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*Editor*
MURRAY F. BUELL

## THE NATURAL HISTORY AND TAXONOMY OF *COMANDRA* (SANTALACEAE)

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# THE NATURAL HISTORY AND TAXONOMY OF *COMANDRA* (SANTALACEAE)

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*Comandra umbellata* subsp. *umbellata* in early flower, Cheboygan County, Michigan (30 May 1960).

# INTRODUCTION

The genus *Comandra* is the most widespread North American representative of the Santalaceae, a family rarely encountered otherwise on this continent since it is predominantly tropical. *Comandra* consists of a small group of perennial herbs bearing terminal clusters of small whitish flowers. The plants are of more than usual interest biologically because of their parasitic behavior. Also, they play a role in forest pathology as alternate hosts of the comandra-pine blister rust.

## Common Names

The American representatives of the genus, as it is treated here, are known in the common vernacular as bastard-toadflax or false-toadflax. Because these names were earlier applied to members of the related genus *Thesium*, and the name toadflax is also used for species of *Cymbalaria* and *Linaria* of the Scrophulariaceae, use of comandra as a common name, as already found in some works, seems desirable. Plants of western North America have been called pale comandra. Infrequently used names for eastern American plants include star-toadflax (Seymour, 1960) and Richardson's (*sic*) bastard-toadflax for *C. richardsiana* Fernald (Jennings, 1953).

The existence of several names should not be taken to mean the plant is widely known; conversely, the comparatively generalized physiognomy of the sterile shoots, in particular, may account for the fact that it is recognized by relatively few persons other than those directly concerned with floras.

## Taxonomic History and Scope of the Present Study

Taxonomically the genus dates from 1818 when Nuttall gave a detailed and generally accurate description of it based on the single member, *Comandra umbellata*, which he segregated from *Thesium*. *Thesium umbellatum* was originally described by Linnaeus in 1753. A second species, *Comandra livida*, was described from boreal North America by Richardson (1823); this was soon followed by Rochel's *Thesium elegans* from the Balkans which was first published by Reichenbach (1824) and later transferred to *Comandra* (Reichenbach, 1849). In 1825 Sprengle transferred *C. umbellata* and *C. livida* to the genus *Hamiltonia* Willd., apparently failing to see the close relationship of these two species to the Balkan plant, which he retained under *Thesium*.

In 1857 De Candolle added two new taxa, *Comandra pallida* and *C. pallida* β *angustifolia* from western America. He also included *Darbya umbellulata* Gray (*Nestronia* Raf.) as *C. darbya*; this made up the second section of the genus which he had divided into sections *Eucomandra* and *Darbya*. Subsequent workers have retained *Darbya* as a distinct genus. A second division of *Comandra* into sections was made in 1880 by Bentham and Hooker. The distinctiveness of *C. livida* was apparent to these workers who placed it in a monotypic section *Haplocomandra*, the remaining three species recognized by them making up section *Eucomandra*.

In 1905, Fernald, largely on the basis of several vegetative characters, segregated a northern and western element, *C. richardsiana*, from the eastern *Comandra umbellata*. Fernald (1928) also noted that *C. livida* formed a separate element in the genus and separated it as a monotypic genus *Geocaulon*, failing, however, to point out that its distinctiveness at the sectional level had been recognized nearly a half-century earlier.

As is evident from the above, a comprehensive study of *Comandra* as a genus does not exist. During the period following the last of the above taxonomic changes, a number of systematists have indicated their dissatisfaction with the taxonomy of the genus. In fact, the distinctiveness of every American species, as well as the generic segregation of *Geocaulon*, has been questioned or denied, in some cases many times (e.g., by Jepson, 1914; Deam, 1940; Jones, 1950; Gleason, 1952; Harrington, 1945; and Moss, 1959).

While compiling the published information on *Comandra*, I soon discovered that relatively little was known about it. In an attempt to fill some of the gaps in our knowledge of these plants it seemed desirable to implement my taxonomic research with observations in such allied areas as anatomy, cytology, ecology, morphology, and palynology. Also, I felt that only a broad analysis spanning the entire developmental pattern could assure information of sufficient scope for the synthesis of a systematic treatment reflecting the natural history and natural relationships of the genus. Because of its availability the widespread eastern North American representative, previously known as *C. umbellata* (L.) Nutt., was studied most intensively to formulate a concept of tendencies in the genus as a whole. However, some 15,000 miles of travel enabled me to study the remaining American taxa in their natural habitats. In addition, about 150 plantings were made at the University of Michigan Botanical Gardens primarily to study germination and seedling development, dormancy, parasitism, and variation in uniform culture.

With a knowledge of some of the major structural and environmental tendencies at hand, the genus-wide variation for some 30 characters was considered. The composite variation pattern for all of these characters formed the basis for the new systematic treatment.

As a result of these studies, I now interpret the genus as consisting of a single widely varying species, *C. umbellata*, which is itself made up of four elements—subsp. *umbellata*, subsp. *pallida*, subsp. *californica*, and subsp. *elegans*. The evidence for this treatment will be given in its proper place, but these names will be used throughout the paper.

## Acknowledgments

I am especially indebted to Professor W. H. Wagner, Jr., for his interest, provocative discussions, and encouragement. I also wish to express my thanks to the curators of the herbaria from which specimens were borrowed and to numerous others who assisted me in locating and collecting specimens, identifying associated invertebrates, and in other ways.

The extensive field work was supported in part by the Society of the Sigma Xi, the University of Michigan Graduate Student Research Fund, and the H. H. Bartlett Plant Exploration Fund. A portion of this study was conducted under the tenure of a University Fellowship, a Rackham Predoctoral Fellowship, and National Science Foundation Summer Fellowships.

## MATERIALS AND METHODS

For most of the anatomical and morphological studies, materials were collected from the field or greenhouse and used either fresh or fixed in formalin-acetic acid-ethyl alcohol (FAA). These materials were supplemented in a few instances by dried material obtained from herbarium specimens, particularly in the case of the European *Comandra umbellata* subsp. *elegans*. Anatomical features were determined from sections prepared by the standard tertiary butyl alcohol and paraffin method (Johansen, 1940) and in a few instances by use of a freezing (clinical) microtome. Sections were cut at thicknesses of 10 to 50 μ and double stained in 1% safranin and 0.5% fast green. In some cases this stain was preceded by 1% tannic acid and 3% ferric chloride. The epidermal features and vasculature of flowers and foliar appendages were studied from whole-mounts cleared in NaOH, bleached in "Clorox," and stained in safranin-celestine blue (Gray and Pickle, 1956) which proved superior both to safranin alone and tannic acid-ferric chloride. Pollen obtained from herbarium specimens was prepared for morphological study by the Erdtman acetolysis method at the University of Michigan Pollen Laboratory. To determine the extent of abortion, pollen was placed in 95% alcohol on a slide, and stained with basic fuchsin in glycerin jelly and mounted directly. Flower buds used in chromosome counts were fixed in Newcomer's Fixative (Newcomer, 1953). Squashes of the young anthers were prepared in acetocarmine (1% carmine in 45% acetic acid).

All drawings were made with a microprojector except where otherwise specified. The photography was done by the author using 35 mm. film. Photographs of all type specimens examined are on file at the University of Michigan Herbarium. Sets of specimens I have collected and those given me have been deposited at 1) The University of Michigan, 2) United States National Museum, 3) University of California, Berkeley, 4) Gray Herbarium at Harvard University; fewer specimens will be distributed to other herbaria, and a sizeable collection has been retained in my personal herbarium.

The herbaria from which specimens were borrowed are: University of Alberta; University of Arizona, Museum of Northern Arizona; Museum of Natural History, Budapest; California Academy of Sciences; Carnegie Museum, Pittsburgh; Department of Agriculture, Ottawa; Conservatoire et Jardin Botaniques, Geneva; University of Georgia; Gray Herbarium, Harvard University; Academy of Sciences of the U.S.S.R., Leningrad; University of Michigan; Milwaukee Public Museum; Mississippi State University; University of Minnesota; University of Nebraska; The New York Botanical Garden; Ohio State University; Oregon State University; National Museum, Prague; University of Tennessee; United States National Museum; University of Wisconsin; and the University of Washington. Additional specimens were examined at the University of California, Berkeley; Missouri Botanical Garden; Pomona College; and the Rancho Santa Ana Botanic Garden.

## ANATOMY AND MORPHOLOGY[1]

### Stem

The stem system consists of the aerial stem and an extensive, much-branched rhizome. Sterile as well as fertile shoots are produced, with the former tending to be more leafy and taller, but also showing greater variation in height. The sterile often outnumber the fertile shoots. The fertile shoots are commonly about 1.6 dm. tall, and often develop lateral, rarely fertile, branches from their upper portions, the greatest develop-

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[1] These observations, plus those given below under the headings Karyology and Ecology, are based primarily on studies of subsp. *umbellata* in Michigan (particularly about the University of Michigan Biological Station in the Mackinac Straits region, Cheboygan County, and near Ann Arbor, Washtenaw County). However, features of other subspecies that stand in marked contrast to those discussed are mentioned.

ment of the laterals occurring in early summer while the fruits are forming. The lateral branches often overtop the central axis which is terminated by the inflorescence. The occasional fertile shoots which bear reduced inflorescences and resemble sterile shoots in stature appear to be formed, for the most part, late in the season. Variation in the form of the shoot has resulted in its being considered as both excurrent (Butler, 1954) and deliquescent (Randall, 1952). The stem is often reddish rather than green for a short distance just above the soil, and occasionally the anthocyanins may extend into the upper half, particularly on the ridges. The leaves are alternate, and axillary buds form and often enlarge at the lower nodes. The upper portion of the shoot is annual, but the base of a shoot which has formed axillary buds may persist (except in subsp. *pallida*), its buds giving rise to shoots the following season(s), and producing a rather bushy aspect. As many as 12 shoots have been noted from a single base. The axillary buds are rounded and covered with several imbricate scales.

AERIAL STEM. The aerial stem is glabrous and terete, and as mentioned in the literature, may have low longitudinal ridges, which Holm (1924) found corresponded in position with the phloem fibers. The ridges become particularly evident with drying. The epidermis is covered with a thin cuticle and the outer cortical cells contain chlorophyll. Starch grains and crystals were generally not found in the cortex and pith, nor was a distinct pericycle or endodermis observed. The eustele consists of collateral bundles with phloem fibers capping the primary phloem in the familiar fashion[2] (Plate 1, A). The primary xylem extends as V-shaped projections into the pith which here and in the rhizome is of the solid type and consists of large thin-walled cells. Swamy (1949) describes the vessel elements of the secondary xylem of herbaceous members of the Santalaceae as short (60 μ), and the nodes as characteristically unilacunar. Concerning the anatomy of the annual portion of the shoot, my observations agree largely with those of Holm (1924).

I have not studied the anatomy of the basal, persistent portion of the aerial stem; the following observations are from Holm (1924). The outer primary tissues are said to persist with some collapse of the cortex, although periderm, "secondary cortex," phloem fibers, and secondary vascular tissues develop. However, Holm also states that the shoot base has a "constantly identical structure" with the rhizome, where he describes all tissues outside the cork as being lost early. The cork cambium arises centripetal to the primary phloem fibers as it does in the rhizome (see

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[2] However, Behm (1895) reported that phloem fibers were not found, and that the cork cambium develops in the epidermis. Holm has suggested that Behm's material was incorrectly identified.

below). The "secondary cortex" contains crystals, and it and the outer pith contain starch.

RHIZOME. My studies of the rhizomes show that the terminal buds are enclosed by the scale-like leaves and are usually reflexed so that the meristem is above and behind the curved portion which apparently protects the meristem as the tip region grows forward. The rhizome is characteristically enlarged just behind the reflexed tip, with a conspicuous narrowing farther back where primary tissues exterior to the cork have been lost. The enlarged terminal region is white and stands out in contrast to the beige cork covering older regions. Scale-like, caducous leaves occur at the nodes; those away from the apex are thicker than those near the apex and are often reflexed, apparently because of the forward growth of the apical portion of the rhizome (Plate 2, F). They subtend axillary buds which are slightly recessed into the cortex.

The surface of the rhizome lacks the shallow longitudinal ridges of the aerial stem. The wood best fits the diffuse porous type, and, as reported for *Exocarpus* (Fineran, 1962), rather indistinct growth layers have been noted, which in *Comandra* appeared to occur occasionally in the large rhizomes of the "crowns" in subspecies *pallida* and *californica* only. The rhizome generally resembles the aerial stem in regard to the epidermis, cortex, bundle and stele type, pith, and the lack of pericycle and endodermis; however, the outer pith contains some starch and it and the cortex occasionally contain crystals (largely druses). Crystals were considered absent from the cortex by Holm (1924). The rhizome has proportionately less pith and more cortex than the aerial stem and differs most in its development of an extensive amount of primary phloem. The phloem occurs in the usual position opposite the xylem, and projects outward as very narrow, radial extensions which sometimes end in clusters of phloem fibers (Plate 1, B). Between these extensions unusually wide rays are found. In the older rhizome the phloem extensions are usually shorter and become broadened inwardly, and the rays, broadened outwardly, take on the V-shape commonly exemplified in botany courses by the *Tilia* stem. The rays contain crystals and much starch, the starch grains being both simple and compound with the concentric layers rather indistinct. A short distance behind the rhizome tip, the cork cambium appears in the inner cortex and traverses the phloem just inside the fiber clusters. The cork cambium at first displays an undulating boundary in transverse section, but later becomes approximately circular. Small groups of secondary phloem fibers may appear, and a considerable amount of parenchyma tissue develops outside the phloem. It seems best not to refer to this parenchyma tissue as "secondary cortex" as Holm (1924) and others have done, but to reserve the term cortex for the usual primary region. The epidermis, cortex, and outer phloem soon break down and are lost, accounting for the decrease in diameter of the rhizome mentioned previously. The comparatively large amount of both primary and secondary phloem and the large food storage capacity of the massive phloem rays may deserve further consideration, particularly in view of the parasitic nutrition of the plant.

In the older rhizomes of subspecies *californica* and *pallida* the cells of the phloem rays and the parenchyma outward from the phloem possess a bluish pigment which, as we will see in the discussion of variation, has proven very useful taxonomically. The bluish pigment is due to an intercellular deposit which under microscopic examination appears to have the form of irregular fragments (Plate 8, C). As mentioned later, the pigment may be due to an oily substance which appears under low magnification when the intact rhizome is submitted to pressure. A similar deposit may occur in lesser amounts in the other subspecies; regardless, these tissues never acquire a blue coloration macroscopically in those taxa. The color does not seem to be changed by alcohols, formalin-acetic acid-alcohol, nor, according to Woodcock and De Zeeuw (1920), by several strong acids and alkalis. The deposit does not take up safranin, fast green, or similar stains. However, in sectioned material examined microscopically in transmitted light it often appears brownish (sometimes blackish-brown to reddish). The deposit is opaque and can hardly be called crystalline as was done by Woodcock and De Zeeuw (1920), who apparently were the first to call attention to the blue color of the roots and rhizomes.

## Root

The primary root system has both primary and lateral roots well developed, and in the classification of Cannon (1949) best fits his Type I. Both it and the adventitious root system may be present the first few years. At least portions of the primary system have been observed in 4 year plants and presumably could be found later. The adventitious system fits into Cannon's scheme with more difficulty (he does not mention root parasites) but seems closest to Type IX, which has adventitious roots scattered and of one kind.

Adventitious roots tend to be most abundant near the rhizome tip, occurring only sporadically along the older portions of the rhizome. The roots remain thin, only occasionally exceeding a few millimeters in diameter, and even the young ones have comparatively few root hairs.

The older roots are short, relatively little-branched, and frequently bear haustoria, which as mentioned in the discussion of parasitism, may terminate the root even though they are initiated laterally. A weakly developed root cap is present. The cells of the cortex are thin-walled, and the cortex is delimited on its inner side by an endodermis with rather obvious Casparian thickenings. The secondary wall thickenings of the primary xylem are coarsely reticulate, while those formed later are either finely reticulate or pitted. Earlier descriptions suggest that the root is tetrarch (Holm, 1924); however, I have sectioned seedling primary roots and found them to be diarch. This aspect of the stele is known to vary considerably from one part of the root system to another in many plants (Esau, 1953). Holm (1924) describes the cork cambium as developing from the pericycle; thus the tissues outside of this zone are lost. I observed a cortex-like band of parenchyma containing abundant starch in older roots. Fibers are reported (Holm, 1924), but were not present in my material. Tyloses were noted in the xylem elements of a root invaded by haustoria of *Pedicularis canadensis* (see Piehl, 1963).

## Foliar Appendages[3]

These structures differ primarily in size and shape, forming a spectrum from the minute bud scales at the shoot base through the largest foliage leaves situated about midway along the axis. At the upper end of this series are the tiny bracteoles of fertile shoots (Plate 3). In this discussion "leaves" refers to the ordinary foliage leaves as contrasted to the other appendages to be described after them.

The simple, deciduous leaves are generally sessile (rarely short petiolate), estipulate, alternately arranged, and display a divergence from the stem ranging from acute to obtuse. Reference to their being held in "an erect position" (Holm, 1924) is inaccurate. I have found the phyllotaxis of the aerial stem to be highly variable. Occasional specimens, particularly sterile ones in shaded sites, attract one's attention because the leaves are rather strongly 3-ranked or are arranged in a conspicuous helix (Plate 9, E). The ptyxis (cf. "vernation") of the leaves seems to fit the "Curvative" type as given in Davis and Heywood (1963). The leaves are always glabrous and characteristically soft and thin with the veins protruding below. The slight whitening of the lower surface, which is related to the presence of stomata, differentiates it from the upper. The much thicker leaves of subsp. *pallida*, with the veins inconspicuous and surfaces similar,

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[3] "Foliar appendages," used here as a matter of convenience, excludes appendages making up the flower which are, of course, also foliar in a phylogenetic sense.

contrast with the situation described above for subsp. *umbellata*. Some degree of leaf dimorphism is apparent particularly when the leaves of the main axis are contrasted with those of the branches. The relationship of the occasional formation of unusually large lower leaves in subsp. *umbellata* to shoots with decumbent and persistent bases is indicated under "Developmental History." The formation of similar large leaves in a collection from California (*Piehl 63763* GH, MICH, UC, US) appeared to be related to the removal of the upper part of the stem.

The general anatomical features of the leaves have been reported by Holm (1924), who mentions the thin cuticle and straight lateral walls of the epidermal cells. He describes the stomata as being "surrounded by four ordinary epidermal cells," but neglected to say that two of the surrounding cells are, with occasional exceptions, elongated parallel to the guard cells which have a syndetocheilic origin. From my observations, I feel these two cells are best designated as the accessory cells as was done by Behm (1895) for *Comandra umbellata* subsp. *elegans*, since the other epidermal cells usually touch only the ends of the guard cells. Holm's description may be the basis for recording the stomata as ranunculaceous (Metcalfe and Chalk, 1957); however, they are better considered as rubiaceous (anomocytic), as those of the Santalaceae are characterized by Swamy (1949). Stomata are restricted to the lower surface (in subsp. *umbellata* only), except for a few at the base of the blade, and tend to be arranged parallel to each other, and at nearly right angles to the midrib. Although such an arrangement of stomata with respect to the midrib is the only condition given for subsp. *elegans* (Behm, 1895), exceptions are found in all subspecies (Plate 4).

I have found the mesophyll to consist of densely organized, nearly isodiametric cells, with only sporadic, short palisade cells (Plate 1, E-G). Sclerenchymatous cells are rare. Some leaves contain groups of thick-walled cells which tend to be associated with vein endings particularly near the leaf margin. The individual cells are somewhat angular, but several of them together form a rounded group (Plate 2, C). These may be silicified cells as they were called by Behm (1895); however, I was able to note only that the lumina are usually filled, and that the walls show concentric rings, but pits were not visible. Further study is needed. Absence of such thick-walled cells in some leaves is unexplained, for they have been found both in the spring and later in the season; however, they tend to be more common as the season advances.

The venation is reticulate and of the camptodromous type, following von Ettinghausen's terminology as given by Foster and Gifford (1959). The vein endings are free and usually have a dilated aspect due to the presence of from two to several clustered storage tracheids. The tracheids are comparatively short and broad, and may be somewhat angular in outline (Plate 2, A & B). They reportedly store water (Holm, 1924); if they do, further study aimed at elucidating their relationship to the parasitism and general water relations of the plant would be desirable.

The outer bud scales lack a vascular trace, have few or no stomata, have scattered stone cells in the epidermis, and contain many loosely-grouped crystals (druses). The inner scales also have the crystals, but have a simple vascular trace (Plate 5), and display stomata on both surfaces. The scale-like leaves on the lower part of the stem become chlorotic and often fall at the time of flowering. The lowest scale-leaves have crystals but those farther up tend to lack them. The scale-leaves have bifacially distributed stomata, and at their tips possess a few grouped sclerenchyma cells (as described above), which were lacking in the bud scales. At the level of the foliage leaves, sclerenchyma cells, when present, occur nearly the full length of the leaf.

The bracts which subtend the flower clusters are much like foliage leaves structurally. The bracteoles subtending the individual flowers are caducous, and have a few stomata on the upper in addition to those on the lower surface. Their venation is similar to that of leaves, but they appear to lack both crystals and silicified cells.

The subterranean, caducous rhizome scales are rather distinctive due to their deltoid shape and the coarse, blunt serrations along the margin. Those of subsp. *umbellata* have a simple vascular trace, while in subsp. *pallida* the vasculature tends to be much more complex and resembles that of other foliar organs except that all veins are remarkably broadened by numerous cells resembling storage tracheids (Plate 5, A). Stomata occur on both surfaces.

## Inflorescence

The fully developed inflorescence varies from one which is loose, with the individual clusters at different levels and thus tending to be paniculate, to one which is denser, the peduncles more elongated proportionately, bringing the flowers together in a generally flat-topped, corymbose group (Plate 3, Q). However, the inflorescence can be said to be paniculate or corymbose in outline only, since the component flower clusters are always cymose. The difficulty in applying the terminology for inflorescence types to certain cases has already been emphasized by Rickett (1955).

The inflorescence is composed largely of clusters of few to several flowers produced on axillary penduncles which are subtended by foliaceous bracts. The basic unit of the ultimate clusters is a 3-flowered cymule (dichasium) which by reduction or compounding makes for a range in flower number of from one to five (Plate 8, G), as has been described by Holm (1924). Five-flowered cymules are common on the lower peduncles, while fewer flowers, commonly three, occur in upper cymules. The individual flowers are subtended by bracteoles (prophyllary bracts) the number of which was apparently misinterpreted as 4 by Linnaeus (1753) for subsp. *umbellata*, and as 2 by Reichenbach (1824) for subsp. *elegans*. Fertile axillary branches occasionally occur at the base of the inflorescence; sometimes these are prolonged and overtop the main axis. The inflorescence is terminated by several solitary flowers with very short internodes between them; each flower here is also subtended by a bracteole. Anthesis occurs at about the same time over the inflorescence as a whole, but the central flower of the component cymules tends to open shortly before the laterals.

## Flower

CALYX. The flowers are actinomorphic, and typically 5- (sometimes 4-, rarely 3-, 6-, or 7-) parted, and essentially odorless. They are bisexual and have a uniseriate perianth, composed morphologically of sepals (Plate 2, G). Below the sepals, the perianth is fused with other floral parts to form a floral tube, which in turn is fused with the ovary at a still lower level. A slight constriction is often evident just above the ovary. The sepals are whitish (rarely pinkish) at anthesis but become yellowed with age, drying, or chemical fixation. This color change in preservation is believed to be responsible for interpretations of the flower as cream or yellow; e.g., see Reichenbach (1849). Descriptions of the flower as greenish may be due to an eventual change in calyx color as discussed under "Developmental History"; also, the sepal bases and floral tube are green even at anthesis. The aestivation is valvate. The vasculature of the sepals resembles that of the leaves. Each sepal is supplied by a single vascular trace which, although it branches at the sepal base, continues as the midvein of the sepal. The vein endings are composed of storage tracheids, which are unusually abundant in the upper part of subsp. *pallida* sepals (Plate 5, I).

A few stomata occur in the outer epidermis of the sepals. Stomata occur also in the floral tube, including the lower levels where it is fused to the ovary, and according to Ram (1957) in the inner ovary wall as well. Tannins occur in the sepals, floral tube, style, and in the filaments and endothecial cells of the anthers. Crystals (druses) occur in the parenchyma cells of the sepals and floral tube. Trichomes are rare in *Comandra*; those on the shoot system are largely restricted to the sepals. The outer epidermal cells of the sepals protrude to make the outer surface gently papillate. Those of the inner surface are prolonged into single- (rarely few-) celled, pointed hairs which give this surface a papillate or shallowly serrate aspect (Plate 2, D-E). In the bud these hairs are somewhat interlocked at the summit and margins of the sepals.

A very unusual feature of the sepals is the prolonged, yellowish hairs which become attached to the anthers. These unicellular hairs are produced from modified inner (i.e., adaxial) epidermal cells near the sepal base. Van Tieghem (1896) incorrectly described such hairs for the Santalaceae as hypodermal. Although mentioned in the original description of the genus (Nuttall, 1818), the hairs have not previously been described in detail. Quite similar hairs are found in many other santalaceous genera of the Osyrideae and Thesieae *sensu* Pilger (1935).

In unopened buds where the anthers have not yet dehisced, the then whitish hairs are closely appressed to the anther, but are not usually attached. Since the inner flower parts are very closely packed in the bud, it appears that during development the mass of hairs becomes crowded into the longitudinal indentation of the anther which marks the location of the connective. The attachment of the hairs to the anther appears to occur after dehiscence of both the anther and hairs. In flowers that have been open for some time the hairs often take the form of an intertwined cluster, and are generally attached to the upper part of the connective of the anther (Plate 7, B), usually remaining securely attached even on herbarium specimens. In old flowers the ends of the then largely empty hairs sometimes become frayed. The similar hairs reported for *Santalum album* are said not to be attached to the stamens (Rao, 1942).

