to 2.0 cm long; leaves 1.0 to 3.5 cm long, entire or with one pair of lateral lobes, subulate, awn-tipped; lobes to 7.0 mm long; heads few to numerous, densely floccose, few-flowered, small, 0.5 to 1.0 cm broad excluding tips of bracts; bracts 1.0 to 1.5 cm long, exceeding the heads, with one or two pair of lateral lobes; calyx lobes unequal, 5.0 to 8.0 mm long, joined by a hyaline membrane; corolla regular, narrowly funnelform, 6.0 to 7.5 mm long, dull straw yellow or cream yellow; lobes elliptic, 2.25 mm long and 1.0 to 1.5 mm broad; throat 0.75 mm long, sinus to stamen insertion 0.25 mm, tube 4.0 mm long; stamens equal, 1.0 mm long; filaments 0.50 to 0.75 mm long; anthers versatile, sagittate-cordate, 0.75 mm long; stigma 0.50 to 1.0 mm



Fig. 6. *Eriastrum sparsiflorum* subsp. *sparsiflorum*. a. Habit, Alice Eastwood 1-13 VII 99 CAS 516 (type), X 6. b. Habit, E. C. Twisselmann 2316 CAS 399515, X 6. c. Habit, R. Bacigalupi and G. T. Robbins 5417 CAS 107771 X 6. d. Calyx, H. M. Pollard 18-VI-49 CAS 352063, X 4.6. e. Corolla and stamens, H. M. Pollard 18 VI 49 CAS 352063, X 4.6.

long, style ca. 3.5 mm long, ovary three-loculed, locules approximately two-seeded.

Type: P. A. Munz & R. D. Harwood 3589. POM 7622. Blythe Junction, Riverside County, California.

Range: Eastern Mohave Desert in eastern Riverside and San Bernardino counties, California.

9. *Eriastrum wilcoxii* (Nelson) H. L. Mason, Madroño 8:85. 1945.

Gilia floccosa Gray, emend. Syn. Fl. N.A. 2:143. 1878. Not type of *G. floccosa* Gray, Proc. Amer. Acad. Sci. 8:272. 1870.

G. wilcoxii Nelson, Bot. Gaz. 34:27. 1902. *Wehutschia wilcoxii* Rydberg, Fl. Rocky Mtns. 688. 1917.

Hugelia filifolia var. *floccosa* Jepson, Fl. Calif. 3:166. 1943, as to lectotype, not as to type.

The following in part as to text, not as to type (See discussion in Mason, 1945):

Gilia floccosa Gray, Proc. Amer. Acad. Sci. 8:272. 1870.

Navarretia floccosa (Gray) Kuntze, Rev. Gen. 2:433. 1891.

H. floccosa (Gray) Howell, Fl. N.W. Amer. 458. 1903.

G. virgata var. *floccosa* (Gray) Milliken, Univ. Calif. Publ. Bot. 2:40. 1904.

N. virgata subsp. *floccosa* (Gray) Brand in Engler, Pflanzenreich IV, 250:168. 1907.

W. floccosa (Gray) Rydberg, Fl. Rocky Mtns. 688. 1917.

H. virgata var. *floccosa* (Gray) Jepson, Man. Fl. Pl. Calif. 793. 1925.

Annual, to 30.0 cm high, racemose, corymbose, or branched from the base; herbage floccose, often densely so, gray green, becoming rigid and brittle, coarse in appearance; internodes 1.0 to 4.0 cm long; leaves 1.5 to 3.0 cm long, commonly 2.0 to 2.5 cm long, subulate-tipped, usually with one pair of lateral lobes or with two pair or entire; heads several to numerous, 0.70 to 1.75 cm broad, densely floccose, several-flowered; bracts prominent, 0.7 to 3.0 cm long, equalling or exceeding the heads, with one or two pair of lateral lobes; calyx lobes unequal, 5.5 to 10.0 mm long, joined by a hyaline membrane; tips of lobes sometimes conspicuous; corolla regular or slightly irregular, funnelform,

9.0 to 14.0 mm long; lobes blue, tube and throat yellow; lobes 3.5 to 6.0 mm long, elliptic to broadly so, 1.50 to 2.25 mm broad; throat 0.5 to 2.0 mm long, sinus to stamen insertion 0.5 to 2.0 mm, tube 5.0 to 7.5 mm long; stamens unequal, 1.5 to 4.5 mm long, varying in one flower by 0.5 mm or 2.5 mm, exerted beyond the sinus (occasionally on the same plant some stamens may be nearly equal and shorter; the anthers barely surpassing the sinus, thus simulating a characteristic of *E. sparsiflorum*); filaments 1.5 to 3.5 mm long; anthers sagittate, versatile, 1.0 to 2.0 mm long and to 1.0 mm broad; stigma 0.50 to 0.75 mm long, style ca. 6.0 mm long; ovary three-loculed, approximately three-seeded.