The base of the hair is enlarged, and contains a nucleus which, because of its great size, contrasts markedly with the nuclei of neighboring cells. The upper portion of the hair contains yellowish globules. For *Thesium*, Ewart (1892) described these globules as a balsam-like resin, and the hair apices as having three constrictions which mark the points where the tip may break off, affording release of the globules. In *Comandra*, a protruding tip usually with one or two constrictions occurs, and it also becomes detached from the rest of the hair. Shed pollen is frequently found attached to the hairs in *Comandra* and may accumulate near the distal end of a cluster of hairs as a large mass. The stickiness of the pollen combines with the secretion of the hairs to facilitate such adhesion. I have found no comment on the wall sculpturing of these hairs, which at high magnification was seen to be granulate (Fig. 1).

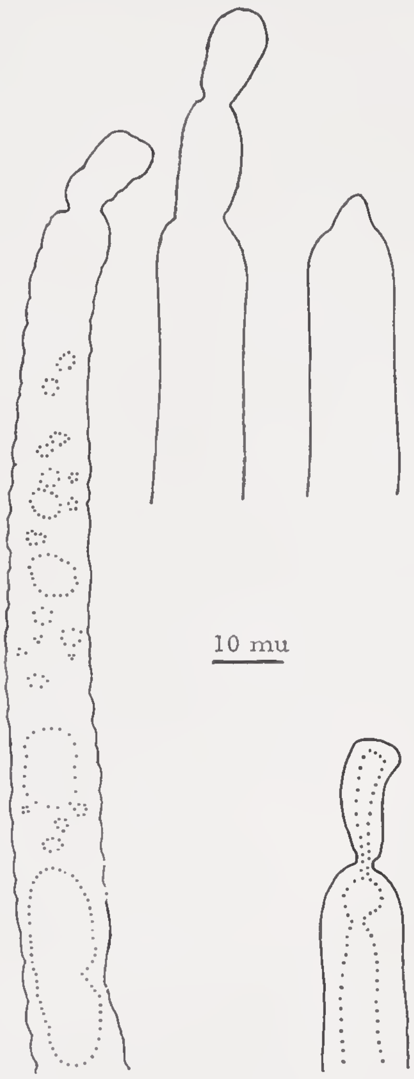

FIG. 1. Post-staminal perianth hairs. Distal portions showing roughened surface and globular contents (l.); others are outlines only (contents extending into tip, lower r.; early development of tip, upper r.).

I have not studied the function of the hairs in detail, nor is it established with certainty in previous works. In *Thesium*, Kerner (1895) found the hairs facilitated closing of the anthers under wet conditions by transferring moisture from the perianth. Also in *Thesium*, release of the sticky globules near the anthers was suggested to be a means of catching and holding pollen (Ewart, 1892). Paliwal (1956) believes the hairs of *Santalum* are related to *in situ* pollen germination, perhaps providing a suitable medium for the germination and growth of the pollen tube over the anther wall. The presence of hairs in the male flowers of *Osyris arborea* Wall. but not in male-sterile flowers again suggests a relationship to pollination (Paliwal, 1956). I have noted that the globules produced in the hairs resemble those associated with the disc; thus, the possibility that the hairs function in attracting flower visitors needs consideration. Future studies of the hairs might profitably be directed to such genera as

*Thesium*, where the development of perianth hairs in some members far exceeds that in *Comandra*.

ANDROECIUM. The stamens are about 1.4 mm. in length; the filaments are short (ca. 1 mm.), rather stout, and much tapered. The smooth, oblong anthers undergo longitudinal, introrse dehiscence, and are dorsifixed, the filament being attached near the anther base. The anthers are 4-celled, becoming bilocular at maturity with the locules slightly divergent basally. Undehisced anthers range from pale yellow to brownish or purplish, but all tend to become pale after the pollen is released. The xylem of the single trace is represented by from one to a few rows of cells. Fully developed endothecial cells possess rather elaborate stellate thickenings which diverge from a thickened plate on the inner tangential wall, pass along the radial walls and terminate as free points on the outer tangential wall. The maximum thickening does not seem to be developed until about the time of anthesis, and perhaps that thickening described as "feebly developed" (Ram, 1957) had not reached maximum development. Rather similar endothecial thickenings occur in *Osyris*, *Santalum*, and *Thesium* (Paliwal, 1956).

The sticky pollen is released as a shiny yellow mass, and most of it can be removed from the locule on the tip of a dissecting needle. The pollen grain is 2-nucleate when released according to Ram (1957) and although my observations suggest it may sometimes be other than 2-nucleate, further observations are needed. I have found that the pollen grains are comparatively small and thin walled. The acetolysed grains used for morphological study averaged 19.6 × 15.4 μ and had a wall thickness of ca. 1.4 μ (subsp. *californica* and subsp. *pallida* pollen is slightly larger). The size was observed to be greatly modified by the mounting medium used: Fresh pollen mounted in water measured 28.0 μ across the equatorial axis; it decreased in this dimension by about 25% when the water was replaced by acetocarmine. From 3 to 5% of the pollen is usually found to be abortive. The morphology of the pollen is influenced by the tetrahedral arrangement of the microspores, and using Erdtman's (1952) terminology, my observations indicate that the pollen is isopolar, angulaperturate, tricolpate, and suboblate (average ratio of polar to equatorial axis is 0.81) (Plate 9, A-B). The exine is finely reticulate, although it has been described as "smooth" (Ram, 1957). The furrows (colpi) measure about 11.2 × 0.98 μ, and have a somewhat fimbriate margin and a somewhat flecked surface, although the last feature needs additional study. These observations generally agree with the brief descriptions of subsp. *pallida* pollen given by Erdtman (1952). Microsporogenesis is described by Ram (1957).

Fresh pollen was transferred to 2.5, 5.0, and 9.0% aqueous sucrose solutions, and was found to germinate best in the 9.0% solution. Subsequent attempts with a higher concentration of sucrose were less successful. After the pollen tubes had developed to about 0.2 mm., growth stopped, probably because the environment was unfavorable. Although not studied in detail, no unusual features were noted in the development of the male gametophyte.

Germinated pollen was discovered *in situ* in undehisced anthers of subsp. *umbellata* and subsp. *pallida* collected in nature. Additional observations indicate this condition is occasional, and suggest that it is prompted in part, at least, by high humidity. This unusual germination has not been previously described for *Comandra,* but has been observed in other Santalaceae, e.g., *Thesium* (Rao, 1942), *Leptomeria* (Ram, 1959), and *Santalum* where the pollen tube has been observed to grow between the cells of the anther wall toward the stigma (Paliwal, 1956). Penetration of the undehisced anther by the pollen tube has not been noted in *Comandra.* Should it occur, the distance the pollen tube must grow to permit fertilization is only slightly greater than that involved when pollen is deposited on the stigma, since the anther is closely appressed to the stigma in the bud. Perhaps it is through irregular behavior of this type that complete cleistogamy, which in some of the many cases recorded is prompted by environmental factors, has evolved. However, there is a lack of agreement concerning the probable origin of cleistogamy (Maheshwari, 1960).

DISC. Above the ovary the inner surface of the floral tube is lined with a shallowly lobed, non-vascularized, nectariferous disc (Plate 2, G). Its rounded lobes, which average 0.5 mm. in length, alternate with the sepals and equal them in number. The lobes are composed of small, densely protoplasmic, isodiametric cells. Just below the lobes some of the inner epidermal cells may be prolonged into short pointed hairs resembling those on the sepals; similar but more rounded hairs occur near the base of the disc. At the top of the ovary, hairs of the rounded type are again found, which Ram (1957) describes as multicellular but illustrates as both single- and few-celled. Those I have observed have been unicellular only. I have not found the lobes ciliolate anywhere in the genus, as was given by Reichenbach (1824) for subsp. *elegans* (see discussion under "Formal Classification"). In newly opened flowers the disc surface shines with a thin film of nectar which attracts insects; however, droplets do not appear to accumulate.

GYNOECIUM. The ovary is inferior, and is sometimes termed "semi-inferior," as the top is free from the floral tube. The style is filiform and has a slightly expanded stigma situated at the level of the anthers. A rather poorly defined stylar canal appears to develop schizogenously, and I have noted a lining of upwardly directed papillate cells as described by Ram (1957) only at its base. In the present work, weak vascular traces were observed to enter only the base of the style, as was described by Smith and Smith (1942b). Although Lawrence (p. 470, 1951)[4] described the ovules of the family as "borne pendulously on the ovary floor . . . the placentation basal," the placentation is best described as free-central in view of the presence of a conspicuous and comparatively long placental column at the mature "embryo sac" stage. The 3 (2-4) anatropous ovules are suspended from the apex of a spirally-twisted or, less frequently, a straight placental column arising from the base of the single locule. The ovule is covered by a single, distinct (for the Santalales) integument which is early consumed by the endosperm (Ram, 1957). The unicarpellate and unilocular condition is considered reduced from the 3-5 parted condition, which exists in some members of the family today (Smith and Smith, 1942b; Paliwal, 1956).

The nature of the inferior ovary of the Santalaceae has received considerable attention in connection with the long-debated appendicular versus receptacular (axial) theories, and particularly since the appearance of the work of Smith and Smith (1942a; 1942b). In a "primitive" member of the family, *Darbya umbellulata* A. Gray (*Nestronia* Raf.), Smith and Smith found that the vascular bundles of the ovary wall occurred in two rings, the outer with normal orientation of xylem and phloem, and the inner reversed. This feature, together with the origin of carpellary traces from the inverted strands and the occurrence of downward pointing residual tissue beyond the point of departure of the carpellary traces, was taken as evidence for the invagination of the tip of the axis, followed by the fusion of the ovary to the axis, and the consequent receptacular origin of the inferior ovary. The authors related this basic ovary type to 23 other, mostly more specialized, genera of the Santalaceae and to related families. Although the interpretation of the santalaceous ovary by Smith and Smith has been opposed wholly or in part by some workers (e.g., Berkeley, 1953; in part by Puri, 1952, and Paliwal, 1956) the receptacular nature of at least a portion of the ovary wall has been generally accepted (Eames, 1961; Puri, 1952; and Paliwal, 1956). A very

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[4] The ovary pictured in Lawrence is mislabeled: "Ba" is a habit drawing (not vertical section) of a partly developed ovary and other floral parts, and "Bb" a longitudinal (not cross) section of same.

brief discussion of the *Comandra* flower from the currently unpopular viewpoint of carpel polymorphism is given by Dowding (1931).

Smith and Smith (1942b) interpret the vascularization of *Comandra* and other specialized Santalaceae in light of their findings in *Darbya*, pointing out that reduction has made the interpretation of the ovary difficult. They find amphicribral bundles in the ovary wall resulting from "phylogenetic" fusion of ascending and recurrent receptacular traces, and residual tissue appears as scattered xylem strands in the pith region of the pedicel tip. This downward pointing residual tissue is considered to be derived from recurrent traces, as still exist in *Darbya*. Following this interpretation the tubular portion of the flower is thus a "hypanthium," but because this term has been variously used, I have adopted the term "floral tube" as used by Parkin (1955) and Benson (1957).

Megasporogenesis and the development of the female gametophyte have been described by Ram (1957),[5] and the following summary is from that source. The female gametophyte is of the *Polygonum* type. The placental column is invaded by the remarkable growth of the endosperm haustoria of the female gametophyte. Peculiar types of female gametophytes are not uncommon in the Santalales, and they become more extreme in certain Loranthaceae, where they may extend up into the style and even into the stigma where fertilization occurs (Maheshwari, 1950). Johri and Bhatnagar (1960), referring to Ram's findings, point out that as far as is presently known *Comandra* has the unique feature in the Santalales of producing a lateral caecum which develops from the micropylar region. The caecum serves as primary endosperm haustoria during early post-fertilization development. Secondary haustoria develop, and the placental column and parenchymatous endocarp are early consumed. However, I have noted that the endocarp is not entirely consumed, for some of the tissue remains in the mature fruit and appears as such in Ram's illustration (1957, p. 33). Ram indicates that endosperm is usually initiated in all ovules, but reaches maturity in only one; however, no information is available on whether embryo development also begins in all ovules. The zygote divides only after considerable development of the endosperm, and the initial division is longitudinal, unlike that known for other members of the Santalaceae. The embryo lacks a suspensor.

Some interesting embryological notes and drawings which I am quite certain are the work of Asa Gray are among the specimens at the Gray Herbarium.

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[5] Because of the geographic sources of materials used in Ram's work (p. 25) and an illustration of a bud (Fig. 4), it appears that her study included material of subsp. *pallida* and subsp. *californica* in addition to subsp. *umbellata*, the only taxon mentioned by Ram (as *Comandra umbellata* (L.) Nutt.).

## Fruit

The early ontogeny of the endosperm and embryo have been described above in connection with the gynoecium. The indehiscent, mature fruit is crowned by the persistent calyx, stamens, style, and often by the upper part of the floral tube which becomes constricted into a short neck. The fruit is nearly globose (slightly longer than wide) and is about 5 mm. in transverse diameter in subsp. *umbellata*. It has been classified as both a drupe (Fernald, 1905; Gleason, 1952), and a nut (Fernald, 1950).

A drupe is generally defined as a single-seeded, fleshy, indehiscent fruit with a hard inner pericarp. The pericarp of the young fruit of *Comandra* has three regions—epicarp, mesocarp, and endocarp—well differentiated. The endocarp is parenchymatous and largely consumed as noted above. The mesocarp becomes hardened as its parenchyma cells dedifferentiate into brachysclereids (stone cells) with conspicuously pitted walls and a narrow lumen. The epicarp is the vascularized, photosynthetic, outer layer (Plates 2, H; 7, C) which often remains leathery while the fruit is on the plant, and hardens as the fruit falls and dries.

Since the thin epicarp in *Comandra* is sometimes dry when found in the field and may give the appearance of having been dry when fresh in herbarium material, it is not surprising to find it described as a nut. However, if the later stages of fruit development are carefully observed, it is apparent that the fruit is normally still soft and leathery when it falls from the plant. (Occasional dried fruits remaining on the plant are often abortive.) After the fruit is detached the epicarp normally dries and hardens.

In this connection one should consider the generally similar, but distinctly fleshy and conspicuous epicarps of closely allied genera, such as *Geocaulon* and *Pyrularia*. These fruits must be considered drupes, and it seems best to consider the fruit of *Comandra* as a drupe also, even though it is somewhat less fleshy. The rather intermediate fruit condition in *Comandra* calls attention to the inadequacy of the terminology for fruit types. Attempts at a so-called natural system of fruit classification (Winkler, 1939) have still not resolved the difficulties imposed by distinguishing fruits on the basis of gross morphology alone without sufficient knowledge of such aspects as their histology and ontogeny.

The endosperm of *Comandra* is apparently cellular from the beginning (Ram, 1957), and in the mature fruit it completely fills the locule. The mature embryo is embedded in an inverted position within the endosperm. Its cotyledons are from linear to almost lanceolate, and its hypocotyl is obtuse. A few embryos were excised from fruits stored at room temperature, and were found to vary considerably in length (1.6 mm. in subsp. *umbellata* to 4 mm. in subsp. *pallida*). In some a single vascular strand had differentiated.

## KARYOLOGY

The chromosomes of *Comandra* have not been previously described, nor have numbers been reported, although Ram (1957) does discuss meiosis briefly. My studies are based almost entirely on microsporogenous meiotic material, as it proved more favorable than mitotic material. Because it is rather difficult to get plants grown from seed to flower under greenhouse conditions, nearly all of the buds used were collected in nature. Meiosis was found to occur while the buds are greenish (not yet white) and still partly enclosed by the larger foliage leaves. The actual dates of meiosis are indicated in Table 2. Young anthers were prepared by the squash method and stained with acetocarmine as described under "Materials and Methods."

In the non-dividing nucleus and during prophase, what I at first interpreted as nucleoli stain brightly, and several (up to seven[6]) are sometimes observed in one cell. The meiotic chromosomes are very small (2-3 $\mu$ at metaphase I), and are usually oblong to nearly spherical at the stages used for counting. Although little information is available on the chromosomes of other Santalaceae, Rao (1942) describes both mitotic and meiotic chromosomes of *Santalum album* as small, and from rounded to oblong. My counts were made at metaphase I, anaphase I, and rarely, anaphase II. Especially valuable were cells at mid-anaphase I, where the chromosomes had already moved toward the poles, but had not elongated and grouped together. Diakinesis was not a particularly useful stage for counting.

Several observations of chromosomes were made on each of the North American subspecies. Meiosis appears to be normal in all of them, and the chromosome morphology was generally similar. All appear to have the number of $N = 14$ (Plate 7). A few preparations which were not favorable for counting gave questionable counts of $N = (12)$ 13 or 15, but these deviations from $N = 14$ are believed due to the difficulties in interpreting these particular cells. Unfortunately, I was unable to obtain cytological material of subsp. *elegans*. However, in view of the situation elsewhere in the genus and its close relationship to other members, it may well display a similar karyology. The cytological uniformity of the subspecies that I

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[6] As this is an unusually high number of nucleoli, perhaps other structures, e.g., heterochromatic chromosome segments, were involved.

have studied correlates well with the evidence from other sources in supporting my contention that the previous separation of these plants at the species level is unjustified.

It appears that *Comandra,* as well as most other Santalaceae for which numbers are available (see below), are already polyploid, since it is generally believed that the original base numbers in angiosperms were of the magnitude of 6, 7, and 8 (Stebbins, 1950). My count of N = 14 for *Comandra,* which suggests a base number of X = 7, is new for the family. Since so few numbers are known for the Santalaceae, the relation of this number to the rest of the family is uncertain. The previously-recorded gametic numbers as summarized for the Santalaceae (Darlington and Wylie, 1955; Tischler, 1950) are: *Santalum* 10; *Thesium* 10, 12 and 13[7]; *Buckleya* 15; *Osyris* 10 and 15; *Pyrularia* 19; *Iodina* 36 (12). Baksay's count of 2N = 14 for *Thesium linophyllon* as reported by Löve and Löve (1961) contrasts with other numbers reported for that genus and suggests this species is at the basic number, unless perhaps, gametic rather than sporogenous tissue was involved, in which case this number would equal that in *Comandra.* Löve and Löve also list *Thesium alpinum* subsp. *alpinum* as 2N = 12.

In the allied Loranthaceae, Wiens (1964) and other workers have reported N = 14 as a common number in *Arceuthobium* and *Phoradendron,* and Gill and Hawksworth (1961) report N = 13-14 for 2 species of *Korthalsella.*

## ECOLOGY

### Life-form

*Comandra* has been classed as a "cryptophyte," following the life-form classification of Raunkiaer, and as a "geophyte (parasites and saprophytes)" according to Turrill's "extended scheme" (McDonald, 1937; Randall, 1952, respectively). Although some buds of the buried horizontal rhizome contribute to spring flushing, the majority of the overwintering, shoot-forming buds occur at or just above the soil or duff level on either the vertical extensions of the rhizomes or the persistent bases of the aerial shoots. Thus the plant is better classed either as a hemicryptophyte or chamaephyte or as both. Subspecies *pallida* displays a strong tendency toward the hemicryptophyte form; subsp. *californica* and subsp. *elegans* are often chamaephytes. The leaves were assigned to Raunkiaer's nanophyll size category (Randall, 1952), but I have found them to vary greatly in size.

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[7] N = 13 for *Thesium rostratum* was reported by Ruthishauser (Tischler, 1950); however, that record was deleted by Darlington and Wylie.

## Habitats

The characteristic habitats are rather dry, partly to completely open sites. *Comandra* is often found at the tops of roadcuts and similar clearings in otherwise wooded areas where its growth appears to be stimulated by the removal of the overstory. Common habitats for subsp. *umbellata* include grasslands, savannahs, and semi-open forest margins (see Plate 12).

Among the larger cryptogams and seed plants occurring most frequently in the *Comandra* stands studied in the Mackinac Straits region, Michigan, were the following: *Ceratodon purpureus*, *Cladonia* spp. *Polytrichum* spp., *Pteridium aquilinum*, *Carex pensylvanica*, *Danthonia spicata*, *Poa compressa*, *P. pratensis*, *Acer rubrum*, *Amelanchier* spp., *Aster laevis*, *Gaultheria procumbens*, *Gaylussacia baccata*, *Pinus resinosa*, *Populus gramdidentata*, *Quercus rubra*, *Rhus glabra*, *R. typhina*, and *Vaccinium angustifolium*.

For Wisconsin plant communities Curtis (1959) gives the following data: *Comandra* reaches its highest frequency in the "oak barrens" (dominated by *Quercus velutina* and *Q. ellipsoidalis*); it is also "prevalent" in "oak openings" (largely *Q. macrocarpa* and *Q. alba*), cedar glades (largely *Juniperus virginiana*), and several types of prairies ranging from wet to dry. *Comandra* occurred in 21 of the 34 native communities distinguished by Curtis, indicating a rather broad ecological amplitude, but it favored the warm and dry portions of temperature and moisture gradients, respectively. Soil analyses of the communities in which it was prevalent showed considerable variation in the available nutrients studied (Ca, K, P, $NH_4$ [*sic*]), a pH range from 5.6-7.8, and a generally low water retaining capacity.

I believe an even wider tolerance of soil pH is indicated by the rare occurrence of *Comandra* in swamps as stated on herbarium sheets, and by my observations of it in an acid bog. I have also found it growing in gravelly limestone, and wet, somewhat marly swales near the Great Lakes' shores in the Mackinac Straits region. However, *Comandra* is most commonly found in porous, often rocky, soils that tend to be acidic, but frequently ranges from sands to sandy loams and loams. The rhizomes commonly occur within the A horizon at a depth of ca. 4.5 cm., but varying from almost superficial to about 10 cm. deep. Along Lake Michigan, rhizomes were found buried to depths of nearly 1 m. due to accumulations of washing and drifting sand.

In the Mackinac Straits region where it is unusually abundant (see below), *Comandra* may occur as one of the first invaders of loose sand near the shore. It is common in the semi-open, forested dunes, and also occurs in the successionally later communities up to and including dense woods dominated by medium-sized aspen (ca. 25 cm. DHB), probably persisting through the herb to the herb-shrub, and finally the early tree stages. In this same area of Michigan, Gates (1930) classified *Comandra* as a "secondary species" (as opposed to "dominant," "relic," and "invading").

## Dominance, Frequency, and Possible Weediness

*Comandra* rarely becomes a dominant member of the herb stratum since the comparatively short and slender shoots are quite widely spaced. An exceptional density was recorded at the margin of an abandoned field bordered by several large trees in Emmet County, Michigan. Here, forming a stand ca. 7 × 12 m., it tended to be the dominant species, with a maximum density of 19 stems per square decimeter. This plant also covers fairly extensive areas in this region. Where it is common on forested dunes at Sturgeon Bay (also Emmet County), *Comandra* occurred in 59 of the 100 one-square-meter quadrats which were laid out five meters apart along compass lines.

When searching for stands of *Comandra*, remnants of the original vegetation, or approximations of it, were most rewarding. *Comandra* is slow to invade disturbed sites, unless the site is adjacent to an established *Comandra* stand, and then it does so by rhizomes. It cannot be called weedy from the standpoint of being an aggressive invader. If it were desirable to to control *Comandra* as has been suggested because it is a parasite (Hedgcock, 1915b) and a host for a pine rust (Hedgcock, 1915a), some difficulty would likely be encountered. As long as the extensive rhizomes remain in the soil intact, or even broken, it is likely that the plant would persist (see "Vegetative Reproduction"). Futhermore, fruits may lie in the soil for at least a few years and still be viable (see "Germination").

## Relation to Fire

The maintenance of some native vegetation types in which *Comandra* occurs, e.g., prairies and oak openings, is considered to be related to fire, particularly in the prairie-forest ecotone region (Curtis, 1959). Also, in forest areas, fire functions locally in removing the overstory, which as indicated above, appears advantageous to *Comandra*. The direct effect of fire was observed only once in this study. In this instance an early spring grass fire in Minnesota did not appear detrimental to *Comandra*.

## Parasitic Behavior[8, 9]

Parasitism is effected by modifications of the roots known as haustoria which invade the subterranean parts of associated plants. The haustoria develop laterally along the *Comandra* roots, although as was also noted by Woodcock and De Zeeuw (1920), they may appear to be terminal in some cases because root growth beyond the haustorium has been arrested. These conical to hemispherical structures are most often attached to roots, but other host organs such as rhizomes may be also involved. Though highly variable in size, haustoria are commonly 3-4 mm. in diameter on woody hosts and 2 mm. on herbs. On small host organs, haustoria tend to be clasping, sometimes nearly encircling the host, while on larger organs they tend to be bulb-shaped, contacting a proportionately smaller part of the surface of the parasitized organ (Plate 10, G). I have found haustoria attached to roots up to 5.5 cm. in diameter. My observations of the other American subspecies of *Comandra* agree with those reported here for subsp. *umbellata*, as does the information available on subsp. *elegans* (Heinricher, 1924).

Hosts are usually invaded to the outer xylem, but sometimes the haustorium penetrates considerably farther (Plate 10, H). Intimate contact and continuity is established between the xylem of host and parasite. In addition to the physical force of the growing haustorium, penetration appears to be promoted by the digestive action of a secreted substance, which Moss (1926) states is produced by a gland in some cases. A safranin-stainable band delimiting host and parasite tissues seems to be due to the presence of this substance. It would seem desirable to obtain more information on the nature of this secretion.