Type: E. D. Merrill & E. N. Wilcox 752. RM 30221. Seven miles W St. Anthony, Idaho.

Range: Central Washington, central and eastern Oregon, south along the Sierra Nevada to Inyo County, California, southwest to San Luis Obispo and Santa Barbara counties, southern Idaho, Nevada, and western Utah.

Eriastrum sparsiflorum and *E. wilcoxii* are closely related. There is a wide range of variation and much overlapping in the expression of the characters. *Eriastrum wilcoxii* plants tend to be more floccose, more robust and thicker-stemmed; the leaves tend to have one or two pair of lateral lobes and to be somewhat rigid. The heads are usually larger and have more flowers per head. The flowers are slightly larger and the filaments are longer and unequal. The lobes of the corolla are sometimes broader, and the vascularization of the corolla is less reduced. The previously reported level of stamen insertion as 2.0 mm below the sinus (Mason 1945) does not hold, as it varies from 0.5 to 2.0 mm.

The plant body of *E. sparsiflorum* is a little less brittle, less rigid, and less floccose than *E. wilcoxii*. The plants may be tall and racemose, or they may have many branches which individually have few leaves. Perhaps the best characters for identification of *E. sparsiflorum* are the short, equal stamens, which quite consistently become free 0.5 mm below the sinus; the anthers, which lie just above the sinus level; the slightly smaller corolla, apparently always with narrow elliptic lobes; the smaller heads; and the greater frequency of short, entire leaves. It seems that *E. wilcoxii* is the most nearly intermediate between the large-flowered forms, e.g., *E. eremicum* and the small-flowered forms, e.g., *E. sparsiflorum* and *E. diffusum*.

10. *Eriastrum diffusum* (Gray) H. L. Mason, Madroño 8:76. 1945.

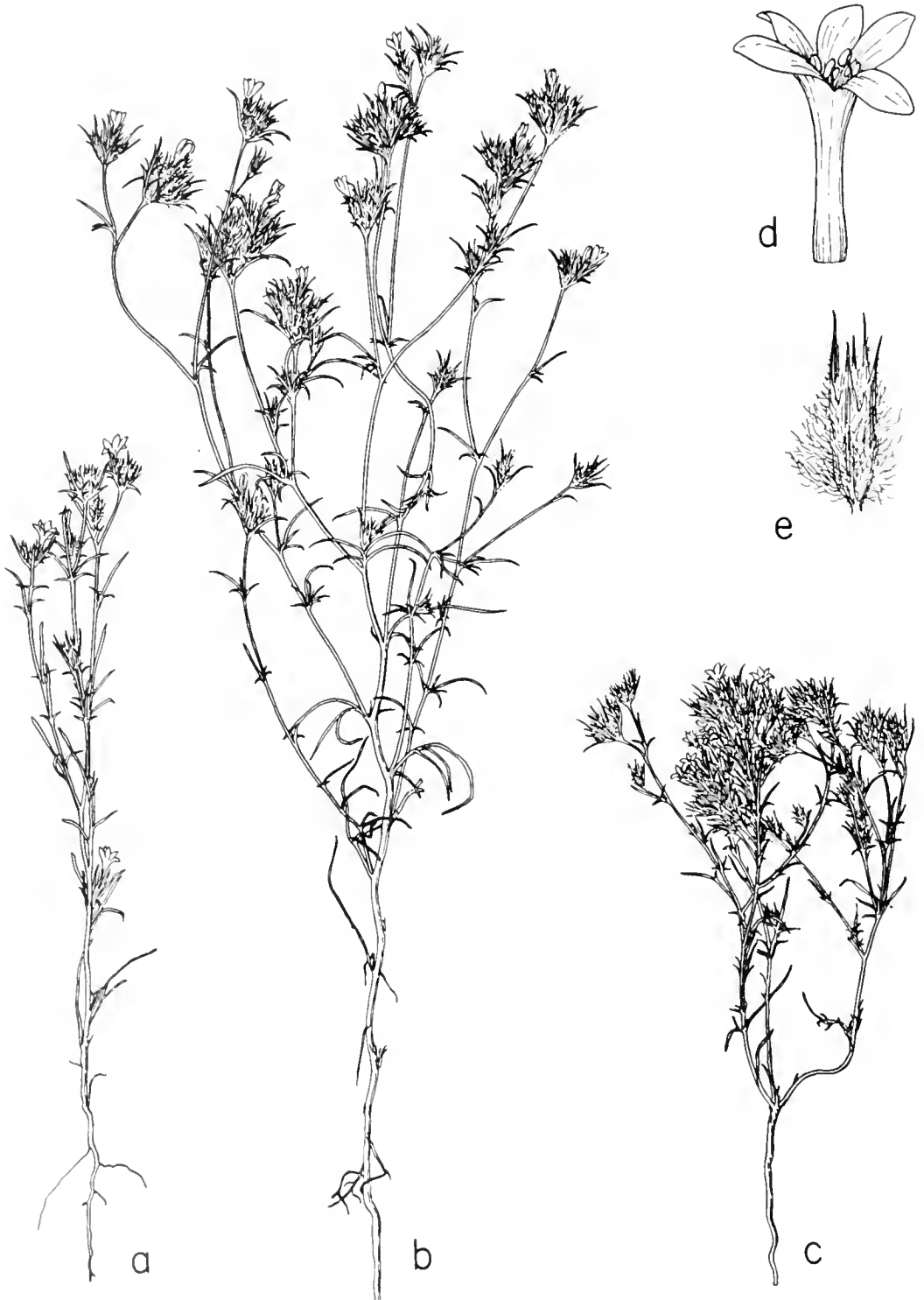


Fig. 7. *Erastrium wilcoxii*. a. Habit, P. A. Munz 11, 077 POM 153278, X .6. b. Habit, Ynez W. Winblad 26-VII-38 CAS 297740, X .6. c. Habit, E. D. Merrill & E. N. Wilcox 952 RM 30221 (type), X .6. d. Corolla and stamens, P. A. Munz 11, 077 POM 153278, X 3.4. e. Calyx, P. A. Munz 11, 077 POM 153278, X 3.4.

- Gilia filifolia* var. *diffusa* Gray, Proc. Amer. Acad. Sci. 8:272. 1870.
Navarretia filifolia var. *diffusa* Brand in Engler, Pflanzenreich IV, 250:167. 1907.
Welwitschia diffusa Rydberg, Fl. Rocky Mtns. 688. 1917.
W. filifolia diffusa Tidestrom, Proc. Biol. Soc. Wash. 48:42. 1935.
G. eremica var. *yageri* Craig, Bull. Torrey Club 61:420. 1934, as to lectotype only, not *G. virgata* var. *yageri* Jones.
Hugelia diffusa Jepson, Fl. Calif. 3:167. 1943.
Eriastrum diffusum subsp. *jonesii* H. L. Mason, Madroño 8:77. 1945. (See discussion under *E. eremicum* subsp. *yageri*.)

Annual, 3.0 to 15.0 cm high, commonly 8.0 cm high, diffusely branched from the base or racemose, often spreading to twice the height; herbage lightly floccose or subglabrous; stems slender, 0.5 mm to 1.0 mm in diameter, often becoming red brown; leaves slender, ascending, light green, small, 1.0 to 2.5 cm long, usually with one pair of short lateral lobes (2.0 to 7.0), less commonly with two pair or entire, subulate, awn-tipped; internodes 1.0 to 2.0 cm long; floral heads few to several, small, 0.5 to 1.0 cm in length and breadth excluding tips of bracts, few-flowered, moderately or lightly floccose; bracts 0.75 to 1.50 cm long and exceeding the heads, with one or two pair of lateral lobes; calyx lobes unequal to nearly equal, 5.0 to 6.0 mm long, joined by a hyaline membrane; corolla funnelform, 7.0 to 10.0 mm long, regular to slightly irregular; lobes light blue to cream, 2.5 to 4.0 mm long and 1.25 to 2.0 mm broad; sinus to stamen insertion ca. 0.25 to 0.75 mm, throat ca. 1.0 mm long, tube ca. 3.0 to 4.5 mm long; stamens adnate nearly to sinus, 2.0 to 3.0 mm long; anthers sagittate, cordate, versatile, 0.50 to 0.75 mm long, occasionally to 1.0 mm long; filaments 1.5 to 2.5 mm long, stigma ca. 0.5 mm long, style ca. 5.0 mm long, ovary three-loculed.