Anatomically, the haustorium is largely comprised of parenchymatous cells forming two regions: an inner region of small, densely protoplasmic cells which is the center of the supposed secretory action, and which includes the tracheary connection to the host; and an outer region of larger, vacuolate, often partly-collapsed cells. In fully-developed haustoria the cells making up the xylary connection often form two strands when viewed from the plane of cross section of the host organ.

Particularly since *Comandra* produces extensive rhizomes, the possibility of attachments to several hosts is evident. This in fact regularly occurs in nature—a single *Comandra* plant parasitizing separate and often unrelated plants simultaneously. Over 200 species have been determined

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[8] Because the parasite in this case is photosynthetic, it is sometimes referred to as hemi-parasitic.

[9] This subject will be treated in more detail in a separate paper.

to serve as hosts for subsp. *umbellata* in the Great Lakes region alone. The hosts are remarkably diverse taxonomically, representing 61 families that are distributed over 2 phyla,[10] in one of which 3 subphyla, 3 classes, and 2 subclasses are involved. Most common among these are angiosperms and conifers, but attachments may also be formed to various pteridophytes and even to non-vascular plants. Among the hosts most frequently parasitized were both woody plants, e.g., *Populus* and *Gaylussacia*, and herbs such as *Aster*. Conversely, haustoria were very rare and sometimes non-functional on certain other species.

Self-parasitic attachments to the rhizomes of other individuals of *Comandra* have also been found. Furthermore, connections to other parts of the same plant have been observed. The manner of attachment and penetration does not differ significantly from that involving other species. This study apparently extends the known host range considerably, since only angiosperm hosts had been previously reported (e.g. by Harrington, 1945; Hedgcock, 1915a).

It has frequently been asked whether *Comandra* is always parasitic. Hundreds of clones covering many substrate conditions have been examined for parasitism in this study, and every clone bore evidence for parasitism in the form of haustorial connections. Even if an apparently isolated *Comandra* plant was found, close examination revealed attachments to wide-ranging host roots.

Variation in the relative vigor of *Comandra* appeared correlated to some degree with the amount of parasitism. The less vigorous clones, showing little or no rhizome growth, and often death of some shoots and rhizomes, proved to have few haustoria. Plants with vigorous, often fertile, shoots and rapidly invading rhizomes (see Plate 9, F) always had strong parasitic connections. Additional evidence on the importance of parasitism is supplied by both greenhouse and outdoor grown seedlings planted either individually in separate pots, or in association with other species to serve as hosts. Those without hosts were much less vigorous, yellowish, and failed to develop rhizomes. Many of the cultures without hosts did not survive the second season and those which did were less vigorous than those with hosts. Second year plants with hosts were, in contrast, a healthy green and had spread by rhizomes. (See also "Seedling Development.")

With the exception of the more succulent forms of subsp. *pallida*, the plants commonly wilt when growing in full sun or when collected, even if kept in a vasculum with a segment of rhizome attached. The fact that *Comandra* grows most commonly in comparatively dry sites and displays a preference for porous soils may seem to present a paradox;

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[10] Classification of Tippo (1942).

however, since I have observed by using tracers that water is one of the products obtained from its hosts, parasitism appears to play a very significant role in circumventing this problem.

Occasionally haustoria are found attached to dead plant tissues, ranging from those which are dead but intact to those which are much decayed. Although haustorial invasion has been (infrequently) observed to result in death of that part of the host organ beyond the haustorium, the presence of haustoria of the current season on much-decayed wood indicates that dead tissue is actually sometimes invaded. It has not been ascertained whether such haustoria become functionally equal to those which invade living tissues. If *Comandra* does obtain substances from such material it may also be considered a hemi-saprophyte. Comparable observations are recorded for several Scrophulariaceae, including *Melampyrum lineare* and *Pedicularis canadensis* (Piehl, 1962; 1963) and other Santalaceae, e.g., *Exocarpus* (Fineran, 1963).

*Comandra* thus appears to have a rather broad range of nutritional sources, invading essentially any higher plant with subterranean organs in proximity to its own roots even, in some instances, if the organs be dying, dead, or decayed, and yet is partly autotrophic. According to the usual definitions of parasitism and saprophytism, these two phenomena are separated on whether the substrate is living or dead. The situation in *Comandra* directs attention to how tenuous the distinction between these two modes of heterotrophic nutrition are, and may provide a living example of the continuum which exists between them.

## Pathogens

A rather large number of organisms parasitize or otherwise consume *Comandra*. Among the pathogenic microörganisms, those producing the most conspicuous effects on the plant were several rust fungi occurring on the leaves and rarely elsewhere.

The heteroecious comandra-pine blister rust fungus, *Cronartium comandrae* Pk., tends to produce the most severe infections, and I found it widespread in the Great Lakes States. It was particularly abundant in the Mackinac Straits region, Michigan, where the following observations were made. Uredial stages only were present in mid-July, but later both uredial and telial stages occurred on a single leaf. By August essentially all lower surfaces of the leaves in heavily infected plants took on a golden cast from the rust infection, which because of the projecting telial columns gave the leaves a peculiar thick and roughened aspect. Pines (*Pinus resinosa*) are common nearby, but show very little damage from this rust. In spite of the high incidence of infection at some sites it appears that this pathogen poses little threat to *Comandra* populations. In 1958 three one-square-meter quadrats were marked by stakes in both open and open-forest sites of high infestation at the University of Michigan Biological Station, Cheboygan County, Michigan. The infestation appeared largely due to the above fungus, but it is possible that other rusts producing a similar effect were involved also. The quadrats were sampled for macroscopic evidence of infestation and were resampled two years later with the results shown in Table 1.

TABLE 1. *Incidence of rust infection.*

| Date | Shoots infected | | | Shoots uninfected | | | Total % infected |
|---|---|---|---|---|---|---|---|
| | Quadrats | | | Quadrats | | | |
| | I | II | III | I | II | III | |
| 17 August 1958 | 107 | 95 | 46 | 1 | 0 | 2 | ca. 99 |
| 16 August 1960 | 70 | 94 | 55 | 0 | 0 | 0 | 100 |

Another rust, *Puccinia andropogonis* Schw., occurred on the leaves at several localities. Arthur (1934) lists both of the above fungi as occurring on *Comandra*, but gives no report of *P. andropogonis* from Michigan. He reports, however, *P. comandrae* Pk. from Michigan, which I have not found there, but have collected several times in California on subsp. *californica*. I also found an imperfect fungus, *Cercospora comandrae* Ell. and Dearn., on the leaves, and suspect it of causing a reddening of the lamina, particularly of small, unthrifty shoots. All of the above are listed as *Comandra*-infecting by Seymour (1929); in addition, he reports *Tuberculina persicina* (Ditm. ex Fr.) Sacc. Seymour lists *Phoma exigua* Desm. for subsp. *pallida* but not for other members of the genus. The data available are much too meagre to determine if a degree of rust-host specificity exists that might be an aid in the taxonomy of *Comandra* such as Savile (1954) has described for *Carex*.

In the course of this study, the larvae of several Lepidoptera were found feeding on the flower buds and foliage in the spring, causing a characteristic deformation of the stem tops. I have collected and cultured the larvae, and the adults have been identified by Dr. Annette Braun as three moths: *Archips purpurana* Clemens, *Sparganothis reticulatana* Clemens, and *Epermenia bidentata* Braun. The small orange larvae of the latter were the most common and were found only on *Comandra*, which raised the question of whether it might be specific for this plant. This question has since been answered affirmatively (Braun, personal communication). In two stands which I sampled near Ann Arbor, 54 and 22 per cent, respectively, out of a total of 410 plants examined showed evidence of larval activity. Since fertile stems appear to be more frequently invaded than sterile, and because nearly all buds of an inflorescence are consumed, this can significantly diminish sexual reproduction. Larval activity appeared more frequent in the open than near trees.

The terminal part of the stem is disfigured occasionally by cone-like galls. Upon dissection the galls were found to contain larvae, but the causal organism has not been identified. Such infected shoots were sterile. Also, leaves from shaded sites were sometimes infected by leaf miners (Agromyzidae).

Many stems of a stand in Emmet County, Michigan were infected by a scale insect which produced a swelling and often caused the stem to diverge from the vertical at a slight angle, above the point of infection. Some basal branching due to growth of lateral buds which normally do not expand until the following season was also associated with this infection. The insect was identified as *Asterolecanium arabidis* Signoret by Dr. Louise Russell who stated it was the first reported on *Comandra* and the first collection of the insect from the north-central United States.

The persistent floral parts and the upper part of the exocarp are rather frequently removed from full-sized fruits still on the plant. The organism(s) causing this damage occurs over much of the American range of *Comandra*, and although the identity of the organism is unknown, it appears to be the work of an insect.

The younger roots of one clone had proliferated greatly and were locally swollen to form numerous nodular structures, which when dissected were found to contain nematodes (*Meloidogyne*). Goodey (1933) does not list nematodes for any member of the Santalales. Such enlargements of the roots were sometimes difficult to distinguish externally from the young haustoria also present. Once the haustoria have contacted a host organ, their characteristic appearance helps to differentiate them even when detached from the host.

Two kinds of Cecidomyiidae larvae have been identified from *Comandra* leaves, as were aphids (Aphididae). The webs of spider egg masses were observed to cause inrolling of single leaves occasionally.

## Economic Relations

Several species of wildlife utilize *Comandra*. About the University of Michigan Biological Station, students have reported that young fruits are taken by gophers, *Citellus tridecimlineatus tridecimlineatus* Mitchill.

and Dr. F. W. Test reports finding mature fruits in cheek pouches of that species. In one instance I located an underground rodent cache containing many fruits and empty pericarps, which strengthened my suspicion that other rodents such as eastern chipmunks (*Tamias*) and mice (e.g., *Peromyscus*) at times consume the fruits. I have also found evidence of browsing by deer, *Odocoileus virginianus borealis* Miller. The fruits have been described as "much liked by birds and rodents" (Hedgcock, 1915a); however, Martin *et alii* (1951) do not mention *Comandra* as a wildlife food. Records of the U. S. Fish and Wildlife Service (Patuxent Research Center) show one entry for *Comandra*, that being fruits from bobwhite (*Colinus virginianus* (L.)) stomachs from northern Florida. As *Comandra* does not occur in Florida or southern Georgia, and as this bird is non-migratory, this record must be questioned. That fruits may be eaten by birds is suggested by the statement that fruits of *Santalum* spp., which are generally larger than those of *Comandra*, are eaten by pigeons, thrushes, and other birds (Ridley, 1930). An additional economic role is that of providing cover for smaller forms of wildlife.

Seeds of the western subspecies of *Comandra* are said to have been eaten by Indians (Yanovsky, 1936). The seeds of subsp. *umbellata* are considered edible and are described as having a sweet taste (Fernald *et alii*, 1958). A better description of the taste may be nut-like since the seeds are somewhat oily.

Grazing has undoubtedly had some influence on the present abundance of *Comandra*. In the west, it (probably subsp. *pallida*) was rated as slightly or not at all grazed (Clarke, 1930; Hanson *et alii*, 1931), and as a "fairly good forage species" (Mueggler, 1950). Both Mueggler's work and that of Dix (1959) in Wisconsin indicate that its growth and development were hampered by grazing. I have noted in each of the American subspecies that plants grazed or mowed early in the season respond by producing lateral shoots from the axillary buds. Swine are reported to consume the fruits (Piper, 1920).

Since *Comandra* often grows in sterile, easily washed soil, it is of some economic significance in controlling erosion. Also, as a member of a much-destroyed major vegetation type, the prairie, it together with its natural associates serve as remnants of scientific, historical, and aesthetic importance.

## Developmental History

PHENOLOGY. Although flower-bud formation is said to occur the same season the flowers open (Randall, 1952), I have found they are actually formed the previous season. As the young shoot expands, its apex is enveloped by the large incurved leaves situated at what will become approximately the middle of the fully elongated axis. This gives the tip a somewhat dilated outline, particularly in the case of fertile shoots because of the flower buds present (Plate 10, C). Meiosis occurs while the axis is still elongating and the inflorescence is yet unexpanded. The bracteoles and scale-like leaves at the lower part of the stem fall at about the time of flowering.

*Flowering.* Flowering is normally vernal, but an occasional shaded or late-developing plant may still be flowering in summer. Rarely, shoots which develop from basal lateral buds formed earlier in the season produce flowers, the production of which may be related to late summer rains and perhaps other factors. The individual flowers are open for about 2 days, remaining open day and night. The perianths then usually close somewhat, and may close completely during the later development of the fruit (less so in subsp. *pallida*). Partly closed flowers are easily mistaken for fully open flowers, and have been illustrated as such (e.g., in Gleason, p. 59, 1952); closed perianths at the young fruit stage may be mistaken for buds by persons not familiar with the plants. This makes the determination of the time of flowering from herbarium specimens difficult, and some of the flowering dates given in manuals may be inaccurate on this account. The dates for flowering and other phenological events as determined by observations in natural habitats at Ann Arbor, Michigan, are summarized in Table 2.

*Pollination.* Presentation of pollen occurs at the time of or just before flower opening. The sticky pollen is immediately suggestive of entomophily. At several sites in both northern and southern Michigan, the insect visitors which were actually seen probing the flowers were captured, and later sent to entomologists for identification. The visitors comprise a great variety of bees, wasps, and flies, as well as fewer ants, beetles, and Lepidoptera, all of which are listed in Table 3 along with the records of Robertson (1929). When the mouth parts of a few of the Diptera were examined some *Comandra* pollen was found, although nectar appeared to be the primary substance sought. A generally similar diversity of visitors is given for *Thesium* spp. (Knuth, 1909), but data seem to be lacking for other Santalaceae.

Such a variety of visitors probably effects considerable cross-pollination, although the insects may also be responsible for some self-pollination as well, particularly in view of the strongly clonal aspect of *Comandra*. Self-compatibility is indicated by the production of fully-formed fruits

TABLE 2. *Phenology of* **Comandra.** *Compiled from data collected in the vicinity of Ann Arbor, Michigan, 1958-1961. A dotted line indicates an indefinite continuation of the total duration of the event.*

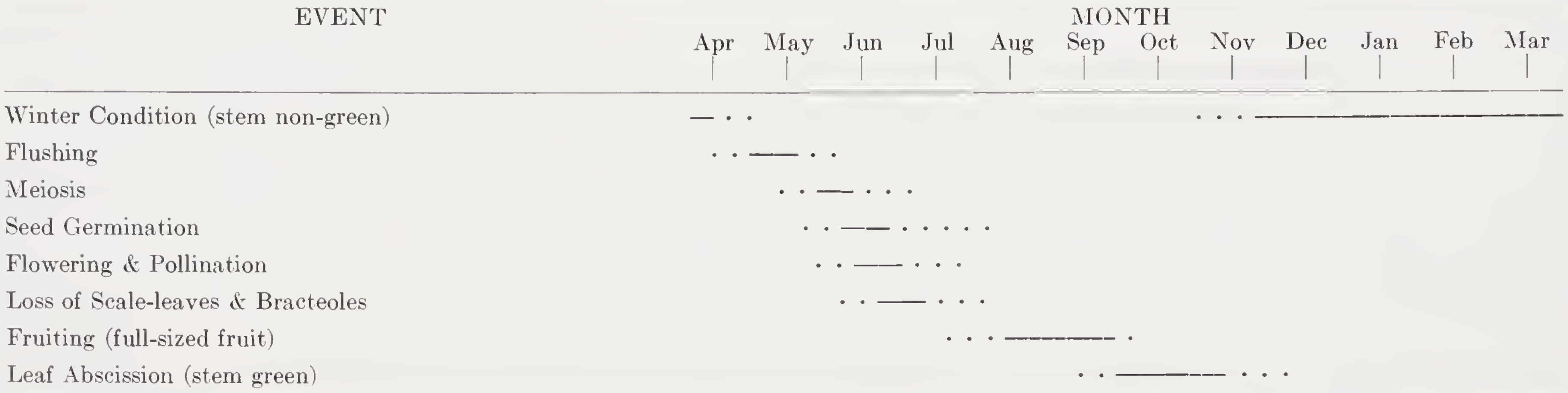

TABLE 3. *Flower visitors of* **Comandra umbellata** *subsp.* **umbellata.** *Unmarked entries are from my collections in Michigan; those with a single asterisk are from Robertson (1929), and those with double asterisks from both my observations and Robertson's.*

Hymenoptera
  *Andrena mariae* Robertson*
  *A. miserabilis* Cresson*
  *A. sayi* Robertson*
  *Andrena* sp.
  *Apis mellifera* L.**
  *Bombus americanorum* (Fabricius)
  *Bracon* sp.
  *Ceratina calcarata* Robertson
  *C. dupla* Say
  *Formica* sp.
  *Halictus rubicundus* (Christ)*
  *Harmolita (Tetramesa)* sp.
  *Lasioglossum albipenne* (Robertson)*
  *L. tegulare* (Robertson)*
  *L. versatum* (Robertson)*
  *Leptothorax* sp.
  *Nomada superba* Cresson*
  *Nomada* sp.
  *Osmia pumila* Cresson*
  *Osmia* sp.
  *Prenolepis imparis* (Say)
  *Sphecodes dichrous* Smith*
  *Tapinoma sessile* (Say)
  *Tetralonia dilecta* (Cresson)*

Diptera
  *Bithoracochieta leucoprocta* (Wied.)*
    (syn. *Coenosia antica*)
  *Bombylius varius* Fabricius
  *Bufolucilia silvarum* (Mg.)*
  *Calliphora vicina* R. D.*
    (syn. *C. erythrocephala*)
  *C. vomitoria* (L.)*
  *Cryptolucilia* sp.*
  *Cynomyopsis cadaverina* (R. D.)*
  *Eristalis arbustorum* (L.)
  *E. dimidiatus* Wied.*
  *Eucalliphora lilaea* (Walker)*
    (syn. *Lucilia latifrons*)
  *Gonia capitata* (DeGeer)*
  *Graphomyia maculata* (Scopoli)*
    (syn. *G. americana*)
  *Helophilus latifrons* Loew*
  *Hylemya platura* (Mg.)*
    (syn. *Delia platura*)
  *Limnophora marona* (Walker)*
  *Liriomyza* sp.
  *Lucilia illustris* (Mg.)*
  *Odontomyia pubescens* Day*
  *Peleteria anaxias* (Walker)
  *P. taxensis* Curran
    (syn. *P. robusta?*)
  *Phaenicia sericata* (Mg.)*
  *Pherbellia grisescens* (Mg.)*
    (syn. *Sciomyza humilis*)
  *Phormia regina* (Mg.)*
  *Sarcophaga cimbicis* Tns.*
    (syn. *Boettcheria cimbicis*)
  *S. sinuata* Meigen*
  *Siphona geniculata* (DeGeer)
    (syn. *S. cristata*)
  *Sphaerophoria cylindrica* (Say)*
  *Stratiomys normula* Loew*
  *Syritta pipiens* (L.)**
  *Tachina robusta**
    (syn. *Peleteria robusta?*)
  *Tropidia mamillata* Loew*
  *Volucella vesicularia* Curran*

Lepidoptera
  *Eurytides marcellus* (Cramer)*
  *Strymon melinus* (Hübner)*

Coleoptera
  *Cantharus bilineatus* Say*
  *Coleomegilla maculata* DeGeer*
  *Meligethes nigrescens* Stephens

on a part of a clone of subsp. *umbellata* transplanted to a glasshouse. However, due to the difficulty of culturing *Comandra*, sufficient data have not been obtained on this subject, although more studies would be desirable.

*Post-flowering Changes.* Soon after the flower closes somewhat, the gynoecium begins to enlarge noticeably as the development of endosperm and embryo progresses. The formerly white sepals frequently develop pigments, often becoming somewhat green and, less frequently, reddish, or both (they were green previously in early bud stages). A multiple function is thus suggested for the sepals, including the attraction of pollinators at anthesis, photosynthetic activity, and, perhaps, facilitating dispersal, since the eastern chipmunk had been observed to take full-sized fruits from the plant and eat only the calyx and attached parts from the top of the fruit. Perianth color changes apparently occur in other genera of the family, e.g., *Santalum*. The closed sepals may dry at the tips rather early, and eventually dry throughout. A fungus mycelium often develops about the pollen within the recently closed flowers, the hardly macroscopic hyphae sometimes filling the flower. A fungus also develops from the outer pericarp when dried, mature fruits are moistened, which may be the same fungus in the flowers. Whether it plays a role in germination and thus may be symbiotic is unknown.

*Fruit Production and Dispersal.* As has been reported previously (Holm, 1924), a relatively low number of flowers produce fruits. Some spring flowers drop before any enlargement of the gynoecium occurs; it is not known whether this is due to pollination failure or to some other factor. Others drop at various stages of early fruit development. Flowers that develop in summer and autumn are generally caducous. No morphological evidence for unisexuality, which is said to exist in other genera of the family, including closely related *Geocaulon*, has been found, although it appears that the central flowers of the cymule more often produce fruits than the laterals. Rather heavy fruiting occurs occasionally, and a maximum of 29 mature fruits was recorded in Cheboygan County, Michigan for a single shoot in 1960, a year of comparatively high fruit yields. That season 56 fertile shoots examined in that area averaged 3.6 mature fruits per shoot. The idea has been advanced that seed production is high in parasites, particularly complete parasites and those having high host specificity (see Salisbury, 1942). In this connection, the comparatively low fruit production in *Comandra* correlates with its partial parasitism and occurrence on a variety of hosts. Considerable year-to-year variation in flower production is also reported (Fernald, 1926). During a single season considerable variation in the fruit-flower ratio was noted for different stands in a given region.

The fruits tend to change from green to yellow-green just before falling, and become brownish soon after. The majority of the fruits fall in August, with fewer falling in July and September. The nearly round fruits are listed by Butler (1954) as "heavy" (above $20 \times 10^{-3}$g.) and as having no special means of dispersal. Exceptions to the above data on color and size are found especially in subsp. *pallida* and subsp. *californica*. Where there is litter or dense surface vegetation, the smooth fruits usually remain near the parent plant and eventually are worked downward toward the soil. However, where there is little other vegetation, fruits may roll considerable distances. Most fruits sink after being in water a short time; thus water appears to be a rather limited means of dispersal. Animal dispersal is likely of importance as fruits are taken by some rodents and other animals as mentioned above.

*Fall and Winter Aspect.* The foliage may become yellowish in August, and some clones show considerable autumnal coloration, ranging from yellows to yellow-reds and purples; others remain green. However, the most common fall color varies from yellow-green to yellow or brown. The abscission of foliage leaves appears to occur acropetally and rather gradually. The lower foliage leaves of a given plant may fall in August, while the majority drop in September, as is characteristic of many forbs which grow with *Comandra.* The common late-autumn aspect is simply the green stem axis with its tiny leaf scars and basal axillary buds, plus a few, dry, shriveled leaves especially at the tips of sterile shoots. By winter the axis has become brown and dry either down to the persistent base or completely to the ground. The inconspicuous dead axis often remains upright and, although it resembles the stalks of numerous other plants, it can be identified even in midwinter upon close examination.

GERMINATION. The germination studies were conducted at the University of Michigan Botanical Gardens in Ann Arbor from 1959-1961.[11] All fruits used were collected in the field by gathering them directly from the plants or by retrieving newly-fallen fruits from the soil surface. They were air-dried and, if stored, were kept at room temperature until planted. All were planted at a depth of 1-2 cm., although some soil was often washed away during the extended period before germination took place.

Germination was first attempted using subsp. *umbellata* fruits from the Mackinac Straits region, Michigan, which were planted in a glasshouse with the following variables: soils ranging from sand to rich loam and peat, acid pre-treatment (and a control), and several germination temperatures (from about 40-75° F). None of the fruits germinated, however. These results, plus a brief statement that dormancy may last 2 years, and that it is broken by exposure to freezing (Hedgcock, 1915b), prompted me to use outdoor stratification the following winter. (Artificial refrigeration seemed less successful; however, further study is needed.)

During the second winter (1959-60) a few plantings were brought indoors periodically. In February the first seedlings appeared (plantings of

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[11] Weather Bureau records for Ann Arbor based on a recent 30 year period show freezing temperatures from November through April, and the following winter mean daily minima and maxima respectively: December 22.8 and 35.5, January 18.9 and 32.8, and February 19.2 and 34.3 (degrees Fahrenheit).

7 March 1959). Other plantings of the previous winter also produced seedlings when moved indoors during subsequent weeks. In the light of this direct evidence that stratification was important for germination, more fruits were planted on February 22nd, and were immediately placed outdoors. However, none of these fruits germinated during the following growing season, suggesting that stratification subsequent to this date was insufficient. These second plantings were again placed outdoors in the fall of 1960 and were taken indoors in late February 1961, whereafter some fruits germinated.

Fruits were again collected in the Mackinac Straits region in 1960, and were immediately placed outdoors for stratification. In mid-March a few of these plantings were brought indoors; others remained outdoors into the 1960 growing season. A low percentage of those brought indoors germinated, showing that the first-year cold period up to this time is sufficient; a similar number of those kept outdoors also germinated.

The minimum duration of outdoor stratification required was not determined. However, although stratification subsequent to February 22nd was generally insufficient, that occurring over the winter prior to that date was sufficient. Germination was greater the second year after planting than the first in some cases, ranging from 0-10.7% (% of total seeds sown) the first year and from 3.7-54.5% the second year. Germination occurred at a much reduced rate the third year; whether it continues in subsequent years is not known, although tests are underway. A rather low percentage of germination (ca. 10 to 20%) both the first and second year is reported for subsp. *elegans* (Heinricher, 1924). For the related genus *Thesium*, germination is recorded from the first through the fourth years (Heinricher, 1924). I have planted fruits both among potential hosts and alone, but no significant difference in percent germination was noted. Host roots do not appear to stimulate germination as they do for some scrophulariaceous parasites (cf. Saunders, 1926).

The time required for germination (here meaning appearance of the epicotyl above ground) of plantings taken indoors during the winter was commonly from 8 to 9 days; however, a few continued to germinate throughout the summer. A planting of 1958 fruits made in the fall of 1960 germinated well the following spring. This suggests that storage of the dried fruits for over a year at room temperature does not appreciably affect germination, although Heinricher (1924) believed that drying hindered germination in subsp. *elegans*.

Fruits of subspecies *pallida* and *californica* were collected in Wyoming, New Mexico, Arizona, and California in 1959. These fruits have a much thicker and more sclerified mesocarp than those of the eastern subspecies, and several treatments were given them to determine whether I could influence germination by modifying the pericarp. The treatments included (1) removal of the leathery epicarp (after soaking), (2) removal of the epicarp and the hard mesocarp, and (3) scarification of the entire pericarp with a file to produce a small opening. All plantings were made during the fall and winter of 1959-60. Although based on small numbers of fruits the results show that removal of the hard mesocarp increased germination the first year, and also promoted germination without exposure to freezing. Neither removal of the epicarp nor scarification appeared to influence germination. Although the control plantings, which were kept indoors, did not germinate, additional plantings kept outdoors germinated both the first and second years. The Wyoming material appeared to require more cold treatment than did those from the Southwest, indicating adaptation to the climatic conditions of the respective regions. The above results suggest that chemical changes, e.g., the removal of inhibitors, which are necessary for germination occur when the entire mesocarp is removed.

SEEDLING DEVELOPMENT. Germination is of the hypogaeous type, the linear-lanceolate cotyledons (except for the very base) remaining within the fruit and functioning as absorbing organs that supply the seedling with food from the endosperm. Seeds which germinate at the surface, rather than underground behave similarly; however, the exposed bases of the cotyledons may become photosynthetic. The pericarp often cracks during germination. In some cases it may already be softened and partly decayed. The hypocotyl, the first structure to appear, emerges from the distal end of the fruit (Plate 9, C). It lengthens to ca. 4 cm. before the epicotyl appears; thus, in the strict sense, germination may actually occur a few days before it is evident above the soil. The epicotyl is characteristically arched as it breaks through the soil, and upon emerging usually becomes green, but anthocyanin pigments may mask all chlorophyll in some cases. Leaves of the newly exposed shoot are linear in shape and are closely appressed to the stem. They soon diverge as the stem becomes erect and elongates. Growth of the shoot is quite rapid in the early stages as compared to a vegetatively-produced shoot of similar stature. The primary root has but a moderate number of root hairs, and in my material lengthened as much as 5 cm. before it produced secondary roots. Many seedlings have been cultured for 2 years and a few for 4 years; none have flowered as yet, although optimum growth conditions have not prevailed.

*Seedling Parasitism.* Haustoria are evident 2 weeks after germination, and attachments are soon formed if host roots are available. In the absence of host roots, haustoria are also formed, as has been reported by Barber (1904) for *Santalum*. A few haustoria are produced on the primary root, but the majority develop on lateral roots.

Individual seedlings from a single collection of fruits were transplanted into 2-inch pots of sandy loam devoid of foreign roots, while control specimens were left growing with other *Comandra* seedlings and plants of other species. At 8-10 weeks the following differences in general appearance were noted: Those with associated plants were green and had begun vegetative reproduction by rhizomes; those grown separately were shorter, yellowish, had lost some leaves, and had not in any case produced rhizomes. Parasitism thus becomes important soon after the nutrition supplied by the seed diminishes.

A few young plants retained in 3-inch pots with only small volunteer plants as hosts are still alive after 4 years, but are even smaller than seedlings and have very depauperate (but not potbound) root systems. This and observations of vigorous growth of comparable rhizome-bearing plants in flats suggest that often a shift in the major area of parasitism from the primary to adventitious roots with the development of rhizomes is likewise a significant step in the establishment of the young plant. Photosynthetic surface is, of course, also added with rhizome development.

*Rhizome Development.* The first rhizome development takes place at an age of about 8 weeks. The rhizome is initiated in the transition or cotyledon region of the root-stem axis, and at this stage tends to be shallow, sometimes becoming partly exposed in culture. Growth below the surface often occurs for 3-6 cm. before a new, sterile shoot is formed from the rhizome tip. Ramification of the rhizomes subsequently produces the characteristic clonal colonies.

*Seedlings in Nature.* Although *Comandra* was observed in the field during the growing seasons of 1956 and 1957, and studied intensively in 1958 and 1959, seedlings were never found. After they were obtained in culture during the winter of 1959-60, a definite effort was again made to find them in nature in the summer of 1960. Several visits to stands in the Ann Arbor area during the spring failed to give results. In July, the Mackinac Straits region was revisited, a site found in 1958 on the Lake Michigan shore at Sturgeon Bay, Emmet County, Michigan, having been selected for the initial search. There the plant grows on the lee side of, and up to, the crest of the sandy berm formed by wave and wind action (Plate 12, A), and it was reasoned that the fruits would roll onto the non-vegetated beach sand (lakeward) so that seedlings, if present, would be conspicuous. The lake level was higher than in recent seasons, keeping more of the sand moist. The hypothesis proved correct, and a few seedlings were found in the very area expected. Subsequently, seedlings were found in an aspen woods, where most of the seeds had germinated in or just below the duff, their roots extending down into the much humified soil. At this site some were attached to hosts; others, generally less vigorous, were not. Observations of seedlings both in nature and in cultures suggest they are rather sensitive to drought. No fungus-caused mortality was noted.

A major factor in my failure to locate seedlings earlier was the very close resemblance between seedlings, with their hypogaeous germination, and the smaller vegetatively produced sterile shoots. Differentiation between them is generally uncertain until they are excavated, when the primary root system, lack of rhizome, and remains of the pericarp of the germinated fruit identify a seedling. However, after locating the first seedlings, many other sites were examined for them, but few were found. This suggests that the number of seedlings present at any one time is usually quite small.

VEGETATIVE REPRODUCTION. *Clone Formation by Rhizomes.* The primary means of vegetative reproduction is by branching, horizontal rhizomes (Plate 9, F). Shoots (''ramets'') are usually produced laterally, but in young plants particularly, one or a few vegetative shoots may occasionally be produced from an upturned rhizome tip. The rhizomes may extend considerable distances without producing shoots; thus, a space of several decimeters barren of shoots between what appear to be two stands does not necessarily mean they are two clones. In old clones the shoots tend to be rather widely and evenly spaced, resulting in loose colonies which may not be recognized as clonal. Large, generally continuous stands occupying some 75 sq. m. or more may have developed vegetatively from a single clone. A few large clones may give the false impression that *Comandra* is common unless a sufficiently large area is examined. Separate colonies are established within an old clone with death and breakage of rhizomes, and new clones may be formed through seeding. The limits of individual clones are often very difficult to determine since the morphological differences between them may be rather subtle and considerable variation occurs within individual clones. In young, vigorous clones which are spacially separated from other clones, one may detect a gradual decrease in shoot height from the center of the clone outward, producing the low parabolic aspect which characterizes some arborescent clonal plants.

A clone excavated on a semi-open, sandy hill in Cheboygan County, Michigan, was carefully mapped to show the root-rhizome system including haustorial connections, and all aerial stems (Plate 11). The major rhizomes tended to be centered around a few haustoria on a single *Populus grandidentata* root about 4 cm. in diameter; no other haustorial connections were found. The shoots were sterile and weak-looking; some of the rhizomes were dead and decayed. Few, if any, roots with young, non-suberized tips were present. There was little or no invasion of the adjoining area and previous invasions were evident only as dead remains of rhizomes, all of which suggest that this was a senile clone.

A small, apparently young, clone excavated the same month (July 1958) was generally elliptical in outline and measured 12.6 × 10.5 dm. It was situated at the open margin of a gravel road and had produced 50 shoots, many of them fertile, and had 20 invading rhizomes around its periphery. Several of the rhizomes had produced growth increments of ca. 10 cm. that season. (In September, elsewhere, I have found maximum increments of from 13 to 29 cm.) In contrast with the clone described in the previous paragraph, this one had many young roots; it also had several haustorial connections to grasses and probably other plants.

An attempt was made to determine the age and rate of spread of clones by means other than the length of the rhizome increments of the current season. (After becoming suberized, individual increments can no longer be detected.) Annual growth layers are poorly or not at all differentiated into spring and summer wood in subsp. *umbellata*. However some degree of differentiation occurs in the periderm, although the transient nature of this tissue may make its use rather limited.

*Experimental Rhizome Breakage.* The possible significance of rhizome fragmentation as a means of vegetative reproduction was tested experimentally. Cultures were made by planting bare rhizomes (and whatever roots remained attached), cut most often to lengths of about 50 cm. Rhizomes taken indoors periodically during the winter at Ann Arbor, Michigan, indicated that dormancy is broken by December 13, and further study may show it can be broken even earlier. Shoots rising from these segments were usually frail and yellowed, and they often died back rather soon. Occasionally flower buds were initiated but these sometimes aborted early in development. Growth appeared to be largely dependent upon stored food in the rhizome, but as roots were formed which eventually effected parasitic connections to associated plants, *Comandra* became more vigorous, and some strong fertile cultures have developed from this type of propagation. Six months after planting, one 20-cm. segment had numerous small connections to a cottonwood seedling which developed in the culture. Transferring segments of rhizomes along with the surrounding sod into flats, thus maintaining haustorial connections, gave better results.

*Aerial Stem Bases.* Another, much less effective case of what might be considered vegetative propagation involves the persistent lower portion of aerial stems from which lateral shoots arise and produce a somewhat bushy, suffrutescent aspect. In some populations of subsp. *umbellata* in Michigan this growth form appeared to be more common in situations where the base of the plant was protected; however, suffrutescence is a well-fixed character in subspecies *californica* and *elegans*. An exceptional type of persistent base involves decumbent shoots (often with large, somewhat two-ranked leaves). The decumbent shoots do not form roots at the nodes, however. As many as 14 shoots have been recorded from such caudices which tend to be proportionately longer than those of erect specimens. The decumbent shoots have been observed previously by Ward (1881) who described them as ''runners or prostrate shoots,'' and by Hill (1884) who described such material as a new variety. In Hill's material, basal, lateral shoots were formed the same season as the initial, decumbent stem. I have found this rarely and believe its formation is dependent on the stem becoming decumbent early in the season, disrupting the usual apical dominance, and resulting in the expansion of basal, axillary buds. Persistent stem bases are not normally found in subsp. *pallida*.

TOTAL REPRODUCTION. It appears that *Comandra* has achieved a reproductive balance between vegetative and sexual reproduction, each contributing to the survival of the species. Since the sexual reproductive capacity is rather low initially, vegetative reproduction seems of much importance in bolstering total reproduction. I believe vegetative reproduction is of particular importance to the species on a local and short-term basis. It enables the plant to persist or invade sites unfavorable for sexual reproduction because of failure in seed production or the inability of seedlings to survive. Vegetative reproduction has been observed in the complete shade[12] of early forest communities, and under such conditions, stands may be totally sterile, yet they appear to persist for years. Such persistence may be advantageous to the species in the event of local clearing of the forest, as the plants would then probably resume sexual reproduction. In addition to its role in the survival of unfavorable periods, vegetative reproduction is important as a means of building up nutritional reserves for sexual reproduction.

Sexual reproduction is also important in carrying the species over un-

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[12] The light intensity in an aspen stand where *Comandra* grew was recorded with a photometer on a July day as 1.3% of full sunlight.

favorable periods, since the hard-walled fruits appear capable of retaining their viability for rather extended periods. Although important in local propagation, sexual reproduction is probably of greatest importance in more distant dispersal. Its major role in the total propagation picture appears to be in migration, and, of course, in providing new genetic combinations for previously unoccupied or gradually changing environments.

## FAMILIAL AND GENERIC RELATIONSHIPS

Relatively little information is available as to the relationships of genera within the Santalaceae. In fact, the family itself has been suggested for revision on the basis of wood anatomy (Metcalfe and Chalk, 1957) and pollen morphology (Erdtman, 1952), and its evolutionary relationships have been variously interpreted. The Santalaceae along with the few other families comprising the Santalales are placed in a relatively low position near the Urticales, Aristolochiales, and Polygonales in the widely-used Englerian system. More recent systems have the Santalales in a more advanced position; for example, according to Lawrence (1951), Hallier places it near the Guttales, while Bessey puts it near the Celastrales, as does Hutchinson (1959). Cronquist (1957) places it close to the Celastrales, also, and mentions a possible direct connection to the Rosales. It has also been placed near the Umbellales (Benson, 1957), and in an advanced position of independent origin along with the Proteales (Wettstein, 1935). As late as 1950, Pulle has retained it along with the Balanophorales in a rather basal position (Lawrence, 1951). Paliwal (1956) has mentioned some similarity in embryological features of the Santalaceae and Rubiaceae.

In difference to the great majority of descriptions, I would be much surprised if the *entire* family is not hemi-parasitic, the majority of its members parasitic on roots, but others displaying a transition to stem parasitism. The strongly stem-parasitic Loranthaceae, conversely, displays transitions to root parasitism. I envision the Santalaceae as very closely related to the Loranthaceae, a view also indicated by Lawrence (1951), who noted it was united with that family by Baillon.

Within the Santalaceae, *Comandra* has been placed in the Osyrideae along with 22 other genera on the basis of ovary position and disc features (Pilger, 1935). However, Van Tieghem (1896), on the basis of its ovules and placentae, placed it in a separate tribe, Comandreae, a division which Ram (1957) and Johri and Bhatnagar (1960) find in agreement with other embryological characters. Present divisions of the family appear unsatisfactory; however, a new arrangement must await more complete studies of additional members. One of the promising characters, in my opinion, concerns germination and the morphology of the seedling, as mentioned below in connection with the segregation of *Geocaulon.*

The nearest relative of *Comandra* is monotypic *Geocaulon.* I agree with Fernald's (1928) segregation of *Comandra livida* as *Geocaulon,* which is differentiated from true *Comandra* by its smoother, more slender, darker rhizome; its fewer-flowered, axillary rather than terminal inflorescence; its (entirely) greenish flowers, short conical style, and floral tube entirely adnate to the ovary; its scarlet, distinctly fleshy fruit; and by its more boreal distribution. Also, it was discovered in the present study that the shoot of the *Geocaulon* seedling elongates only a short distance (often just above the soil) the first season, while that of *Comandra* is often about 1 dm. tall and displays several expanded leaves. Marie-Victorin (1935), Abrams (1940), Gleason and Cronquist (1963), and C. L. Hitchcock *et al.* (Vascular Plants of the Pacific Northwest, in ms.) are among those who do not recognize the separation of this genus from *Comandra. Comandra* is also rather similar to monotypic *Nestronia* (Gray, 1846; Fernald, 1928), a localized shrub of the piedmont area of the southeastern United States. I have made field observations of *Nestronia* and the only other North American Santalaceae, *Pyrularia* and *Buckleya,* which are also shrubs and occur in the mountains and foothills of the southern and central Appalachians. Both *Pyrularia* and *Buckleya* exist in America as single isolated species of genera that have other members in Asia. The first, *Pyrularia pubera* Michx., which has usually pentamerous flowers, alternate leaves, and rounded fruits, bears considerable resemblance to *Comandra. Buckleya distichophylla* Torr., on the other hand, differs considerably with its tetramerous, conspicuously unisexual flowers, opposite leaves, and distinctive elongate fruits.

Smith and Smith (1942b), on the basis of floral anatomy, consider *Comandra* as belonging among the more advanced forms of the Santalaceae in a series beginning with *Colpoon* and *Nestronia,* and see it as having close affinities with *Geocaulon, Pyrularia,* and *Nanodea.*

Since I have found no record of fossil material of *Comandra* in the literature, this source does not help to clarify generic relationships. Likewise, little seems to be known about the biochemistry of the genus and family, although recent introductory work by Hatt *et al.* (1960) on the acetylenic fatty acids in the family has included *Comandra.*

## CHARACTERS, THEIR VARIABILITY AND TAXONOMIC IMPLICATIONS

Although the variability of populations was studied in the field over a sizeable area of North America as well as in culture, herbarium specimens served as the primary source of data for studies of the genus-wide variation pattern. For the initial sampling purposes North America was divided into geographic areas which conform largely to individual states and provinces with the exception of very small states and those from which little material was available. In the latter cases two or three adjacent states were combined. The Balkan range of *Comandra* was likewise included in the broad variation survey as a single geographic area.

Except for the Balkan States and geographic areas from which fewer specimens were available, 10 specimens were selected for detailed analysis from each of the 43 geographic areas. In the case of the Balkans, 40 specimens were studied in an effort to get a better indication of the variability in this isolated population. Specimens were selected in part on the basis of how many of the characters being studied were available; also, an attempt was made to use specimens from different parts of a given geographic area and to avoid specimens which did not seem comparable due to artificial influences. Characters of two structures, fruits and rhizomes, were less frequently available on the specimens; thus specimens which displayed them were given preference to those which did not. The data for presence-absence characters, e.g., suffrutescence, were quantified by expressing them as percentages. An arbitrary scale was used to evaluate leaf texture and foliage color.

### Morphological Characters

Several of the characters enumerated below have not been previously employed taxonomically in *Comandra*. The characters studied in the greatest detail will be considered first. These are followed by several additional characters, the majority of which supported trends indicated by the first group of characters.

Characters Studied in Detail. *Fertile Stem Height.* This character was measured from the soil surface to the top of the central axis. In this way either flowering or fruiting specimens could be evaluated, since the size of the reproductive structure at the top of the axis did not influence the data (the central axis does not elongate appreciably after flowering). Occasionally some difficulty was encountered in determining soil level from herbarium specimens, but ordinarily the presence of pigments in the outer tissues just above the soil surface, in contrast to their absence below the surface, made this apparent. Decumbent specimens and those in which the stem was broken off above the soil were not used when evaluating this character.

*Leaf Length-width Ratio.* The largest foliage leaves, which are usually found in an approximately median position along the stem axis, were used for this measurement. Measurements were made at the widest portion, and since the leaf is essentially sessile, from the tip to the point of juncture with the stem.

Although there is considerable plasticity in this character even within very limited populations, it does not involve near the diversity displayed by some dicots, since all but rare teratologic leaves conform to the single plan of undivided, entire leaves tapering at the base and apex. Evidence obtained from cultures suggests that this character is varied to some extent by the environment, and that nutrition (including parasitism) can be influential. Also, shoots formed later in the season have smaller, often narrower, leaves than those formed early.

*Leaf Texture.* This character concerns the variation in thickness of the mesophyll and the concomitant differences in the conspicuousness of the veins. ''Texture'' here refers not to actual measured thickness but rather was evaluated under low magnification, and was based upon three criteria in particular: 1) the visible thickness, translucence, and rigidity of the leaf, 2) the protrusion and conspicuousness of the veins on the abaxial leaf surface, and 3) the tendency of the leaf margin to curl. An arbitrary scale expressing eight gradnated character states was used in which extremes ran from a decidedly thin leaf, the margin curling when dried and with strongly protruding veins, to a firm, thick leaf, with no curling at the margin and with deeply immersed and obscure veins (Plate 8, D-F).

*Inflorescence Structure.* With the inflorescence ranging from densely corymbose to loosely paniculate, the best measurement found to express the relative length (or ''looseness'') was the vertical distance between the top of the lowest peduncle and the top of the main axis (Plate 3, Q). Occasionally the lowest peduncle extends above the main axis, so that negative values are possible.

*Sepal Length.* Sepal length was found to be generally proportionate to the length of other floral characters, e.g., floral tube, style, or that of the total flower, and since it could be measured without dissection of the flowers, sepal length was chosen as generally representative of floral parts. Measurements were made under low magnification, and only the free portion of the sepal was included (where fused with the floral tube the sepal continues slightly below this level in a shallow V-shaped extension; see Plate 7, A).

*Fruit Diameter.* Since mature fruits and those in the later stages of development look very much alike, particularly after drying, it was necessary to exercise care in selecting fruits for measurement. Only unbroken fruits in which the mesocarp had sclerified to the extent that they were not flattened in pressing, and in which the exocarp had hardened so that it was not severely bruised when pressed, were considered. Since fruits are frequently lacking from herbarium specimens, ten measurements could not be made from every geographic area, and measurements are entirely lacking from some areas.

*Rhizome Cortical Parenchyma Color.* Although the color of the "cortex" (cf. discussion under "Rhizome") is observable in roots also, the rhizomes, which are larger and more often included on herbarium sheets, were used. However, on many herbarium specimens even the rhizome had been detached from the aerial stem, making it impossible to evaluate this character. As mentioned in the discussion of rhizome anatomy, the phloem rays and parenchyma immediately outside of them are a conspicuous blue macroscopically in living material of subsp. *californica*, subsp. *pallida*, and intergradients between them. In dried material this area varies from light blue to gray and black. The contrasting character state, lacking the "blue" pigment, involves beige or whitish tissues; where the two meet in the Great Plains, an intermediate condition with a brown, rufous or light gray to light blue coloration is found (Plate 8, A-B). The brown or rufous conditions are difficult to differentiate from the darkest expression of the beige character state; however, when herbarium specimens are viewed under low magnification, a difference in textural features which is also characteristic of the blue tissues is noted: It is soft and generally pliable, and when pressure is firmly applied tiny oil droplets appear. Whether there is a direct relation between the oil droplets and the blue color has not been determined. Also numerous lacunae occur in the tissues, while eastern material has few or no lacunae, and though sometimes crumbly, is not oily.

This character was scored on the percentage of specimens with blue or brown rhizomes. Seed cultures of western specimens displayed the blue tissues when grown under essentially the same conditions as eastern material, suggesting a genetic rather than environmental control of the character. Rhizome color, a new character in *Comandra* taxonomy, provided one of the best features for distinguishing western material from that of eastern North America and the Balkan region.

*Suffrutescence.* This character concerns the tendency for the lower part of the aerial stem to be perennating, making the plant somewhat suffrutescent (Plates 13, 14). Some individuals completely lack basal buds that overwinter and develop into shoots the next season; others have from one to several of them. Field observations indicate that both first year stems and stems with perennating bases, i.e., caudices, may occur in a given clone; thus, values for this character can be influenced by what type of stems were collected. However, I believe the large number of specimens used to give the overall trends adjust for this factor so that it distracts very little from the significance of the total picture given by the data. Although it varied rather randomly in the eastern part of the range, this character was found to take on added meaning when the western and Balkan specimens were considered.

*Foliage Color.* The foliage color of herbarium material was considered, although as with many other plants the resultant color is somewhat dependent on how the specimen was prepared. After examining the total color range from gray- and blue-green to green, five arbitrary classes utilizing a sequence of numerical values were established.

ADDITIONAL CHARACTERS. The following characters, though not sampled on the basis of 10 specimens from each geographic area, have either added support to overall trends or have been useful in delimiting one or more taxa in particular. This enumeration of characters is, of course, not meant to be exhaustive, since the number of possible characters available in any detailed study is virtually unlimited.

*Sepal Length:width.* This character was measured in selected parts of the total range after it was discovered that values were unusually low for Balkan specimens, which this character helps to delimit taxonomically. Length was measured as previously outlined under sepal length; the width was measured at the widest portion of the sepal, namely, at its base.

*Flower Shape.* This character proved useful in separating the Balkan subspecies. In that taxon the flowers tend to be campanulate, with the floral tube diverging rather strongly (i.e., dilated) at its point of separation from the ovary. In American material the floral tube above the ovary diverges gradually, and flower shapes range from narrowly funnel-form to rotate or somewhat reflexed (cf. Plate 6).

*Pedicel Length.* Since the pedicels vary in length according to their position in the individual cymules, it was necessary to exercise care in making measurements so that the data were comparable. Data from selected parts of the range indicate that it reinforces the trends shown by other characters.

*Leaf-surface Differentiation.* As indicated earlier, the upper and lower surfaces are distinctly differentiated in material from the Mid-Atlantic States. Besides the whitening of the lower surface as related to the presence of stomata, the less heavily cutinized and less roughened (papillate in herbarium specimens) epidermises and the smaller epidermal (and guard) cells help to distinguish eastern material. Westward, to a lesser extent northward, and in Balkan material, the two surfaces show less contrast. The least contrast occurs in subsp. *pallida* in which the surfaces are essentially undifferentiated (Plate 8, D-F).

*"Neck" of the Fruit.* The "neck" of the fruit is that part of the floral tube above the ovary which appears as a constriction below the dried persistent calyx in some mature fruits. The opposite extreme has the persistent floral parts approximately sessile (Plate 8, H). It has been contended (e.g., by Rydberg, 1932) that the neck is more distinct in specimens from eastern than in those from western North America. My study shows that the neck varies considerably even in a single locality, ranging from quite prolonged to nearly absent. Also, the actual measured length of the neck was found to be greater in some areas of the west than in some places in the east. Although this character was not constant enough to be used to differentiate the American subspecies, it did prove valuable in separating American from Balkan specimens, which (although few fruiting specimens were available) tend to lack the neck entirely.

*Fruit Shape.* Eastern North American and Balkan fruits are subglobose to globose, while in western North America, those of subsp. *pallida*, in particular, tend to be more ovoid (Plate 8, H).

*Pericarp Thickness.* Both the leathery exocarp and the bony mesocarp of fruits of subsp. *pallida* are thicker (exocarp 0.3-0.5 mm. and mesocarp ca. 0.5 mm.) than those of subsp. *umbellata* (ca 0.1 and 0.2 mm., respectively) and those of subsp. *californica*. The thin exocarp of subsp. *umbellata* can scarcely be cut or lifted from the mesocarp after soaking in water, while this can be readily done with the thicker exocarp of subsp. *pallida*. As indicated above, the endocarp is largely lost during the development of the fruit.