Lectotype: George Thurber 326. GH. Pachetiju, south of Copper Mines, Grant to Luna counties, New Mexico, to Arispe, Sonora, Mexico (cf. Gray 1854. pp. 297-302).

Range: Southern California, Nevada, Utah, southeast through Arizona, southwestern New Mexico to Texas.

When Gray described *Gilia filifolia* var. *diffusa* (1870), he wrote, "Forms of this approach the preceding too nearly," by which he meant *Gilia floccosa* and not *Gilia filifolia*. This is evi-

denced by his annotation on an S. Watson 915 collection at the Gray Herbarium to the effect that forms approached *G. floccosa* too closely. However, when the other collections which were studied by Gray (Thurber 326, Cooper Fort Mohave [in part] and probably Thurber 172) are examined together with his description, the variety to which he applied the name can be recognized. The sheet bearing the aforementioned Watson collection has four collections upon it, and they do not represent the elements which prompted Gray to name a new variety, but rather represent the discordant elements which made him qualify his original description as being too similar to *Gilia floccosa*. As the type of *Eriastrum diffusum* has not been indicated, the selection of a lectotype is in order. In the original description, Gray (1870) cited no collector but gave the geographic range as "Fort Mohave and Nevada to New Mexico and the borders of Texas." Reference to the collections confirms the Fort Mohave, New Mexico and Texas border locations.

On the sheet containing the Watson 915 collections, as well as the other collections, the word "type" unsigned has been printed in pencil at the bottom. This cannot be accepted as the type nor as a lectotype, because there is no indication as to which collection was under consideration; since Gray considered the plants of the Watson collection as discordant elements and as being too close to *Gilia floccosa* (*Eriastrum wilcoxii*) to which I refer them, they do not coincide with Gray's intention. The annotation "type," is therefore ambiguous as to its application; it has not been published; and there is no indication as to whose opinion it represents. Therefore, I consider the annotation as having no standing. From the other specimens examined by Gray, it seems proper to select the George Thurber collection 326 (GH) as a lectotype. This collection was made from May to June 1851 at Pachetiju, south of the "Copper Mines" (presumably Grand to Luna counties), New Mexico. In May 1851, Thurber made a journey from the Copper Mines (now Santa Rita) and the Mimbres River south, by way of the Playas Lake area, Animas, Guadalupe Pass, Black Creek to the border at Agua Prieta, and south into Mexico to Fronteras, Bacoachi, and to Arispe (Gray 1854).

The closest affinities of *E. diffusum* are not with *E. filifolium*, and their separation (Jepson 1943) was proper. *Eriastrum diffusum* plants are of small stature with slender, fine stems, a fraction of a millimeter to 1.0 mm in diameter. The diffuse branching from the base is not the

best criterion for recognition, as the branching may be racemose, and since diffuse branching occurs in other species. The vegetative portion has some aspects of *E. eremicum*, chiefly in the usual slender and much-branched habit. The flower of *E. diffusum* is regular and like that of *E. wilcoxii*, being just a little smaller (although sometimes somewhat broader), with similar unequal stamens with smaller anthers.

11. *Eriastrum brandegeae* H. L. Mason, Madroño 8:88. 1945.

Annual, to 25.0 cm high, racemose or virgate; herbage lightly floccose; internodes 1.0 to 4.0 cm long; leaves grey green, 1.0 to 2.5 cm long, subulate, or awn-tipped, with one pair of lateral lobes, less commonly entire; lobes to 1.0 cm long; heads one to few, floccose, 0.5 to 1.0 cm broad excluding tips of bracts; bracts 1.0 to 1.5 cm long, with one to two pair of lateral lobes; calyx lobes unequal, 5.0 to 8.0 mm long, joined by a hyaline membrane; tips not obscured by trichomes; corolla regular to slightly irregular, 8.0 to 11.0 mm long, subsalverform; lobes narrowly elliptic, 3.25 to 5.0 mm long and 1.0 mm broad, lavender blue to white; throat plus tube 5.0 to 6.0 mm long, sinus to stamen insertion 0.5 to 1.5 mm; stamens 1.5 to 2.0 mm long, filaments 1.0 to 1.25 mm long; anthers versatile, sagittate, 0.75 to 1.0 mm long; stigma ca. 0.5 mm long, style ca. 3.5 mm long, ovary three-loculed, each locule one- to two-seeded.