*Fruit Color.* The color of the mature fruit ranges from brownish and not glaucous in eastern North America and the Balkans to dark purplish brown and glaucous in western North America. In the western United

States this character is of some help in differentiating subsp. *californica*, with its light brown to brown and often only slightly glaucous fruits, from subsp. *pallida*.

*Fruit Surface.* This character parallels the thickness and color characters just described, and ranges from a mature fruit with a smooth surface (exocarp) which remains hard when moistened (subspecies *umbellata* and *elegans*) to one which is slightly wrinkled longitudinally (Plate 8, H), and which, due in part to its greater thickness, becomes rather leathery when moistened (subsp. *pallida*). These features are generally also apparent in the ovary and floral tube at flowering, though they are not as conspicuous.

*Rhizome Thickness and Surface.* The rhizomes of subsp. *pallida*, and to some extent those of subsp. *californica*, are thicker than those of other subspecies. Unusually thick rhizomes of subsp. *pallida* may be 2.0 cm. and more in diameter (2.6 cm. in *Piehl 631020* from Colo., GH, US[13]). Also, there is a tendency for the outer periderm of the rhizomes, particularly those making up the crowns, to break into short plates with age in subsp. *californica* and to some degree in subsp. *pallida*, in contrast to a periderm in other members which exfoliates (often only slightly) into thinner elongate strips. The formation of plates may be influenced by a drier climate, but uniform culture observations suggest that at least the tendency persists.

*Leaf and Sepal Anatomy.* Among the useful anatomical features is the structure of the mesophyll, particularly when it involves conspicuous aspects like the amount of what appears to be tannin (Plates 1, E-G; 2, D-E) which is greatest in subsp. *pallida*, where an exudate has also been noted on the flowers and bracteoles in rare instances (e.g., cf. *Zirney 13* (OSC)). The details of vascular patterns, including those of the rhizome scales, afford helpful characters, particularly in differentiating specimens of western North America from those of eastern North America and the Balkans (Plate 5).

*Pollen Diameter.* The pollen of subsp. *pallida* tends to have a greater (equatorial) diameter than that of the other subspecies ($\bar{x} = 26.6\ \mu$ vs. $\bar{x} = 21.9\ \mu$). However, further study of this character is needed.

## Variation Patterns

The genus-wide variation of six of the characters studied in detail—height, fruit diameter, leaf length:width, inflorescence structure, leaf

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[13] Herbarium abbreviations are those of Lanjouw and Stafleu (1964).

texture, and sepal length—is summarized pictorially on a map (Fig. 2), where the values are based on the mean for each character in each geographical area. For most of these 6 characters, gentle gradients exist across much of the North American continent; shorter gradients are exhibited by the others. It may well be that if the geographic variation of the additional characters was examined more intensively certain of these would display similar gradients.

Such gradual changes in individual characters across a continuous population are referred to as clines (topoclines). Certainly one need be aware of the weakness in studying individual characters by themselves as criteria of taxonomic distinctions. However, by demonstrating the continuous variation in characters, such studies may, as stated by Hardin (1957), help to evaluate the adequacy of particular characteristics as a basis for classification. The usefulness of the cline concept in understanding individual taxa is mentioned by Simpson (1961). Stebbins (1950) who feels that clines are often overlooked, points out that if a cline is relatively uniform over a long distance, and if the extreme types are relatively limited in distribution, a basis for classification does not exist. Conversely, if there is a steep gradient in some areas, and a gentle one in others, the different levels of variation in the character may constitute a basis for classification.

When clines exist in several characters, the positions of the more abrupt increases or steps in the gradient for each character can be compared with one another, particularly when the clines are parallel over long distances. If there is a *coincidence* in the occurrence of steps in several clines in a given area, one's basis for taxonomically distinguishing the segments of the population on either side of the step is considerably strengthened.

In the six characters considered in Fig. 2, the most extensive clines run east and west from the Middle Atlantic States into the Great Basin with the exception of that for inflorescence, which ends in the Great Plains region. In Canada, rather similar clines run from Quebec to British Columbia for all characters except height.

The most prominent north-south clines occur east of the Appalachians from the Mid-Atlantic States to the Maritime Provinces and Quebec for all six characters except height. Farther west similar but less distinct clines occur for most characters from the southern part of the range toward the Great Lakes region. Other clines run in a generally northeast-southwest direction from the Dakotas and Saskatchewan to New Mexico and Arizona for all characters but inflorescence. Short north-south clines are evident in the Pacific Coast region, again involving all characters except inflorescence.

If these clines are considered simultaneously, the steps in the gradients for two or more of them become superimposed in a number of places. One of these, demarcating California, and parts of Washington, Oregon, and Arizona, involves the coincidence of four of the six characters. This exceptional agreement (cf. Hubbell, 1954) in these rather long clines delimits what I am treating as subsp. *californica*. A second general concurrence of steps involves four characters and occurs near the eastern margin of the Great Plains, running from eastern Oklahoma and western Arkansas north and northwestward into the Canadian Provinces. This delimits what I am calling subsp. *pallida* from the eastern subsp. *umbellata* (Fig. 2, 3; Plate 16). The correlations of at least major portions of these steps with large-scale physiographic and climatic changes are obvious; further examination of this with reference to subsp. *californica* follows shortly.

A third zone involves correlation of only two characters and minor agreement of two others. This is the Appalachian region from about the southern extent of the mountain system to Maine, which agrees approximately with Fernald's most recent concepts of the area of demarcation between *C. richardsiana* Fern. and *C. umbellata* (L.) Nutt. (see Deam, 1940). However, in general the amount of change in the gradients in this area is definitely less than that which delimits subsp. *californica* and subsp. *pallida*. One exception is between the North Atlantic States and eastern Canada, where a rather abrupt step exists in four characters. This latter step may be due partly to sampling differences with respect to coastal versus inland localities in the two areas. Also the correlation of the steps for separate characters is less exact in eastern North America than in the far west and the Great Plains region, e.g., some include New York and parts of New England while others exclude them. Because this zone involves less concordant, less definite changes in the clines, it is not felt to represent discontinuities which form a sufficient basis for taxonomic separations even at intraspecific levels. To do so, I feel, would have little meaning from a broader biological viewpoint. Further evidence in support of not recognizing these two elements is given by experimental cultures, in which material from east of the Appalachian Mountains in Maryland and New Jersey ("*C. umbellata*") was found to be essentially indistinguishable from Michigan and Wisconsin material ("*C. richardsiana*") grown under uniform conditions at Ann Arbor, Michigan.

Both of the strong composite steps in the gradients—in the far west and eastern Great Plains—are strengthened appreciably when the three


BALKANS
LEGEND:
height
inflorescence
1
2
3
4
fruit diam.
leaf l/w
SCALE IN MILES
ALBERS EQUAL AREA PROJECTION
DEPARTMENT OF COMMERCE
BUREAU OF THE CENSUS

additional characters studied in detail are considered. The character dealing with rhizome "cortex" color provided a good means of differentiating subsp. *umbellata* (and Balkan plants) from the western taxa. The data on suffrutescence showed a strong demarcation of subsp. *californica* and a less sharp distinction between subsp. *pallida* and subsp. *umbellata*. In eastern North America there is an overall increase in the percentage of suffrutescence north and northeastward, the data exhibiting a cline with the gradient steepest in the eastern St. Lawrence region. The highest values (100%) occur in subsp. *californica*, Balkan plants, and subsp. *umbellata* in the Maritime provinces. The data on foliage color again delineate subspecies *pallida*, *umbellata*, and with some exception in the Arizona portion of its range, subsp. *californica*.

With the overall trends of variation evident, attention was focused on the individual specimens from areas where steps occurred in the gradients. When subsp. *californica* is mapped, its eastern limits are found to agree approximately with the eastern border of the Cascade and Sierra Nevada Mountains. *Comandra* is lacking from the Mojave and Sonoran Deserts and the western part of the Great Basin, and in what appears as a peninsula-shaped extension of the "basin effect" northward into the Columbia Plateau, a feature which is common enough to be considered a general phytogeographic feature (Harshberger, 1911). The specimens from either side of this area in Washington and Oregon were found to have quite different mean values for most characters. The California population, however, was considerably more uniform, while that in Arizona was

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FIG. 2. Clinal variation in six characters. Symbols are based on means for 10 specimens from each geographic area except when fewer than 10 specimens were available; fertile material was totally lacking from New Hampshire, South Carolina, and West Virginia. One character is expressed on each side of a square, the values indicated by the cumulative length of the arm(s), e.g., in legend, a value of 1.4 units for height is expressed by one full length arm and another 0.4 of full length. A broken line given for some fruit diameters indicates the value is based on fewer than 3 specimens. Omission of a character means that it was lacking in material from that area. The characters represented by various parts of the symbols are:

(1) Sepal length: size of the square itself.

(2) Leaf texture: sector(s) of the square shaded according to the following index (see legend):

| *Texture values* | *Sector(s) shaded* |
|---|---|
| 1.1- 4.0 | 1 |
| 4.1- 7.0 | 1 and 2 |
| 7.1-10.0 | 1, 2, and 3 |
| 10.1-13.0 | all 4 |

(3) Fertile stem height: arm(s) at top of square.

(4) Fruit diameter: arm(s) at right of square.

(5) Leaf length/width: arm(s) at bottom of square.

(6) Inflorescence structure: arm(s) at left of square.

also divided, the geographical division being much more obscure than in Washington and Oregon, due to the presence of widespread intermediates. Specimens from northern Arizona are similar to those from adjoining areas to the north and east (subsp. *pallida*); only a few from the mountains of the central and southeastern part of the state agree with other material of subsp. *californica*.

In the areas of contact between subsp. *pallida* and subsp. *umbellata* and in some adjoining areas all degrees of intergradation are found. This zone of transition is rather narrow in eastern Oklahoma but becomes extremely broad northward and northwestward until in western Canada it occupies a large region from Manitoba to British Columbia (Plate 16). I consider this broad area of intermediacy indicative of a high degee of interfertility between the two elements. Intermediate specimens are also found in Oregon and Washington where subsp. *californica* contacts subsp.

FIG. 3. Correlations of clinal steps. An individual line (1 mm. wide) represents location of a step in basically east-west gradient for one character. A general concurrence of steps is evident in the far west and eastern Great Plains. The characters involved are the six in Fig. 2, plus those for rhizome color, suffrutescence, and foliage color. (Map projection: Lambert's Azimuthal Equal-area.)

*pallida*; however, they occupy a comparatively narrow zone in this region. Over a sizeable area in Oregon and California there appears to be no contact, which affords at least a partial explanation for the comparative scarcity of intermediates. In contrast, intermediates are widespread in Arizona as indicated above.

Further evidence of the degree of interfertility in both transition areas is given by the lack of pollen abortion. Pollen was examined from each of the areas in which steps occurred in the gradient. Only the low percentage (ca. 3%) of abortion which appears normal in the genus was found. Meiotic material was available from two intermediate areas (S. D. and Ariz.), and chromosome pairing was normal in both, as it was in non-intermediate areas.

Among the types of variation not recognized taxonomically were a few instances that appear to be ecotypic (*sensu stricto*). Some examples are the shore or dune variant of the Great Lakes region and St. Lawrence Valley in subsp. *umbellata*, and the mountain and basin (or desert at White Sands, N. M.) variants in subsp. *pallida*.

Intraclonal variation was examined in Cheboygan County, Michigan, located within the region in which subsp. *umbellata* is most variable. Because the clones were not excessively large every shoot was included. The range of variation within a single genotype for 3 characters—height, inflorescence structure, and leaf length:width—was found to be considerable and approached what one might expect within a less-variable species in a single area. Some temporal variation, such as described by Fassett (1952) in *Quercus*, is believed to occur in subsp. *umbellata*. Further study of temporal and intraclonal variation appears to be desirable.

## Taxonomic Categories

The species concept attained during this study allows for considerable variation over wide geographic and ecologic ranges. One of the more useful criteria in studies at the species and intraspecific levels is the degree of reproductive isolation in areas where two taxa meet, although we have ample evidence that the barriers which operate in natural populations are exceedingly diverse and that reproductive isolation is often only relative and its measurement at best arbitrary. Tests under artificial conditions often provide valuable data; however, observations of reproductive isolation in nature are of generally greater significance.

I feel that the lines of evidence presented above indicate that the three North American entities involved in *Comandra* should be treated at an intraspecific rather than a specific level, with the most accurate taxonomic expressions being at the level of the subspecies or variety (*varietas*). Unfortunately, there has been no unanimity of opinion, even in modern times, concerning which of these categories is to be preferred in a given instance (see Stebbins, 1950; Davis and Heywood, 1963). The term variety appears to have suffered more from inconsistent usage since it has been used both for various levels of distinctiveness ranging from major subdivisions of a species to minor variants and for another purpose in widespread horticultural usage. Some systematists prefer to use only one or the other category to cover intraspecific variation, unfortunately often with little indication as to the level of distinction meant. The use of both (but probably no others) to indicate different levels of divergence may be helpful in some groups. I feel that to a large extent each plant group invokes its own special problems, and that if the subspecies, variety, or other category is used, one should make some attempt to define the level of distinction intended.

The subspecies category has come into common usage in botany comparatively recently, though it has long been used in zoology. One of the most prudent usages of the category is essentially that proposed by Du Rietz (1930) and basically agreed to by a number of modern systematists (cf. Davis and Heywood, 1963). Contemporary thought on the application of this category seems to emphasize three general criteria of a subspecies, viz., some morphological differentiation, geographical distinction, and free intergrading where ranges meet (cf. Wagner, 1960, and bibliography).

It is hardly necessary to point out the close agreement of this usage of the subspecies category to the situation in *Comandra*, and thus I have called each of the four major elements in the genus subspecies. Of the three North American subspecies defined by these criteria, subsp. *californica*, is the least clearly delineated morphologically. Its separation from subsp. *pallida* does not involve one of the best distinguishing characters between subsp. *pallida* and subsp. *umbellata*, namely, rhizome "cortex" color. Also, there is more overlap in the data for leaf length:width, leaf texture, calyx length, and fruit diameter. Nonetheless, fairly definite steps and a high degree of coincidence of steps in the clines for these and other characters, plus its geographical separation and strong tendency toward suffrutescence, support its distinction from subsp. *pallida*.

The Balkan element, subsp. *elegans*, is here also treated as a subspecies in accordance with its geographical isolation and (slight) morphological distinction. Because of the unavailability of seeds and the difficulties in cultivating these plants, tests of interfertility with the other subspecies were not made, but on the basis of observations elsewhere in the genus I would expect it to be interfertile with them. As Davis and Heywood

(1963) point out, the fertility-sterility test for allopatric populations tells us little about what status the populations should be given. Subspecies *elegans* is differentiated to some degree from other subspecies by its strongly suffrutescent habit, greater pedicel length, more campanulate flower, more ovate sepals, and less distinctly by its lack of a neck in the fruit and its shorter inflorescence, although in its entire range of variability it overlaps with one or more of them in each character. Previous workers have accepted its distinctiveness without question, but when it is considered in respect to the variation pattern described for the entire genus by many characters, I do not see how it can be considered other than conspecific with the North American members.

A recent taxonomic study of the related Old World genus *Osyris*, has also resulted in a reduction of the number of species, in that case from several to two (Stauffer, 1961).

## FORMAL CLASSIFICATION[14, 15]

### Comandra

*Comandra* Nuttall, Gen. N. Am. Pl. 1:157. 1818.
*Hamiltonia* Sprengel, Syst. Veg. 1:831. 1825. *Pro parte.*
*Thesium* Linnaeus, Sp. Pl. 208. 1753. *Pro parte.*

Essentially glabrous, perennial herbs or sub-shrubs from extensive horizontal rhizomes; the fertile shoots 0.7-4.0 (6.2) dm. tall, green to blue-green or grayish, branched or unbranched, often sterile; leaves alternate, simple, entire, sessile to rarely short petiolate, estipulate, varying from very thin, soft, and veiny to thick, firm, and with inconspicuous veins; inflorescence terminal, paniculate to corymbose, made up of few to several cymules, the peduncles subtended by foliaceous bracts, each flower subtended by a bracteole; flowers small (ca. 5 mm. wide), the fresh uniseriate perianth white (occasionally pinkish or greenish); with a green floral tube, regular, perfect, epigynous, sessile to pedicellate, persistent; calyx rotate or somewhat reflexed to infundibulate at anthesis; sepals ovate to oblong, slightly shorter than or equaling the floral tube, 5 (occasionally 4, rarely 3, 6, or 7), their adaxial epidermal hairs becoming adherent to anthers; stamens opposite sepals, equaling them in number;

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[14] All measurements given in this section are from herbarium specimens. A more detailed description of most structures will be found under the appropriate heading in the forepart of this work.

[15] Photographs of all types mentioned are on file at MICH (herbarium abbreviations from Lanjouw and Stafleu, 1964). In addition to the lists of selected specimens given for each taxon below, a list of all specimens examined is available from the author upon request.

anthers longitudinally dehiscent, pollen grains tricolpate, exine finely reticulate; disc intrastaminal, its lobes isomeric with sepals; ovary inferior, unilocular; placentation free-central; ovules 3 (2-4), anatropous; integument 1; style filiform; stigma 1, capitate, at level of anthers; fruit, 1-seeded, drupaceous, exocarp thin, drying quickly, mesocarp sclerified; seed without testa; embryo straight; endosperm abundant; nutrition hemiparasitic by haustorial roots on subterranean parts of vascular (rarely nonvascular) plants and perhaps incidentally hemi-saprophytic by the same means; metaphase-anaphase chromosomes small (ca. 3 μ long), rounded to oblong, N = 14.

The name *Comandra* is from the Greek *Kome* (hair) and *aner* (man), alluding to the hairs superficially attached to the anthers, which actually are not staminal, but develop from the base of the sepals as discussed earlier under "Anatomy and Morphology." The name has frequently been misspelled "*Commandra.*"

**Type species:** *Comandra umbellata* (L.) Nutt.

**Distribution.** Temperate areas of North America and the Balkan States, largely between 30° and 60° north latitude. Voucher specimens have not been seen for a report from north of 60° in the Yukon (Hultén, 1944).

## Key to the Subspecies of *Comandra umbellata*

Sepals ovate, tip acute; lower part of aerial stem definitely overwintering, producing a suffrutescent habit; base of the free floral tube somewhat dilated (divergent); plants of the Balkan Region .......................................... 1. Subsp. *elegans*.

Sepals oblong to lanceolate and ovate-lanceolate, tip acute to obtuse; lower part of stem overwintering (subsp. *californica*), or overwintering weakly or not at all; base of free floral tube not dilated (see Plate 6); plants of North America.

Rhizome "cortex" whitish or beige macroscopically; mature fruits less than 6 mm. in diameter; plants green, often with leaves lighter beneath; sepals 2.0-3.0 ($\bar{x} = 2.4$) mm. long, plants of east of the Great Plains ........................ 2. Subsp. *umbellata*

Rhizome "cortex" blue; mature fruits 6 mm. wide or wider; plants often gray- or blue-green, usually glaucous, leaves quite uniformly colored; sepals 2.0-5.0 ($\bar{x} = 3.0$) mm. long, plants of western North America.

Lower part of aerial stem often overwintering; sepals 2.0-3.5 mm. long, lanceolate to ovate-lanceolate; leaves often slightly paler beneath, lateral and mid veins apparent below; plants greenish, sometimes with a gray or blue tinge, 15-40 cm. tall; from Vancouver Is. to California; rarely in mountains of Arizona .................. 3. Subsp. *californica*

Lower part of stem not overwintering; sepals 2.7-4.5 mm. long, distinctly lanceolate to oblong; leaves approximately concolorous, veins obscure; plants gray-green, often very pale, 6-32 cm. tall; from Texas and Mexico to Manitoba and British Columbia; south to Arizona . . . . . . . . . . . 4. Subsp. *pallida*

### 1. *Comandra umbellata* (L.) Nutt. subsp. *elegans* (Rchb. f.) Piehl, comb. nov.

*Thesium elegans* Rochel ex Rchb. f., Icon. Bot. Exot., Hort. Bot., p. 14. 1824.

*Hamiltonia elegans* (Rchb. f.) Rchb. f., Icon. Fl. Ger. 11:547. 1849.

*Comandra elegans* (Rchb. f.) Rchb. f., Icon. Fl. Ger. 11:11. 1849.

Light green to gray-green, occasionally glaucous sub-shrubs or herbs, fertile shoots 0.8-2.65 ($\bar{x} = 1.69$) dm. tall; often much branched due to growth of axillary branches from lower persistent portion of aerial stem. RHIZOME "cortex" whitish or beige. LEAVES 1.3-3.3 cm. long; linear to lanceolate, oblanceolate and broadly elliptic; base attenuate to cuneate, tip acute to obtuse, sometimes apiculate; slightly paler below, stomata on both surfaces; rather thin, veins apparent, protruding somewhat below, the margins weakly or not at all revolute in herbarium material. INFLORESCENCE corymbose to nearly paniculate, pedicels short to long ($\bar{x} = 2.6$ mm.). FLOWERS campanulate to broadly infundibulate; sepals generally ovate, 2.5-3.2 ($\bar{x} = 2.8$) mm. long, thin; anthers ca. 0.5 mm. long. FRUIT subglobose (longer than wide) to globose, 5.0-6.5 ($\bar{x} = 5.5$) mm. in diameter, smooth, brownish, floral tube not extending appreciably above the fruit as a "neck."[16]

LECTOTYPE: "in agro Romanorum Bannatus, 4 June 1815," *Rochel 85* (PR 181687!; photograph 1450, MICH). This specimen, which is part of the original collection, does not appear to be that in the illustration that accompanies the original description or in Rochel's (1828) illustration. Other type material should be searched for further, particularly in European herbaria.

ECOLOGICAL NOTES AND GEOGRAPHICAL DISTRIBUTION. According to the the data accompanying herbarium specimens, the Balkan subspecies is most commonly found on dry, sandy hills, and also occurs in pastures, thickets, and woods, including rocky areas. This plant ranges from Rumania south to western Turkey, and west to east-central Yugoslavia; thence south to Albania and Greece. Many collections come from the sandy steppe of Deliblat in Yugoslavia. The rather numerous older collections from "Hungary" do not fall within the present boundaries of that country.

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[16] Only 8 fruits were available for study; more observations are needed.

Subspecies *elegans* is restricted to areas having the Central European rather than Mediterranean climate. The former allows for growth in spring and summer with a cessation of growth during winter, while the Mediterranean climate involves summer drought (Turrill, 1929). *Comandra* is found in the hilly interior areas rather than in coastal lowlands, and extends into such mountain masses as the Rodope and Stara Planina. It is recorded from almost 5,000 ft. (1,500 m.) at Mt. Vitosha, Bulgaria, and may well occur higher.

Flowering occurs from April to July, and fruiting from June to August (as judged from the relatively little fruiting material seen).

DISCUSSION. Although living material of this representative was not available, herbarium specimens indicated that it is like other subspecies of *Comandra umbellata* in being quite variable. Two forms of the plant were indicated by Velenovský (1891). Some of its variability may well be of an ecotypic nature since the plant occurs in the steppe region and in the mountains. The characters of leaf length:width and leaf texture vary considerably. Inflorescence structure, however, is less variable, and displays a tendency to be more compact here than elsewhere in the genus. Among other rather slight distinctions are those for flower shape, sepal length:width, and the lack of a neck in the fruit. From the data on herbarium labels it seems that its habitat is generally similar to that of the other subspecies.

Turrill (1929) has commented briefly on this plant, giving the following information. It has been considered ''a relict of the tertiary flora . . . formerly common to the North Temperate Region'' (p. 455). He listed it among the plants which indicate connections northward into the old Austro-Hungarian territories. Presumably it is among those which have migrated from the north, and have persisted in the Balkan Peninsula, which Turrill stated is the most important European area of refuge. There is no barrier separating central Europe from the Balkan region. Central Europe was drastically affected by the Ice Age, while in the Balkan Peninsula, although the climate changed, glaciation was limited to high mountains. Presently, both the climate and the vegetation of the high altitudes simulate that of central Europe, in fact, one of the two major vegetation types is termed ''Central European.'' Among its characteristic communities are deciduous ''brushwood,'' steppe-like grasslands, and stony heaths, which are all likely habitats for *Comandra*.

The similarity between the floras of northern North America and Europe is well known, and is accounted for by a free exchange in the floras until geologically recent times (Fernald, 1931). Today many other similar bihemispheric distributions are known where the degree of taxonomic distinctiveness varies from none at all to clear-cut species, e.g., in *Cercis, Platanus, Torara, Liriodendron, Phryma, Symplocarpus, Monotropa* (Fernald, 1931), *Ostrya, Aesculus,* and *Taxus* (Turrill, 1929).

Concerning the geographic isolation of subsp. *elegans* from the other subspecies, I believe the possibility of an introduction from North America should be considered, especially in light of its close resemblance to some American populations. Herbarium labels, though notorious for their lack of information, suggest that it is found in disturbed places, e.g., pastures and vineyards, which might indicate that it is behaving as a weed. However, Turrill (1929) does not include it in his list of weeds. It may be like certain American populations in that it occurs in restricted "islands" of essentially native habitat amid disturbance, as well as in areas relatively little altered because of their inaccessibility. It has been described as rare in Greece (De Halàcsy, 1904).

The original treatment of Reichenbach described and illustrated the nectariferous disc of the flower as ciliolate; however, the discs of all specimens examined were glabrous and very similar to those of the other subspecies. Of interest too is the fact that Reichenbach failed to mention the perianth hairs which become attached to the anthers. Also, most of the descriptions of the plant give the sepals as yellow or yellowish (e.g., Reichenbach, 1849; Hermann, 1956) rather than as white or whitish. Since the whitish flowers of the other subspecies yellow with preservation, it appears that previous interpretations of color in subsp. *elegans* may be erroneous and based solely on preserved material.

Selected Specimens Examined.

**BULGARIA.** Grassy spots in half-shade, Mt. Vitosha, 19 Jun 1951, *Effremov s.n.* (MICH, US); in pratis montanis, Mt. Vitosha, 1 Jun 1927, *Georgieff s.n.* (GH); im Walde, Nova Mahala, 30 Jun 1893, *Stříbrný s.n.* (GH); ad Stanimaka, May 1892, *Stříbrný s.n.* (PR); in fruticetis apud Dragoman, 13 Aug 1923, *Novák s.n.* (PRC); ad quercetorum margines inter pag. Monastir et Bjela, 18 May 1871, *Janka s.n.* (BP, PR); in collinis ad Papazli, May 1909, *Stříbrný s.n.* (BP, PR); in decliv. herbos. calcar. [*sic*], Tirnowo, 1 Apr 1922, *Schirjaew s.n.* (PRC).

**GREECE.** Vodena [Edessa], May 1899, collector uncertain (PR 48295); in m. Parnethe pr. Dekeleiam (hod. Tatoï) [*sic*], Jun 1878, *De Heldreich s.n.* (BP).

**RUMANIA.** In herbidis silvae Comana pr. pagum Comana, Muntenia, distr. Ilfov., *Zitti and Forstner 1671* (BP); infra Orsova, 20 May 1874, *Borbás s.n.* (BP); loco "Porta ferrea," dicto ad Danubiam inferioram, 20 May 1874, *Borbás s.n.* (BP).

**TURKEY.** Ditianis opp. Bilečik, Bithynia, *Bornmueller 13533* (GH).

**YUGOSLAVIA.** Sŭpra Morani in monte Kitka, *Bornmueller 1868* (GH); Mitrovica (Macedoniae Albaniae), *Bornmueller 1869* (GH, BP); silvis Belanovce apud Leskovac, 12 May 1893, *Ilić s.n.* (PR); in vineis ad Niš, Aug 1880, Jun 1881, *Pančić s.n.* (BP, GH, PR); gorica prope Niš, 11 May 1888, *Bornmueller s.n.* (BP, GH, PR); in vinetis ad Vranja, May 1903, *Bierbach s.n.* (LE); in arena mobili ad Grebenacz, Banatus, *Heuffel 120* (BP, LE); Sandhuegeln bei Grebenacz, Banatus, *s.d.*, *Wierzbicki s.n.* (BP, GH, PR); in arenosis herbosis praedii Deliblat loco "Korn" dicto, Temes, 3 Jun 1912, *Lengyel s.n.* (BP, GH, LE, PR); prope Deliblat, (locus classicus), Temes, May 1909, *Wagner s.n.* (GH).

### 2. *Comandra umbellata* (L.) Nutt. subsp. *umbellata*

*Thesium umbellatum* L., Sp. Pl. 208. 1753.

*Thesium corymbulosum* Michx., Fl. Bor. Am. 1:112. 1803.

*Comandra umbellata* (L.) Nutt., Gen. N. Am. Pl. 1:157. 1818.

*Hamiltonia umbellata* (L.) Spreng., Syst. Veg. 1:831. 1825.

*Comandra cuneifolia* Raf., New Fl. N. Am. 2:33. 1836.

*Comandra elliptica* Raf., *ibid.*

*Comandra media* Raf., *ibid.*

*Comandra obovata* Raf., *ibid.*

*Comandra obtusifolia* Raf., *ibid.*

*Comandra umbellulata* Raf., *ibid.*

*Comandra umbellata* (L.) Nutt. var. *decumbens* E. J. Hill, Bot. Gaz. 9: 175. 1884. Lectotype: wooded hills, Poysippi, Wisconsin, 26 July 1883, *E. J. Hill s.n.* (GH!).

*Comandra richardsiana* Fern., Rhodora 7: 48. 1905. Lectotype: Grand River, Gaspé Co., Quebec, June 20-July 10, 1903, *G. H. Richards s.n.* (GH!).

*Comandra richardsiana* Fern. forma *palustris* Jennings, Wild Fls. W. Pa. 1: 181. 1953. Holotype: Pymatuning swamp at Hartstown, Pennsylvania, 29-31 May 1914, *G. K. Jennings s.n.* (CM!).

Light green herbs or sub-shrubs, fertile shoots 0.7-4.0 ($\bar{x} = 2.07$) dm. tall; sometimes much branched due to development of axillary branches on lower persistent portion of aerial stem. RHIZOME "cortex" whitish or beige. LEAVES 0.7-5.0 (7.6) cm. long; lanceolate (occasionally linear) or oblanceolate to broadly elliptic or ovate; base attenuate to acute, tip acute to obtuse, sometimes apiculate; distinctly to slightly paler beneath, stomata on the lower surface only; rather thin to very thin and soft, midrib and often lateral veins conspicuous and protruding below; often minutely revolute in herbarium material. INFLORESCENCE loosely paniculate to corymbose, pedicels short or absent ($\bar{x} = 1.4$ mm.). FLOWERS infundibulate to almost rotate; sepals lanceolate or lanceolate-oblong to nearly ovate, 2.0-3.0 ($\bar{x} = 2.4$) mm. long, thin; anthers ca. 0.5 mm. long. FRUIT sub-globose to globose, 4.0-6.0 ($\bar{x} = 4.6$) mm. in diameter, smooth, dark brown to chestnut, floral tube often forming a "neck" above the fruit.

Intergrading with subsp. *pallida* in the eastern Great Plains and over a wide area northwestward into Canada.

HOLOTYPE: "in Virginae, Pensylvaniae" (Linnaeus, Sp. Pl. 208. 1753.), *Kalm s.n.* (LINN; microfiche 161). Linnaeus also indicated that material illustrated under the name *Centaurium* in Plukenet's Mantissa (1696; tab. 342, D) is the same. Although the habit of the plant illustrated is an excellent match for *Comandra,* the flowers are incorrect since the perianth appears either to be closely subtended by a whorl of bracts or is composed of two whorls instead of one.

ECOLOGICAL NOTES AND GEOGRAPHICAL DISTRIBUTION. This subspecies is commonly an inhabitant of dry, sandy, or rocky soils, varying from rather "sterile" to richer mesic sites; occasionally it is found in swamps or boggy areas. It is common in open sites and savannahs, e.g., "oak-openings" of the Lake States; it may persist in earlier forest stages. It occurs from near sea level to 2,200 feet (670 m.) and likely higher, and ranges from Newfoundland westward south of about latitude 52° N to Manitoba and northwestward in Saskatchewan and Alberta, south along the Atantic Coastal States to Georgia, and west to Arkansas and the eastern parts of Oklahoma, Kansas, Nebraska, and the Dakotas.

This range correlates well with boundaries of several physiographic regions (cf. Lobeck, 1948). The southern limit of its range from Texas to South Carolina agrees approximately with the northern limit of the Coastal Plain. Its western boundary is approximately that between the Central Lowland and Great Plains. In eastern North America its northern limits extend from Newfoundland along the St. Lawrence Valley Section as it occupies a narrow strip along the north shore of the river at the southern boundary of the Laurentian Upland. In the Great Lakes area it extends a short distance into the Laurentian Upland, but from Manitoba to Alberta its range is again in surprisingly close agreement with the Laurentian boundary.

The flowering dates are from late March to May in the south, and from May to July (Aug. in Nfld.) in the north. Mature fruits are found from June to September; however, data are lacking from the Gulf States.

DISCUSSION. Subspecies *umbellata* has been separated into a number of species and varieties by various authors as evidenced by the rather lengthy list of synonyms. There is often a great deal of variation even within the population of a single locality, suggesting a high degree of heterozygosity. Considerable plasticity is found even in a single genotype as indicated by my studies of individual clones. The great vegetative variability in just a part of the range of this subspecies was early observed by Rafinesque, who stated (1836, p. 33) "there are now 7 or 8 sp. of this G. and I will distinguish 5 sp. of it, all blended by our careless Authors." Fernald (1905) has pointed out that Rafinesque's five species (a sixth, *C. umbellulata* Raf., apparently was intended as a substitute for *C. umbellata* (L.) Nutt.) are all variants of *C. umbellata sensu* Fernald. However, as will be discussed below, Fernald himself added a new species.

As indicated in the discussion of variation, it has been the extremes of this subspecies (Atlantic Coastal States vs. Maritime Provinces and the Minn.-Wis. to Ark. region), which compared to the entire population are of narrow distribution, that were separable by the characters traditionally used. In the broad intervening region (the Appalachians to Manitoba, Ontario, and the St. Lawrence Valley) these characters have been found to be of little or no value.

The population restricted to the far eastern states is the *Comandra umbellata* of Fernald, who, although he formerly (1905) envisioned this taxon as ranging beyond the Alleghenies, is said to have later interpreted it as being restricted to east of the mountains (Deam, 1940; apparently Fernald did not publish these later ideas himself). Regardless, it is still not apparent why Fernald (1950) recorded the range as west to Michigan and south to northern Alabama *after* Deam had published the above. Under Fernald's treatment the western and northern extreme was segregated as *C. richardsiana*. It should be pointed out that this epithet has been misspelled "*richardsoniana*" in the literature, an error which unfortunately has been frequently perpetrated in subsequent works and on herbarium labels. Fernald named this variant after its discoverer, George H. Richards; the originator of the above error may have had Sir John Richardson in mind, which adds to the confusion, for it was the latter who named *Comandra (Geocaulon) livida*.

There is some uncertainty concerning the typification of *C. richardsiana*, since no type was designated. The collection data for the first specimen of several cited in the original description are given as "Quebec, sandy alluvium of the Grand River, Gaspé County, July 1903 (G. H. Richards)" (Fernald, 1905). The only Richards specimen I have found and the one I have selected to be lectotype is simply labeled "Grand River" as to locality and dated June 20-July 10, 1903. It appears that Fernald emended Richards' data to agree with that of his own collection, which as the second specimen cited is given simply as "July 1, 1904 (*M. L. Fernald*)." Fernald (1942) later indicated that he considered this to be the type locality. A specimen from Saguenay County, Quebec (Tadousac, 14 July 1904, *Collins and Fernald s.n.* (GH!)) is stamped "Type," but it along with the others cited are syntypes, except for the Richards specimen.

I consider *C. umbellata* var. *decumbens* E. J. Hill to be simply an extreme growth form of subsp. *umbellata* which has a tendency to be decumbent and suffrutescent (see discussion under "Vegetative Reproduction"). The decumbent aerial stems of this form have apparently been confused with the supposedly shallow rhizomes of *C. richardsiana* Fern., and Gleason and Cronquist (1963) consider it synonymous with that species. Another minor variant with allegedly more ascending and narrower leaves is exemplified by *C. richardsiana* Fern. forma *palustris* O. E. Jennings from western Pennsylvania, which I consider to represent a modification found in extreme habitats. I have seen rather similar specimens from wet habitats in Virginia, well within the range of *C. umbellata sensu* Fernald. Concerning Michaux's *Thesium corymbulosum*, Fernald (1905) states that there appear to be no specimens in Michaux's herbarium in Paris, and that probably the name was intended simply as a substitute for the morphologically inappropriate name *T. umbellatum* L.

SELECTED SPECIMENS EXAMINED.

**UNITED STATES.** ALABAMA. Colbert Co.: dry woods between Cherokee and Riverton, *Harper 3930* (GH). ARKANSAS. Clay Co.: Crowleys Ridge, Piggott, *Demaree 30403* (TENN). ILLINOIS. Jo Davies Co.: calcareous slope, dry open woods 7.5 miles NW of Stockton, *Hermann 8808* (GH). INDIANA. Morgan Co.: wooded oak ridge 1/4 mile N of Bethany Park, *Friesner 8693* (GA, PR, WTU). IOWA. Boone Co.: semi-open wooded ridge, Ledges State Park, *Hayden 9178* (GA, GH). KANSAS. Cherokee Co.: 2 miles E of Baxter Springs, *Horr et al. E299* (CAS, GH, OSC). MICHIGAN. Charlevoix Co.: Lake Michigan shore, Cables Bay, SE side of Beaver Island, *Piehl 58197* (GH, MICH, UC, US). MINNESOTA. Hennepin Co.: with *Celastrus*, *Symphoricarpos*, *Rhus*, and *Poa* in sandy loam of open hillside, Ft. Snelling Reserve, Minneapolis, *Piehl 5728* (GH, MICH, UC, US); Redwood Co.: meadow, 8 miles S of Sacred Heart, *Moore 13203* (GH, MIN). St. Louis Co.: dry rocky ledges in Namakon Narrows, *Lakela 14127* (DAO, MIN, WIS). MISSISSIPPI. Lowndes

Co.: calcareous soil, slope, 9 miles E of State College, 25 Mar 1957, *C. Smith s.n.* (MISSA). MISSOURI. Boone Co.: with *Quercus*, *Rhus*, *Aster*, and *Triosteum* on south-facing slope over limestone near Hinkson Creek, S of Columbia, *Piehl 5941* (GH, MICH, UC, US). NEBRASKA. Dixon Co.: Ponca, *Clements 2519* (CAS, GH, NEB). NEW YORK. Suffolk Co.: sandy railroad embankment, South Haven, *Moldenke 18682* (OSC, WTU). NORTH CAROLINA. [Buncombe Co.]: dry grounds, Biltmore, *Biltmore Herbarium 312b* (GH, PR). OHIO. Lorain Co.: Oak Point, 19 May 1895, *Dick s.n.* (CAS, WIS). PENNSYLVANIA. Allegheny Co.: near Stoops Ferry, 12 Jun 1901, *Shafer s.n.* (GA, MIL). TENNESSEE. Van Buren Co.: dry slopes, Fall Creek Falls, *Shanks & Sharp 1326* (OSC, TENN). VERMONT. Addison Co.: rich, rocky soil, in and at margin of hemlock-hardwoods near Bristol, *Piehl 59610* (GH, MICH, UC, US). WISCONSIN. Bayfield Co.: near Port Wing, *Cheney 7052* (MIL, WIS). Kenosha Co.: sandy prairie 4 miles S of Kenosha, *Fuller C-425* (MIL, WTU).

**CANADA.** ALBERTA. River bluff, Wood Buffalo Park, Mackenzie Basin, *Raup 2199* (GH). NEW BRUNSWICK. Grass plain, Portage Island, *Blake 5670* (GH). NEWFOUNDLAND. Limestone barrens, Burnt Cape, Pistolet Bay, *Fernald & Long 28111* (GH). ONTARIO. Bois pourri dans la tourbière du rivage du lac Huron, Oliphant, *Victorin et al. 45992* (CAS, GH). QUEBEC. Sandy woods near Lake Deux-Montagnes, ca. 5 miles NE of Oka, *Piehl 59617* (GH, MICH, UC, US); sandhills, Coffin Island, Magdalen Islands, *Fernald et al. 7325* (CAS, GH). SASKATCHEWAN. Sandy open woods near S shore of Lake Athabaska, *Raup 7015* (GH).

Selected Specimens Examined—Intergradients between *C. umbellata* subsp. *umbellata* and *C. umbellata* subsp. *pallida*.

**UNITED STATES.** KANSAS. Montgomery Co.: sandy loam of open prairie along Sedan-Elk City road 2.5 miles E of Bee Creek, *Piehl 5985* (MICH, UC, US). MINNESOTA. Clay Co.: prairie, Muskota, 14 Jun 1936, *Stevens s.n.* (DAO, MIN); Mahnomen Co.: dry sand dune area near Fertile, *Piehl 5605* (UC, US). MISSOURI. Jackson Co.: rocky barrens, Greenwood, *Bush 6449* (GH). NEBRASKA. Antelope Co.: Neligh, 18 May 1896, *Bacon s.n.* (GH); Dawes Co.: Chadron, *Bates 5907* (NEB). NORTH DAKOTA. Benson Co.: arid prairie, Leeds, *Lunell 13778* (WIS). SOUTH DAKOTA. Walworth Co.: bluffs, Glenham, 16 Jun 1909, *Moyer s.n.* (GH).

**CANADA.** ALBERTA. Sandhill S of Winterburn, near Edmonton, *Moss 4400* (ALTA, DAO); dry edge of woods, Ft. Saskatchewan, *Turner 19* (DAO, GH). BRITISH COLUMBIA. Dry bluffs, Peace River at Taylor Flat, *Raup & Abbe 3577* (GH); grassland plateau, Peace River Bridge, *Taylor et al. 23* (DAO, WTU). MANITOBA. Along railroad, Portage la Prairie, 1 Jun 1906, *Herriot s.n.* (GH). SASKATCHEWAN. Sandy railroad siding, Carnduff, *Coupland 29* (DAO).

### 3. *Comandra umbellata* (L.) Nutt. subsp. *californica* (Rydb.) Piehl, comb. nov.

*Comandra californica* Eastw. ex Heller, Muhlenbergia 2:20. 1905. *Nomen nudum.*

*Comandra californica* Eastw. ex Rydb., Fl. Rocky Mts. 1138. 1922. *Pro parte.*

*Comandra nudiflora* A. Davidson, Bull. So. Calif. Acad. 24:68. 1925. Holotype: Tehachapi Mountains, Kern County, California, 1 May, 1 June 1925, *Mrs. W. W. Hutchinson s.n.* (LAM!, LAM photograph S. 54-T/ 31-3995; isotype US 1243520!).

Light green to blue- or gray-green, somewhat glaucous sub-shrubs or herbs, fertile shoots 1.5-4.0 (6.2) ($\bar{x} = 2.38$) dm. tall; often much branched (and many flowered) due to growth of axillary branches from lower persistent portion of aerial stem. RHIZOME "cortex" bluish in fresh material; sometimes blackish when dried. LEAVES 1.7-5.3 cm. long; broadly elliptic and sub-ovate or sub-obovate to linear and lanceolate (oblanceolate); base acute to slightly attenuate, tip acute, sometimes apiculate; slightly lighter below, stomata on both surfaces; rather thin, veins apparent and somewhat protruding below; somewhat revolute in herbarium material. INFLORESCENCE corymbose to paniculate, pedicels short to rather long ($x = 2.1$ mm.). FLOWERS infundibulate to rotate; sepals lanceolate or lanceolate-oblong to nearly ovate, 2.0-3.5 ($\bar{x} = 2.7$) mm. long, thin to somewhat thickened; anthers ca. 0.6 mm. long. FRUIT sub-globose, 5.0-7.5 ($\bar{x} = 6.4$) mm. in diameter, smooth, brown-light brown, floral tube sometimes forming a "neck" above the fruit.

Intergrading with subsp. *pallida.*

LECTOTYPE: S. Fork Kaweah River, Tulare County, California, 20 July 1904, *Culbertson 4479* (CAS 84511!; isotypes, CAS!, GH!, MO!, POM!; see comment under "Discussion").

ECOLOGICAL NOTES AND GEOGRAPHICAL DISTRIBUTION. Subspecies *californica* occurs primarily in dry places, largely in mountain or foothill areas. Its habitats range from open sites to open conifer forests (especially yellow pine), and at lower elevations it occurs in brushy woodland (especially oak) and about chaparral margins, where it is frequently found near the bases of shrubs or trees. The maximum elevations recorded on herbarium sheets are 8,000 ft. (2,438 m.) in Arizona and 10,000 ft. (3,048 m.; *Grant 206*, G!) in the southern Sierra Nevada, which is the altitudinal record for the genus. It is more often a plant of high elevations than is subsp. *pallida*. However, subsp. *californica* ranges down to elevations below 1,000 ft., particularly in river valleys in Humbolt, Trinity, and Shasta counties in northern California and in the Columbia and Willamette valleys of Washington and Oregon.

Its geographic range extends from Vancouver Island, southwestern and southcentral Washington, western Oregon, and northern California south in the Sierra Nevada to the Tehachapi Mountains, Kern County, California, and, discontinuously, to restricted areas in southeastern and central Arizona. In Washington and Oregon it occurs just east of the Cascade Range from Kittitas County, Washington southward. In most of California it is restricted to the Sierra Nevada and connected ranges, its range bounded on the west by the Central Valley; however, it approaches the Coastal Ranges in northern California and northward. On the eastern side of the Sierras I have collected it at the base of the mountains down to 5,800 ft. (1,768 m.) in Inyo County. Munz' (1959) inclusion of Death Valley in the range is apparently based on a single specimen for which the locality is given only as "Titus Canyon, Death Valley" (*Peirson 13537*, RSA). Since Titus Canyon extends for many miles and displays considerable relief from its mouth (ca. 1,200 ft. or 366 m.) bordering on Death Valley to its head, an attempt was made to locate this site more precisely. Reference to Peirson's notebook has yielded no additional information directly, but the known altitudinal ranges for several other species collected the same day may suggest the *Comandra* collection came from above 3,500 ft. (P. A. Munz, personal communication). It would be very desirable to recollect *Comandra* in this area because the elevation suggested is comparatively low, particularly for an arid region, and because this collection fills in another segment of the gap between localities in southern California and Arizona. Also, *Comandra* has yet to be collected between the Sierras and Titus Canyon in such places as the White Mountains. Eastward, the Titus Canyon station appears to be closest to several stations for subsp. *pallida* and intergradients between it and subsp. *californica* in the Charleston Mountains, Nevada. In northwestern Arizona, intergradient specimens with strong affinities to subsp. *californica* have been found. The few stations of subsp. *californica* in Arizona are in mountain ranges that are included in what has been called the Arizona Highlands (Bowman, 1911) or the Western Sierra Madre (Atwood, 1940).

The flowering dates are from March to July, and mature fruits are found from May to September. The dates vary greatly with elevation. I have observed buds in the field in late July in Arizona at about 5,800 ft. (1,768 m.) which suggests markedly variable flowering dates that are probably determined by when the rains occur.

DISCUSSION. The geographic isolation that exists over a large portion of the California-Washington segment of the range of this subspecies has resulted in relatively little intergradation with subsp. *pallida*. In the coastal mountains and along the Columbia River Valley in Oregon, particularly, the ranges of subsp. *californica* and subsp. *pallida* meet and intermediates are found, while in occasional specimens from California some influence of subsp. *pallida* is apparent, especially in the sepals, floral tube, and leaves.

In Arizona, however, subsp. *californica* is very localized and the majority of specimens from the southern part of the state are intermediate. For several characters, gene flow from this area is evident northward into Nevada and weakly into Utah and New Mexico. Much of the intergradient material from Arizona shows affinities toward subsp. *pallida* with its larger, fleshier flowers and with a surprisingly widespread tendency for all leaves to be narrowly lanceolate (oblanceolate) to linear. Further, many specimens are bluish- or gray-green and somewhat glaucous, although some are a more definite green. In characters of its fruits and in its tendency to be suffrutescent, however, this material is suggestive of subsp. *californica*. A form of that subspecies grades almost imperceptibly into the widespread intermediate element and actually grows with it in such places as Parker Creek in the Sierra Ancha Mountains (Gila Co.). A somewhat less continuous gradient occurs between the intermediates and subsp. *pallida*, a situation which may be accounted for by their being somewhat separated ecologically and geographically. Although only a few specimens of the Arizona form of subsp. *californica* are available, it appears much less variable as to leaf width than is the material from the Pacific States. The Arizona material is not sufficiently distinct to separate it taxonomically from the small-flowered, broader-and thinner-leaved segment of the subspecies in the Pacific States. Furthermore, rather similar material has occasionally been collected in California.

Rydberg (1922, p. 1138) gave the range of subsp. *californica* as also including a considerable area east of the range I have given ("Wash.—Ida.—Son.—southern Calif.;" both the range and year of publication are incorrectly given in the Gray Card Index "corrected reprint"). However, I have found that, except for local populations in Arizona, specimens from east of the Great Basin (i.e., Rydberg's "Ida.—Son.") have larger, fleshier flowers and thicker leaves, and are entirely herbaceous—features which characterize subsp. *pallida*.

A limited number of seed cultures of Arizona material were obtained and grown together with the other American subspecies at the University of Michigan Botanical Gardens. These specimens, although they have thus far remained sterile, indicate that this subspecies retains its morphological distinctiveness, including the perennating bases.

My description of this subspecies differs from that given by Munz (1959) for California material in two minor ways. He describes the sepals as purplish-green rather than whitish; however, I suspect his observation is based on material in which a post-flowering color change has occurred as discussed under "Developmental History." He also describes the sepals as oblong (as in subsp. *pallida*, with which some of his specimens could have been intergradient), although his illustration shows them as ovate.

In 1904 Eastwood's proposed "*Comandra californica*" was used by C. F. Baker in a list of herbarium specimens offered for sale. Heller also took up this name and published it in a list of his collections, but since a description had not yet been given, the name was still invalid according to the International Code of Botanical Nomenclature (Lanjouw, 1961). The correct citation for this taxon is that referring to Rydberg's work, in which case a description was published. I feel it is vital to follow the code closely in such instances by including the name of the publishing author in author citations, and certainly not to delete his or her name in favor of the author who simply proposed the combination as is done by C. L. Hitchcock *et al.* (in ms.). Retention of the proposing author's name when a change in rank is made is optional according to the code.

Since the name *Comandra* alludes to the perianth hairs which become superficially attached to the anthers, it is ironic that an allegedly new species was based largely on the lack of such hairs (Davidson, 1925), particularly since the characteristic hairs are definitely present on the holotype. A pencil annotation on the holotype, "no hairs on stamens," suggests that Davidson erroneously thought the hairs developed from the stamen rather than from the sepals.

It should be emphasized that, although the type collection falls within my circumscription of the subspecies, it tends to have thicker, somewhat narrower leaves and longer sepals than some other collections which better exemplify these characters. Rydberg (1922) did not indicate a type specimen, nor did he annotate any of the specimens now at the New York Botanical Garden as such. I have chosen a lectotype from among specimens Eastwood had considered to be types. C. L. Hitchcock *et al* (in ms.) cite a specimen, but do not state that they have chosen it as the lectotype.