Type: H. L. Mason 12604. UC 693854. Obsidian Ridge southeast of Borax Lake, Lake County, California.

Range: Lake County, California.

Vegetatively, *E. brandegeae* closely resembles *E. tracyi*, *E. wilcoxii* and to a lesser extent *E. sparsiflorum* and *E. filifolium*. The flower, however, suggests a close relationship with *E. tracyi* and differs from that of *E. sparsiflorum*, *E. filifolium*, and *E. wilcoxii*, in that the sides of the opened corolla are more nearly parallel. The corolla tube of *E. brandegeae* is proportionally broader than that of *E. sparsiflorum* or *E. filifolium*. *Eriastrum brandegeae* is further distinguished from *E. sparsiflorum* by its larger leaves, the larger leaf lobes, by a general absence of entire leaves in a mature plant, and in having the stamens inserted at a lower level. It is distinguished from *E. filifolium* by its shorter stamens, slightly smaller anthers, by its more pubescent heads, and by geographic isolation from the latter. There are few distinctions between *E. brandegeae* and *E. tracyi*.

12. *Eriastrum tracyi* H. L. Mason, Madroño 8:87. 1945.

Annual, to 22.0 cm high, branching racemose or virgate; herbage lightly floccose; internodes 1.0 to 3.0 cm long; leaves grey green, 1.5 to 2.5 cm long, subulate, awn-tipped, with one pair of lateral lobes or entire; lobes to 7.0 mm; heads one to few, floccose to densely so, 0.5 to 1.0 cm broad, excluding tip of bracts; bracts to 1.5 cm long, exceeding the heads, with one or two pair of lateral lobes, hyaline membrane between the lobes sometimes present; calyx lobes unequal 7.0 to 9.0 mm long, joined by a hyaline membrane; corolla regular, subsalverform, 9.0 to 10.0 mm long, light blue to white; lobes broadly elliptic, 2.5 mm long and 1.25 to 1.50 mm broad; throat 1.0 mm long, sinus to stamen insertion 0.50 to 0.75 mm, tube 5.5 mm long; stamens equal, 1.0 to 1.5 mm long; filaments 0.50 to 1.0 mm long; anthers versatile, sagittate, 0.75 to 1.0 mm long; stigma 0.50 to 0.75 mm long; style ca. 4.0 mm long, ovary three-loculed, each locule having a single seed.

Type: J. P. Tracy 6463. UC 690662. Hayfork Valley 2600 ft, Trinity County, California.

Range: Trinity County, California.

It is with considerable hesitancy that the author retains *E. tracyi* as a distinct entity, and the only reason for so doing is to avoid unnecessary synonymy until later collections may substantiate the distinction. The only characters by which the entity may be distinguished from *E. brandegeae* are the corolla proportions and the exceedingly slight difference in filament length. The lobes of *E. tracyi* are minutely shorter and broader than those of *E. brandegeae*. When described, *E. tracyi* was said (Mason 1945) to be distinguished from *E. brandegeae* and *E. filifolium* by its branching and by its very small anthers and the corolla proportions. Branching is of almost no value in the recognition of species of *Eriastrum*. When the anthers of *E. brandegeae* and *E. tracyi* are restored (Harrison 1968), they prove to have exactly the same range in size from 0.75 to 1.0 mm. Each specimen of *E. brandegeae* examined has shown narrowly elliptic lobes from 3.0 to 3.5 mm long and 1.0 to 1.25 mm broad, those of *E. tracyi* have measured 2.50 mm long and 1.50 mm broad.

13. *Eriastrum abramsii* (Elmer) H. L. Mason, Madroño 8:90. 1945.

Navarretia abramsii Elmer, Bot. Gaz. 41: 314. 1906.

Hugelia abramsii Jepson and Bailey in Jepson, Fl. Calif. 3:167. 1943.