It is of interest that Jepson (1914) cited a specimen of the type collection as among specimens he considered intermediate between *C. umbellata* and *C. pallida*. Regarding the variability of California material, he mentions he did not find the specimens separable into two consistent units.

Selected Specimens Examined.

**UNITED STATES.** ARIZONA. Gila Co.: abundant; many shoots fertile; in oak scrub near Parker Creek Experimental Forest headquarters, 5,100 ft., *Piehl 59453* (GH, MICH, UC, US); *F. W. Gould 4358* (ARIZ, GH). Pima Co.: S of Molino Basin, Mt. Lemmon highway, Santa Catalina Mts., *Barr 61-501* (ARIZ). Yavapai Co.: Prescott, 8 Jun 1936, *E. H. Jones* (WTU). CALIFORNIA. Amador Co.: with conifers and hardwoods on fine loam of roadbank 20 miles NE of Jackson, 2,700 ft., *Piehl 59504* (GH, MICH, UC, US). Butte Co.: open places in Sierra foothills 3 miles above Centerville, *Heller 11845* (CAS, GH, OSC, WIS, WTU). El Dorado Co.: N side of north fork of Cosumnes River, NW of Youngs (Somerset), *Raven 9114* (CAS). Fresno Co.: trail to Tehipite Valley, W of Simpson Meadow, Middle Fork of Kings River, 5,900 ft., *Howell 34118* (CAS, US). Humbolt Co.: under oak-manzanita, Trinity River Valley, *Tracy 8038* (GH). Inyo Co.: dry slope between Kearsarge Pass and Onion Valley, Sierra Nevada Mts., *Munz 12662* (RSA, WTU). Kern Co.: dry loam at top of roadcut, Cedar Creek Campground, 10 miles E of Glennville, 4,800 ft., *Piehl 59471* (GH, MICH, US). Mariposa Co.: Chowchilla Mt., 6,900-7,000 ft., *Quick 51-76* (CAS). Shasta Co.: Kennet, *Smith 56* (CAS). Siskiyou Co.: Shasta Springs, *Eastwood 6646* (CAS, GH). Tuolumne Co.: Twain-Harte, *Eastwood & Howell 8616* (CAS). OREGON. Benton Co.: roadside 7 miles S of Corvallis, *Baker 5376* (OSC, WTU). [Clackamas Co.]: grassy bluffs of the Willamette near Oswego, *Henderson 910* (OSC). Curry Co.: Rogue River Canyon along edge of Tate Creek, *Baker 3884* (OSC). Douglas Co.: river banks, Umpqua, *Cusick 4547* (OSC, WTU). Jackson Co.: dry Douglas fir and oak woods on Fielder Creek Road, *Dennis 2292* (OSC). Jefferson Co.: rocky dry soil, Black Butte, 5,000 ft., *Johnson et al. 27* (OSC). Jefferson-Deschutes Co. line area: dry, sandy soil, Black Butte, NW of Sisters, 3,800 ft., *Johnson 574* (OSC). Lane Co.: Linton Creek, *Anderson 614* (OSC). Wasco Co.: foothills of Cascades 3½ miles W of Friend, 2,600 ft., *Lawrence 166203* (OSC). WASHINGTON. Kittitas Co.: open gravelly places, pine forest 3 miles W of Cle Elum, *Hitchcock & Muhlick 8119* (WTU). Klickitat Co.: dry hillside, *Suksdorf 614* (GH); White Salmon, Jun 1880, *Suksdorf s.n.* (GH). Skamania Co.: Wind River Nursery, Columbia National Forest, 18 Jun 1928, *Eringer s.n.* (OSC).

**CANADA.** BRITISH COLUMBIA. Dry ground, Elk Lake, Vancouver Island, 29 May 1925, *Bridgman s.n.* (V).

SELECTED SPECIMENS EXAMINED—INTERGRADIENTS BETWEEN *C. umbellata* SUBSP. *californica* AND *C. umbellata* SUBSP. *pallida*.

**UNITED STATES.** ARIZONA. Cochise Co.: dry open slopes of Miller's Canyon, Huachuca Mts., *Goodding 118* (ARIZ, G, GH). Mohave Co.: chaparral area, Cerbat Mts., 3 miles E of Chloride, at falls, *Darrow & Gould 3742* (ARIZ). Navajo Co.: rock slope 10 miles W of McNary, *Goodman & Hitchcock 1323* (CAS, G, MICH). Pima Co.: on coarse decayed granite under open yellow pine and *Quercus hypoleuca*, 9 miles SE of Mt. Lemmon P.O., 6,750 ft., *Piehl 63944* (GH, UC, US). Pinal Co.: oak flats, mountains between Miami and Superior, *Nelson & Nelson 1870* (G, GH, WTU). NEVADA. Clark Co.: near bridge, Kyle Canyon, *Clokey 5554* (GH, WTU). OREGON. Union Co.: stony loam of Whitman forest, *Reid 431* (OSC). WASHINGTON. Kittitas Co.: slopes W of Cle Elum, *Thompson 6193* (WTU).

**MEXICO.** SONORA. E slope of Canyon del Oso, near Bavispe, *White 607* (ARIZ).

### 4. *Comandra umbellata* (L.) Nutt. subsp. *pallida* (A. DC.) Piehl, comb. nov.

*Comandra pallida* A. DC., *in* DC. Prodr. 14:636-37. 1857.

*Comandra pallida* β *angustifolia* A. DC., *in* DC. Prodr. 14:637. 1857. Isotypes: New Mexico, in 1851-52, *C. Wright 1783* (GH!, NY!).

*Comandra umbellata* (L.) Nutt. var. *angustifolia* (A. DC.) Torr., Rept. U. S. Mex. Bound. Surv. (Bot.) 2 (Part 1): 185. 1859.

*Comandra umbellata* (L.) Nutt. var. *pallida* (A. DC.) M. E. Jones, Proc. Calif. Acad., Ser. 2, 5:722. 1895.

*Comandra linearis* Rydb., Fl. Rocky Mts. 818, 1066. 1917. Holotype: Green River, Utah, 19 Aug. 1887, *S. M. Tracy and Evans 716* (NY!).

Pale, generally glaucous, green to gray-green herbs, fertile shoots 0.5-33.2 ($\bar{x} = 16.8$) dm. tall; often much branched. RHIZOME often thick, its "cortex" blue to blackish. LEAVES 0.9-4.2 cm. long; linear or lanceolate to elliptic or ovate, those of lateral branches often distinctly narrower; base attenuate to cuneate, tip attenuate to acute, often mucronulate or apiculate; approximately isolateral, stomata on both surfaces; rather thick (becoming somewhat succulent) and firm, with some xerophyllous anatomical features; veins inconspicuous, not protruding; not revolute. INFLORESCENCE paniculate to corymbose, pedicels absent to rather long ($\bar{x} = 1.6$ mm.). FLOWERS infundibulate to rotate or somewhat reflexed; sepals oblong to lanceolate oblong, 2.5-5.0 ($\bar{x} = 3.3$) mm. long, thick; anthers ca. 0.7 mm. long. FRUIT sub-globose to ovate, 5.5-9.0 ($\bar{x} = 6.9$) mm. in diameter, often slightly roughened, purplish-brown (glaucous), floral tube sometimes forming a "neck" above the fruit.

Intergrading with both subsp. *californica* and subsp. *umbellata*.

Holotype: Clear Water, Oregon (now Idaho), *s.d.*, *Rev. Spalding s.n.* (G!; photograph 1454 (MICH)); two probable isotypes (GH!). Another specimen labeled "plains—Oregon, May 7," (GH!) could also be type material.

Ecological Notes and Geographical Distribution. Subspecies *pallida* commonly occurs on partly open to open, sandy or rocky slopes, sagebrush areas, and occasionally under conifer or deciduous trees, in moist places, and in gypsiferous areas. It rarely occurs in desert areas (Chihuahuan Desert, White Sands, N. M.), the only subspecies to do so. It ranges from Saskatchewan south to Oklahoma and Texas, west to Arizona, eastern Nevada, Oregon, Washington, and British Columbia, and, based on information from herbarium specimen labels, occurs at maximum altitudes of 7,200 (2,195 m., Nev.), 8,000 (N.M.), 9,500 (Colo.), and 9,100 (Wyo.) feet.

As indicated above, the boundary of subsp. *pallida* agrees in general with the eastern limits of the Great Plains. Its western limits are in the basin region from Arizona to Oregon and along the Cascade Mountains farther north. In Arizona only an occasional specimen is known from below the Mogollon Rim. It appears not to have been collected from the Canadian Coast ranges, but is found in the Interior Plateaus, Northern Rockies, and Great Plains of western Canada.

The flowering dates are from March to May (occasionally flowering in early July at White Sands, N. M.) in the south; April to early July in the north. Mature fruits are present from May to August in the south; June to September in the north. These dates are probably influenced considerably by rainfall.

Discussion. This subspecies is also quite variable, but more of the variation appears to be correlated with various habitats such as seen in specimens from moist versus dry sites, low versus high elevations, and in some cases may be related to the variety of substrates in its range. For two of the clines, those for height and sepal length, the east-west gradient is reversed in the western part of its range (B. C., Wash., Ore., Nev.), a trend which may be due to gene flow from subsp. *californica*.

At the eastern and northern limits of its range a rather extensive zone of intermediacy between subsp. *pallida* and subsp. *umbellata* exists. This zone of probable interfertility is narrow in the south, becoming more extensive northward so that it covers a large area in Canada. It is of interest that the northernmost collections are intermediates. Perhaps the contact of populations isolated during glaciation in either the southeastern or southwestern United States or in Mexico afforded phenotypes better adapted to northern areas than either parental type. Since the northern area of intermediacy was more recently occupied than at least some areas within the range of either subspecies, it seems probable that segregation of the subspecies occurred relatively early and that they have contacted each other more recently.

Subspecies *pallida* contrasts with the other subspecies in that it characteristically sprouts from buds which are at or below the soil surface, the aerial part of the plant dying each season. Often a weak but sometimes conspicuous crown is produced from the bases of the aerial stems and may persist just below the soil surface for several years. The crown is usually more fully formed here than in subsp. *umbellata*, in which some semblance of a crown may be formed also. Hitchcock (1900) has mentioned the formation of a crown by subsp. *pallida*.

Greenhouse and garden cultures involving material both grown from seed and vegetatively propagated indicate that the morphological features which best characterize this subspecies, e.g., rhizome "cortex" color, foliage color, and lack of caudex, are genetically rather than environmentally determined.

A rather widespread variant which in its extreme form can be suggestive of small conifers in gross appearance is found particularly in the southern part of the range (mainly the N.M.-Okla. area). De Candolle (1857) described it (as "β angustifolia") from New Mexico at the same time he described the typical *Comandra pallida*. This plant is often profusely branched, including the lower half of the stem (branching of upper part is common in the genus). The branching occurs in the development of an aerial stem which is annual and is not to be confused with the formation of lateral branches from a caudex as is prominent in subsp. *californica*. The leaves of the branches of this variant are linear, and contrast so markedly with the leaves of the main stem that the foliage is distinctly dimorphous. However, throughout the genus there is a tendency for the leaves of branches to be somewhat narrower than those of the main axis. The extreme of a more or less continuous variation pattern involving the single character of linear-leaved lateral branches hardly seems worthy of taxonomic distinction. The type of De Candolle's narrow-leaved form is from New Mexico, and was collected in 1851-52 (*Wright 1783*). When Torrey (1859) used the same name and gave the intraspecific category as variety instead of β, he apparently based it on the same type; however, Wright's collection numbers were erroneously given as *783* and *784*. This error is compounded by the fact that although a *Wright 1784* exists, it is not cited in De Candolle's description.

A second linear-leaved variant described by Rydberg (1917) as *Comandra linearis* is hardly more than a growth form. It is not branched, and was described as having *all* leaves linear (a few basal leaves are linear-lanceolate). The collector of the type of Rydberg's species has heretofore been cited erroneously as simply S. M. Tracy (e.g., by Rydberg, 1917; C. L. Hitchcock *et al.*, in ms.); reference to the type specimen indicates the collection was made by Tracy and Evans.

In addition, an unnamed variant exists which is characterized by large lanceolate leaves with attenuate tips, and to a lesser extent by its greater height and large flowers. It is best expressed in the Washington-British Columbia region, but rather similar specimens also occur farther south, e.g., in Nevada.

SELECTED SPECIMENS EXAMINED.

**UNITED STATES.** ARIZONA. Apache Co.: sandy slope between Tunitcha and Luka-Chukai Mts., *Goodman & Payson 2859* (CAS, GH, WTU). Mojave Co.: rocky slope, Nixon Springs, Mt. Trumbill, *Gould 1708* (ARIZ, CAS, GH). COLORADO. Denver Co.: hilltops, Clear Creek near Denver, *Clokey & Bethel 3260* (CAS, GH). IDAHO. Bear Lake Co.: steep hillsides, Montpelier, *Macbride 3* (G, GH, WTU). KANSAS. Ellis Co.: rocky hills 2 miles W of Hays, *Runyon 68* (ARIZ, CAS, MIL, WIS). MONTANA. Sheridan Co.: Westby, *Larsen 23* (G, GH). NEBRASKA. Thomas Co.: Middle Loup River near Thedford, *Rydberg 136B* (GH, NEB). NEVADA. Clark Co.: Kyle Canyon-Deer Creek, *Clokey 8104* (ARIZ, DAO, G, GA, GH, MIL, OSC, POM, PR, RSA, TENN, WIS, WTU). Elko Co.: Star Canyon, SE of Deeth, *Heller 10583* (CAS, G, GH). NEW MEXICO. Otero Co.: with *Populus*, *Atriplex*, *Poliomintha*, and *Yucca* on gypsum sand, interdunal flat, White Sands National Monument, *Piehl 59348* (GH, MICH, UC, US). Sierra Co.:

south end of Black Range, Kingston, *Metcalfe 950* (CAS, G, GH). OKLAHOMA. Custer Co.: with *Opuntia*, *Yucca*, *Castilleja*, and *Andropogon*, on sparsely-vegetated gypsum hillside 1 mile SW of Weatherford, *Piehl 59172* (GH, MICH, UC, US). OREGON. Malheur Co.: sandy roadbank 11.6 miles SW of Vale, *Chisaki 830* (ARIZ, WIS). SOUTH DAKOTA. Lawrence Co.: rocky open ground near Deadwood, *Palmer 37212* (GH). TEXAS. Garza Co.: with *Juniperus*, *Bouteloua*, *Polygala*, and *Ephedra* on dry exposed rim of caprock, Lott's Ranch, 7 miles SW of Post, *Piehl 59224* (GH, MICH, UC, US). UTAH. Salt Lake Co.: with *Purshia*, *Bromus*, *Ambrosia*, and *Artemisia* in fine reddish loam, Red Butte area, Ft. Douglas near Salt Lake City, 4,400 ft., *Piehl 59550* (GH, UC, US). Washington Co.: sandstone ledges, sandy flats, Diamond Valley, 10 miles N of St. George, *Gould 1552* (ARIZ, CAS, GH). WASHINGTON. Lincoln Co.: sandy hill above Grand Coulee Dam, *Rogers 382* (CAS, GH, POM, WIS, WTU). Whitman Co.: rocky slope 3 miles above Bishop, Snake River Canyon, *Marson 36* (CAS, GA). WYOMING. Albany Co.: gravelly "hogback ridge" 0.8 mile W of Centennial, 8,100 ft., *Piehl 59581* (GH, UC, US). Big Horn Co.: dry sagebrush hillsides near mouth of Antelope Creek, *Williams & Williams 3195* (G, GH, WTU). Sheridan Co.: dry hillside NE of Sheridan, *Rollins 431* (G, GH).

**CANADA.** ALBERTA. Devil's Lake, Banff, *Butters & Holway 24* (GH). BRITISH COLUMBIA. Sandy dry slopes, Summerland Experimental Station, *Calder & Savile 8076* (CAS, DAO, WTU); grassy slopes 4½ miles N of north end of Nicola Lake, N of Merritt, *Calder et al. 17540* (DAO, OSC). SASKATCHEWAN. Dry hill, Eastend, *Russell 85084* (DAO).

**MEXICO.** COAHUILA. Moist stream side, Canyon de Sentenela on Hacienda Piedra Blanca, Villa Acuña, *Wynd & C. H. Mueller 543* (ARIZ, GH).

## SUMMARY

Studies of the genus *Comandra*, a small group of perennial herbs widely distributed in North America and represented by a single member in the Balkan region, have been made from a broad biological standpoint involving essentially the entire developmental history of the plants.

Much new information is revealed in an anatomical-morphological survey of all organs, including data on the unusual blue coloration of rhizome and root cortical parenchyma, which has proven to be an excellent taxonomic character. The chromosomes, not before described, are comparatively small, and the gametic chromosome number is N=14, which constitutes a new number for the Santalaceae.

The findings from studies of the plant's floral biology include information on a wide variety of insect visitors; *in situ* pollen germination; multiple functions for the sepals, which persist and acquire pigments after anthesis; and the unusual secretory hairs which develop from the perianth and become attached to the anthers. Other studies provide data on germination, which is of the hypogaeous type. The seedlings, which can hardly be distinguished from small vegetative shoots of mature plants, are described for the first time. Data are also presented on sexual and vegetative reproduction, phenology, habitats, abundance, economic relations, and pathogens, including several fungi, insects, and nematodes new to *Comandra*.

Parasitic attachments are made to other plants by means of haustorial roots. Attachments were found to over 200 species, which appears to be the largest and most diverse natural host range now known for a root-parasitic flowering plant. Parasitism is evidently important for the optimum development of the plant at all stages, and is of particular significance during the first few years. Possible correlations between parasitism and certain structural and physiological features, e.g., few root hairs, the presence of numerous storage tracheids in foliar organs, generous amounts of phloem in the rhizome, and a propensity to wilt easily, have been indicated.

In North America the variation of characters previously used taxonomically in *Comandra* and of several new characters studied intensively was found, for the most part, to be clinal. Steps in the clinal gradients for several characters show an unusual degree of coincidence in two zones, separating New World populations into three taxa—*umbellata* in eastern North America, and *pallida* and *californica* in the west. In a revised taxonomic treatment these and a fourth taxon, *elegans*, from the Balkan region are shown to be conspecific, and are treated as subspecies of *Comandra umbellata* (L.) Nuttall. Among other alleged taxa in recent works, *Comandra richardsiana* Fernald was found not to merit recognition even at an intraspecific level. Additional evidence is given supporting the somewhat controversial segregation of *Comandra livida* as a monotypic genus, *Geocaulon* Fernald.

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TABLE 4. *Cultures cited in plates.*

| Culture Number | Parts Obtained | Data |
|---|---|---|
| C-18 | rhizomes | White Sands Natl. Monument, Otero Co., New Mexico, 11 July 1959 (*Piehl 59348*,[17]). |
| C-19 | fruits | " " " " |
| C-76 | fruits | Near Parker Creek Forest Experiment Station, Sierra Ancha Mts., Gila Co., Arizona, 23 July 1959 (*Piehl 59454*). |
| C-85 | rhizomes | Three mi. N. of Levels, Hampshire Co., West Virginia, 17 Apr. 1960 (*Piehl 6005*). |
| C-90 | rhizomes | Shore of Lily Lake, Cape May Point, Cape May Co., New Jersey, 21 Apr. 1960 (*Piehl 6022*). |

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[17] Specimens cited without herbarium abbreviation indicate material in my personal herbarium.

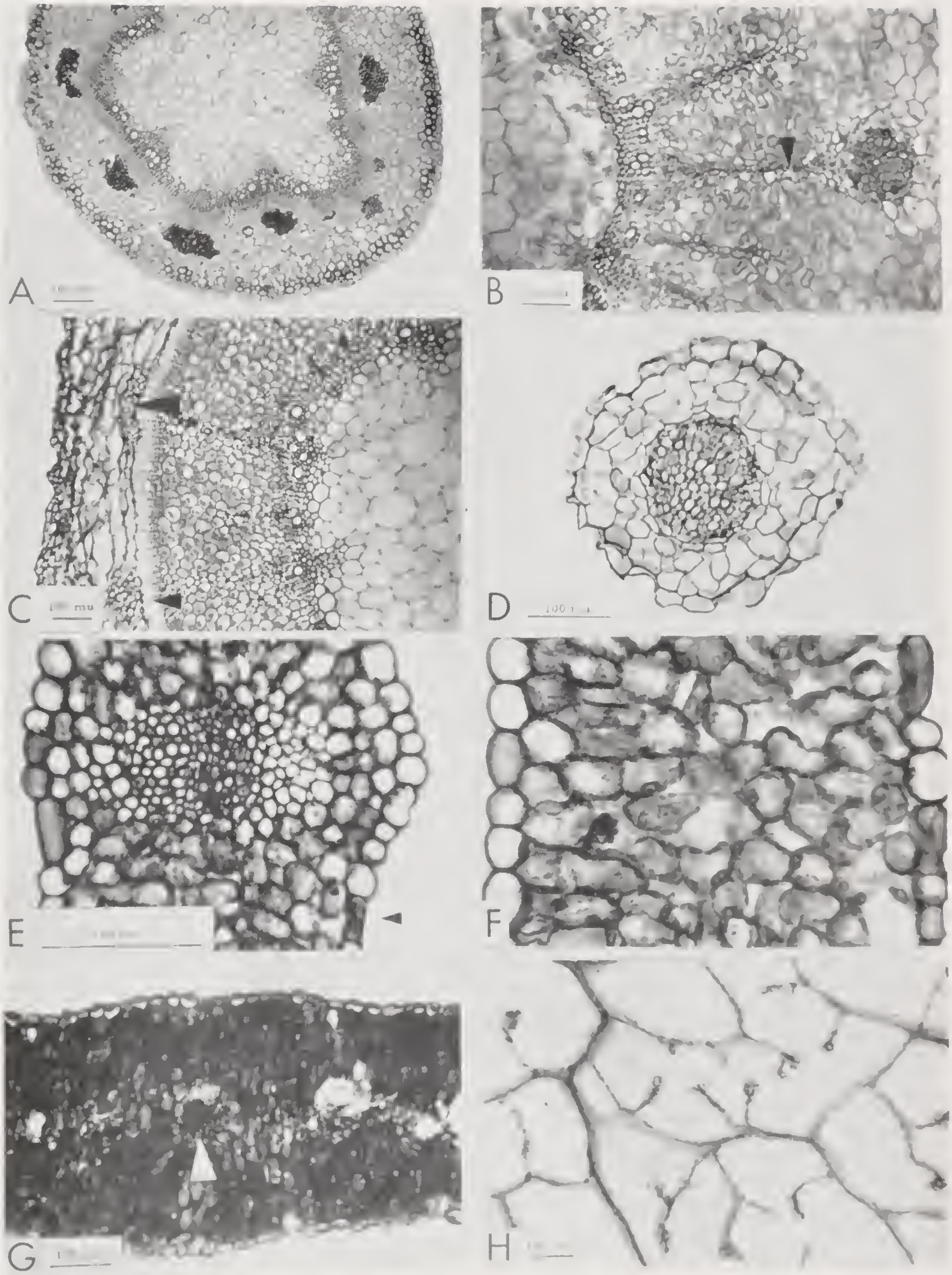

Plate 1.[18] Stem, root, and leaf anatomy. A. Cross section of aerial stem with irregular zone of (largely) primary xylem bordering pith (center) bounded by vascular cambium, phloem, phloem fibers (irregular black patches) and cortex. B. Cross section of swollen rhizome tip of subsp. *pallida* showing broad band of primary phloem including radial extensions (pointer; pith at left), some of them terminated by fibers; abundant parenchyma between the extensions. C. Cross section of older rhizome with primary phloem fibers (large pointer) and collapsed cortex outside of cork cambium (small pointer). D. Cross section of young root showing loosely organized cortical cells surrounding stele. E. Cross section of leaf showing midvein; a stoma is evident on lower surface (pointer). F. Cross section of leaf in non-vein area displaying weak differentiation of palisade (lower surface at r.). G. Cross section of subsp. *pallida* leaf showing abundant "tannin" bearing cells (dark), more compact structure, sclerenchyma cells (light areas), and lack of differentiation of upper and lower surfaces (midvein at pointer). H. Vasculature of leaf between midvein and margin from cleared whole mount

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[18] Unless otherwise specified, material of subsp. *umbellata* from Michigan study areas is shown in all plates.