Annual, to 15.0 cm high, stems solitary or branched racemously, corymbosely, or diffusely from the base; herbage floccose, often densely so below the floral heads; internodes 0.5 to 2.5 cm long; leaves when present filiform, light green, 1.0 to 4.5 cm long or with one to three pair of lateral lobes, not rigid, subulate, awn-tipped; heads one to many, densely floccose, 1.0 cm broad, excluding tips of bracts, several-flowered; bracts to 2.5 cm long with one to three pair of lateral lobes, exceeding the heads by 1.0 to 1.5 cm, light green; the bases often completely obscured by dense, white wool; calyx 5.0 to 6.0 mm long; lobes unequal, joined by a hyaline membrane, embedded in white wool; corolla regular, salverform or very narrowly funnel-form, 5.0 to 8.0 mm long; lobes elliptic, 2.5 mm long, blue or white; throat 1.25 mm long, tube 3.5 mm long, sinus to stamen insertion 1.5 mm; stamens adnate to base of throat, equal or subequal, 1.5 mm long; filaments 1.0 to 1.25 mm long; anthers versatile, subsagittate, 0.50 to 0.75 mm long; stigma ca. 0.50 mm long, style 2.0 mm long, ovary three-loculed, capsule spreading at dehiscence, locules one-seeded.

Type: A. D. E. Elmer 4586. DS. Black Mountain, Santa Clara County, California (Black Mountain of the Santa Cruz Mountains, not Black Mountain of the Mount Hamilton Range, cf. Sharsmith 1944).

Range: Santa Cruz Mountains and Mount Hamilton Range in Santa Clara County south to San Benito County and north in Lake County.

Eriastrum abramsii is known from Lake County and from the Santa Cruz Mountains and the Mount Hamilton Range, where it is more common. It is remarkable for the contrast between the light green of the leaves and bracts and the very dense white mass of wool, which obscures the bases of the calyces and the bracts and continues to a short way down the stem. The plants are of short stature, usually 15.0 cm or less high; and the stems may be solitary, branched racemously, corymbosely, or diffusely from the base. Flowering may occur when the plant is a few centimeters high or when the floral head is just above the ground level. As the first leaves may wither, the plant may be

almost leafless; and a large part of the photosynthesis may be carried on by the bracts. The corollas are white and protrude above the mass of wool so slightly that they are quite inconspicuous. The species was first described as *Navarretia abramsii* (Elmer 1906) and, as discussed by Sharsmith (1944) and Mason (1945), is more closely related with *Eriastrum*. It occurs as an associate of *Adenostoma fasciculatum* chaparral (Sharsmith 1944) and is found "chiefly confined to dry gravelly soil immediately bordering thickets of the California Chamiso (*Adenostome fasciculatum*)." (Elmer 1906).

14. *Eriastrum hooveri* (Jeps.) H. L. Mason, Madroño 8:89, 1945.

Hugelia hooveri Jepson, Fl. Calif. 3:167. 1943.

Annual to 15.0 cm high, racemose, corymbose, virgate, or branched from the base; herbage lightly floccose to subglabrate, internodes 0.5 to 3.0 cm long; leaves filiform, 0.5 to 2.5 cm long, entire or with one pair of lateral lobes; lobes to 5.0 mm long; heads one to few, commonly 0.50 to 0.75 mm broad excluding tips of bracts, two- to eight-flowered, floccose to lightly so; bracts 0.8 to 1.5 cm long, exceeding the heads, with one pair of lateral lobes; calyx lobes unequal, 4.0 to 6.0 mm long, joined by a hyaline membrane; corolla regular, subsalverform, 5.0 to 6.0 mm long, white; lobes 2.0 to 2.5 mm long and 0.75 to 1.0 mm broad; throat 1.0 mm long, sinus to stamen insertion 1.0 mm; tube 2.0 to 2.5 mm long; stamens 1.0 to 1.25 mm long, equal; filaments 0.75 to 1.0 mm long; anthers sagittate-cordate, versatile, 0.50 mm long; stigmas 0.25 to 0.50 mm long; style ca. 2.0 mm long, ovary three-loculed, each locule one- to four-seeded.

Type: R. F. Hoover 1846. JEPS. Shafter, Kern County, California.

Range: Southern San Joaquin Valley, Fresno and Kern counties, California.

Eriastrum hooveri occurs on alkaline areas and dry stream beds in the San Joaquin Valley. The slender plants of short stature and heads of two to five flowers suggest a relationship with *E. diffusum*. The flowers of *E. hooveri*, in their small size, resemble those of *E. abramsii*.

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