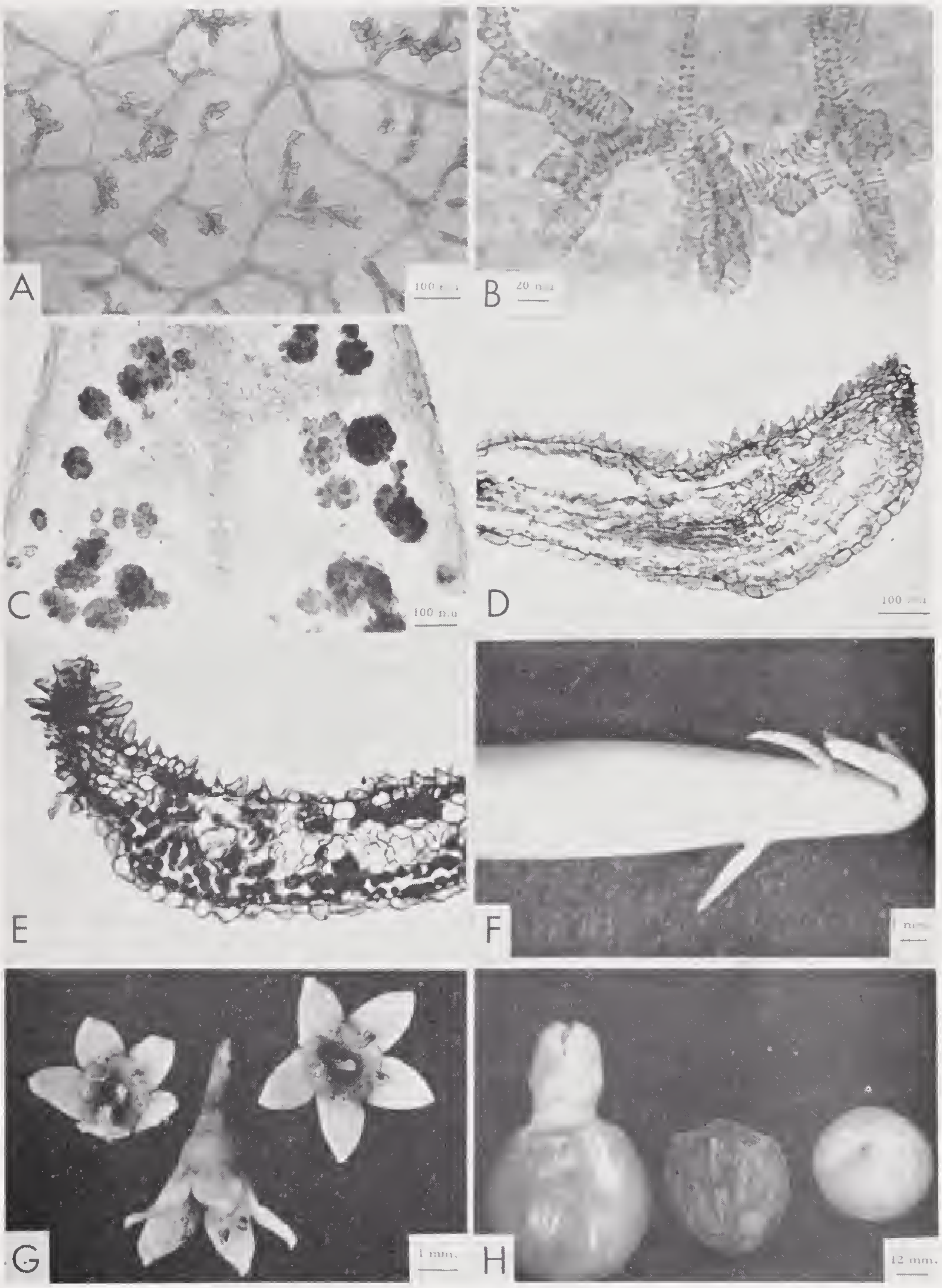

PLATE 2. Leaf and sepal anatomy and general morphology. A. Vasculature of subsp. *pallida* leaf between midvein and margin (A-C are cleared whole mounts). B. Close-up of A showing dilated vein endings composed of storage tracheids. C. Groups of sclerenchyma ("silicified") cells in subsp. *pallida* leaf. D. Longitudinal section of upper part of subsp. *umbellata* sepal with pointed hairs along adaxial surface (top). E. Same for subsp. *pallida* showing abundant "tannin"-filled cells (black). F. Terminal part of rhizome with reflexed tip and scales. G. Newly opened flowers with sepals pushed back (upper r.) to show stamens, disc, and style. H. Mature fruit, entire (l.); epicarp and floral parts removed (middle); seed only (r.).

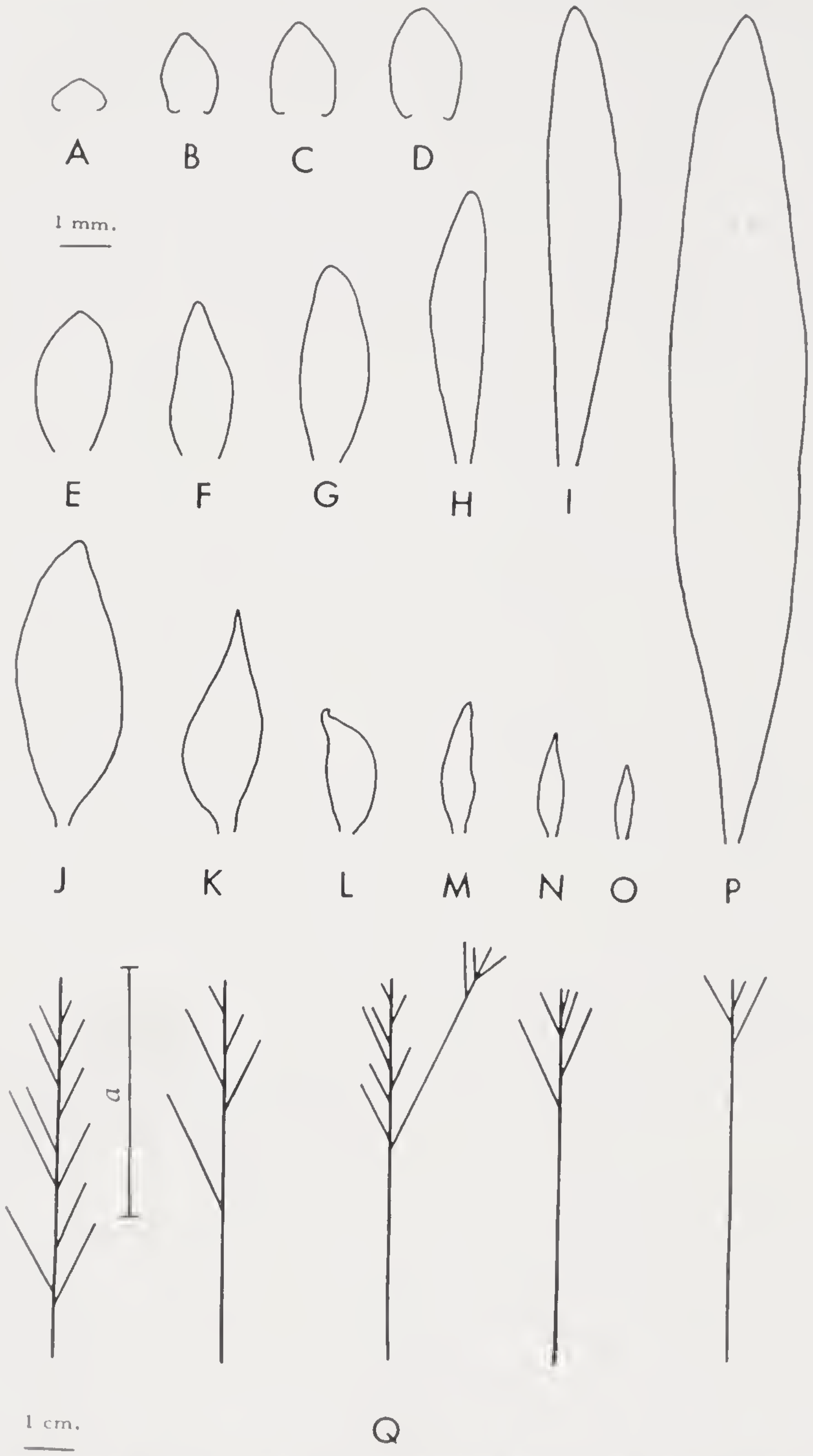

Plate 3. Foliar appendages and inflorescence structure. A-P. Spectrum of foliar appendages: A-D. bud scales (outer to inner), E-G. scale leaves, H-I. lower leaves, J-M. bracts, N-O. bracteoles, P. leaf from mid-portion of stem. Q. Diagramatic representation of variation in inflorescence form; distance measured when evaluating inflorescence structure is indicated at a.

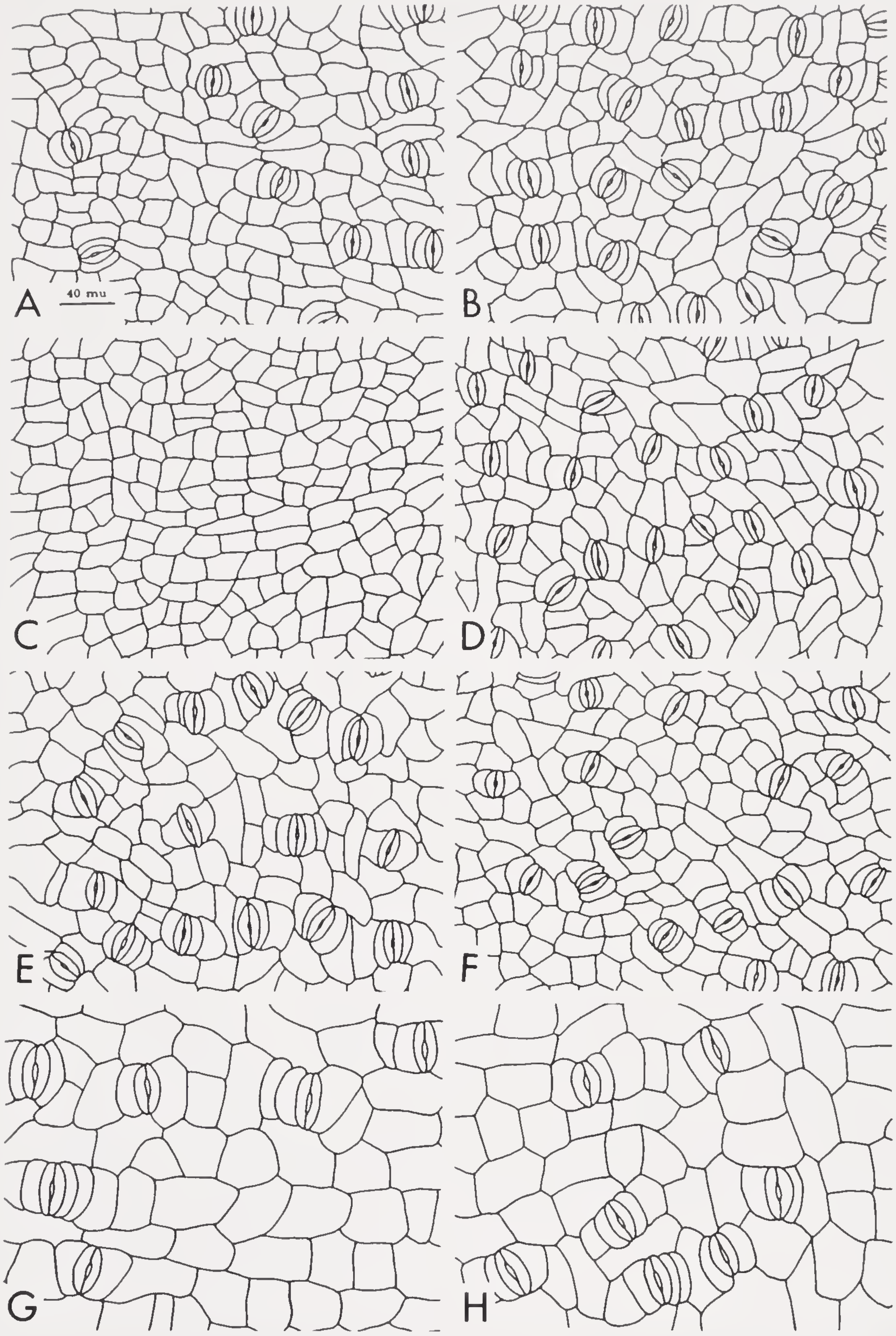

Plate 4.[19] Leaf epidermis patterns. A-B. Subsp. *elegans* (*Effremov* in 1951, MICH). C-D. Subsp. *umbellata* (*Piehl 5809*, MICH). E-F. Subsp. *californica* (*Heller 7937*, GH). G-H. Subsp. *pallida* (*Piehl 59172*, MICH).

[19] Upper (adaxial) epidermises are at left, lower at right; midrib of leaf toward top of page in each case.

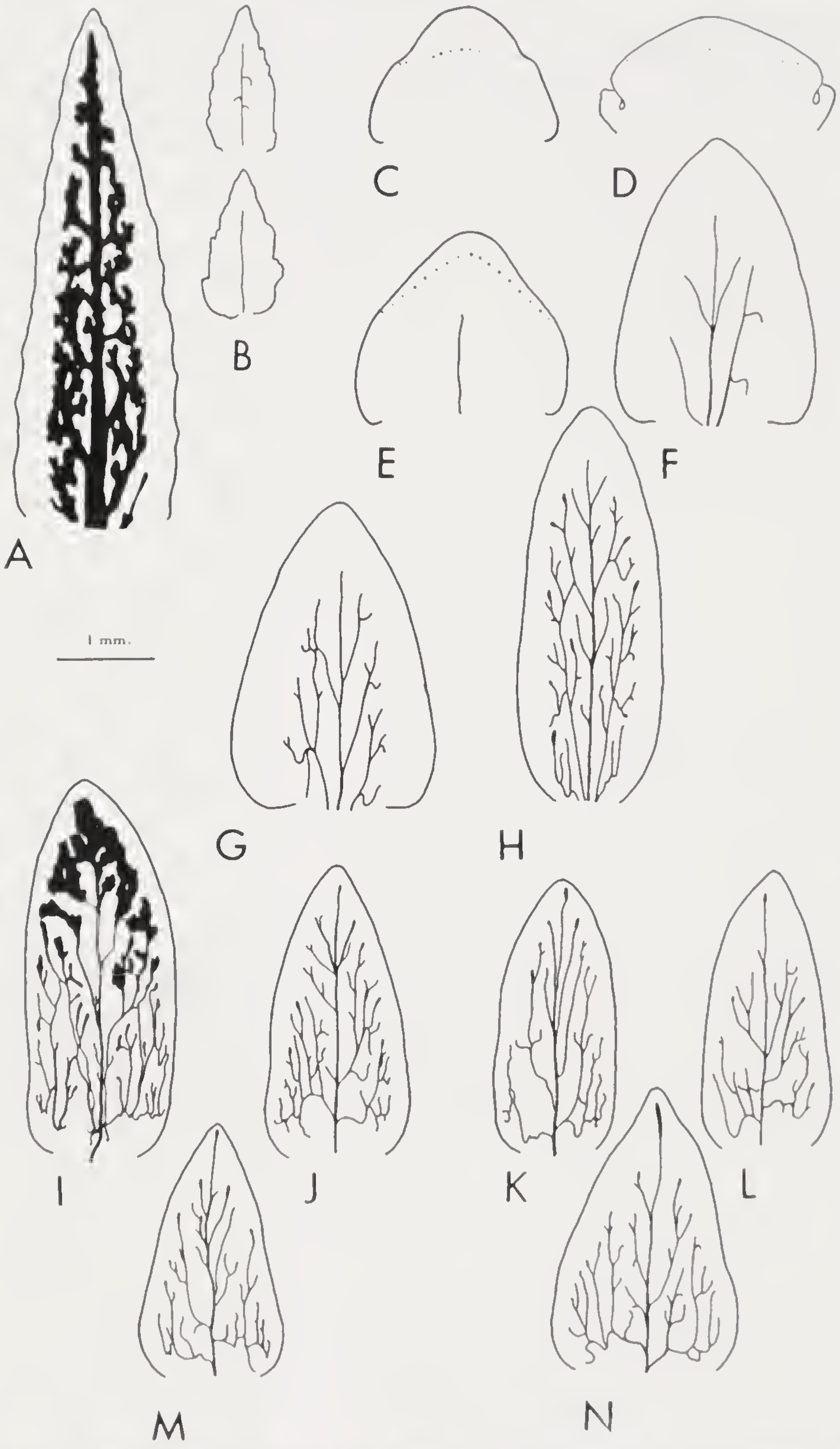

PLATE 5. Scale, scale-leaf, and sepal morphology. A. Rhizome scale of subsp. *pallida* showing veins greatly broadened by abundant storage tracheids. B. Rhizome scales (subsp. *umbellata*) showing simple venation (and no storage tracheids) and irregularly toothed margin. C-E. Bud scales showing scarious tip (dotted line) and either lack of veins or only a single trace (E). F-H. Inner bud scales and lowest scale leaf (H) showing progressively more complex venation. I-N Sepal shape and venation pattern: I. Subsp. *pallida* showing veins much widened near sepal tip by storage tracheids. J. Subsp. *californica* displaying some vein endings dilated by storage tracheids (also in K-N), K-L. Subsp. *umbellata* from Michigan (K) and Virginia (L). M-N. Subsp. *elegans* from Bulgaria (M) and Yugoslavia (N).

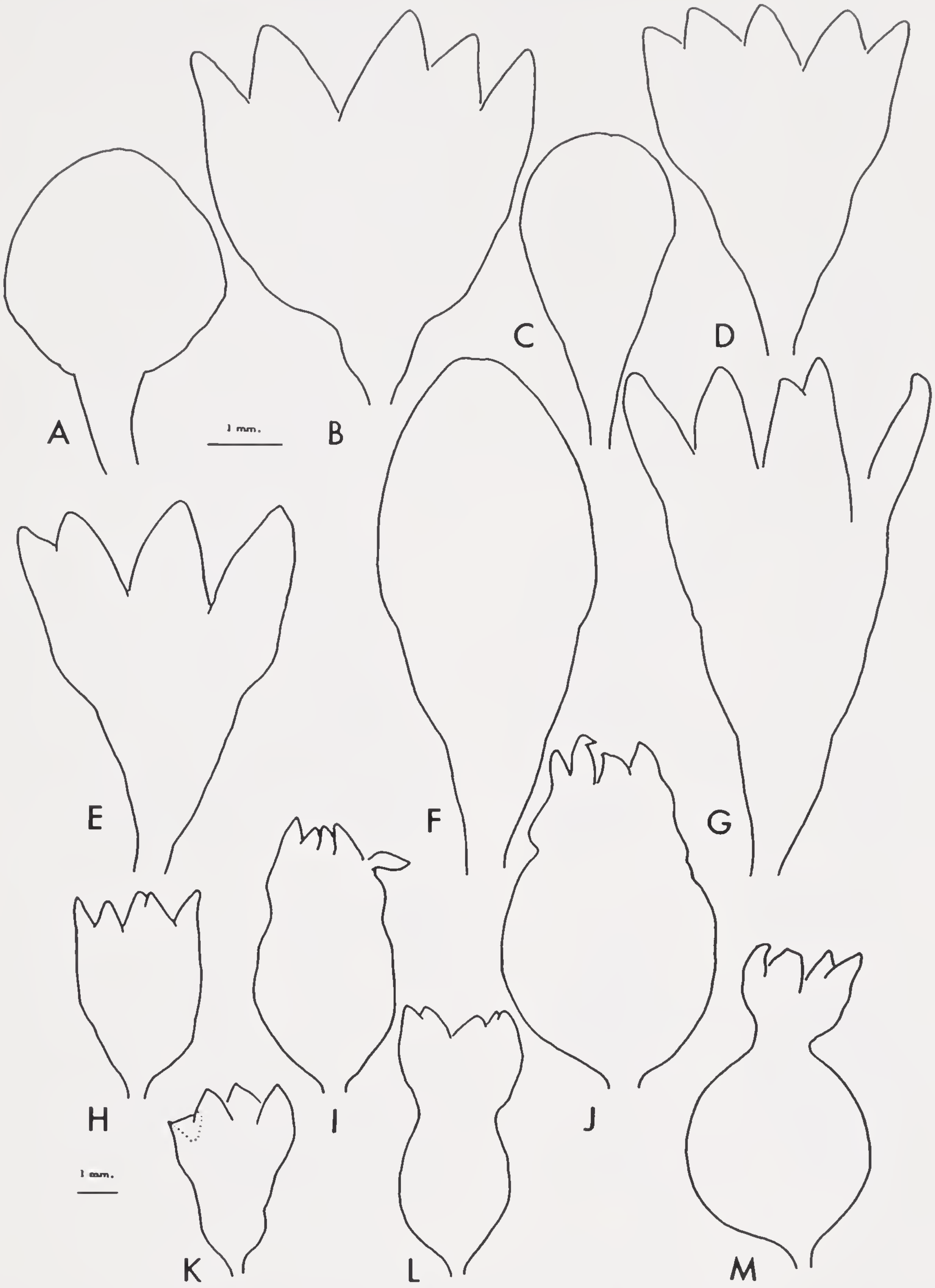

PLATE 6. Bud, flower, and fruit shape. A-B. Bud and flower of subsp. *elegans* (*Pančić* in 1880, PR). C-D. Bud and flower of subsp. *umbellata* (*Fernald and Long 11820*, GH). E. Flower of subsp. *californica* (*Heller 13013*, GH; bud similar to C). F-G. Bud and flower of subsp. *pallida* (*Clements & Clements* in 1903, GH). H-J. Progressively later stages in development of fruit of subsp. *elegans* (various collections) showing lack of neck above fruit. K-M. Similar stages for subsp. *umbellata* (*Piehl 5809*) showing short neck formed by fused portion of floral tube above ovary.

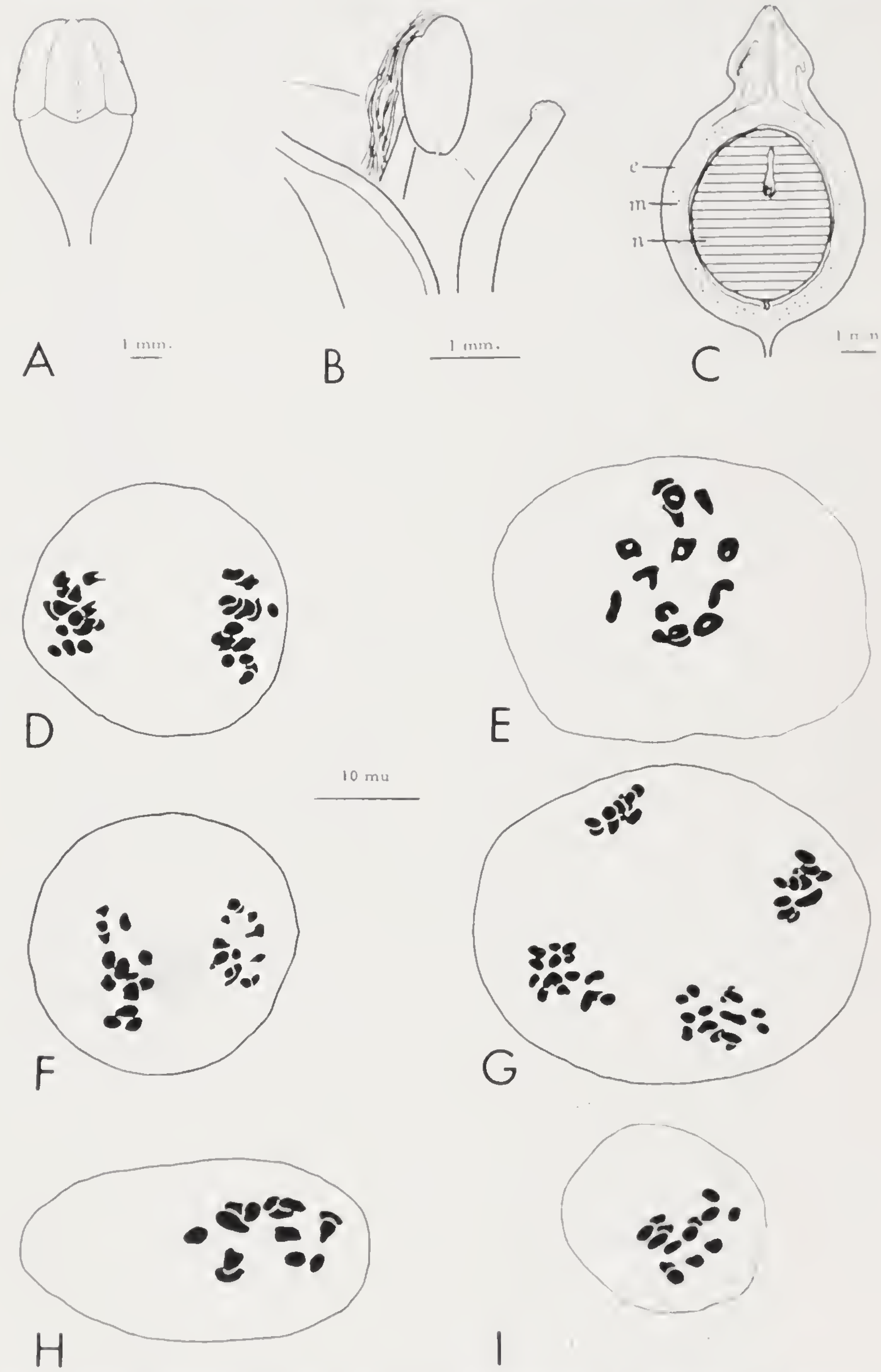

Plate 7. Floral morphology and meiotic chromosomes. A. Flower bud showing valvate aestivation just prior to opening (A-C are free-hand drawings). B. Bud as in A dissected to show relation of perianth hairs to anthers (hairs still unattached; sepal and style have been tilted away from stamen). C. Longitudinal section of mature fruit. Embryo (upper center) is embedded in endosperm (n); pericarp comprised largely of leathery epicarp (unshaded outer part, e) and bony mesocarp (m); a small amount of endocarp (unshaded) persists just inside mesocarp. Persistent flower parts crown the fruit. D-I. Camera lucida drawings of meiotic chromosomes; all N = 14: D. Subsp. *umbellata* at anaphase I (N. J., *Piehl 6023*) E. Subsp. *umbellata* at early metaphase I (Mich., *Piehl 6037*) F. Subsp. *umbellata* at anaphase I (Minn., *Piehl 6044*) G. Subsp. *pallida* at late anaphase II (S. D., *Peterson* in 1960) H. Intermediate between subsp. *californica* and subsp. *pallida* at metaphase I (Ariz., *Piehl 5944S*) I. Subsp. *pallida* at metaphase I (N. M., *Piehl 5951S*; mother cell wall indicated as a dotted line).

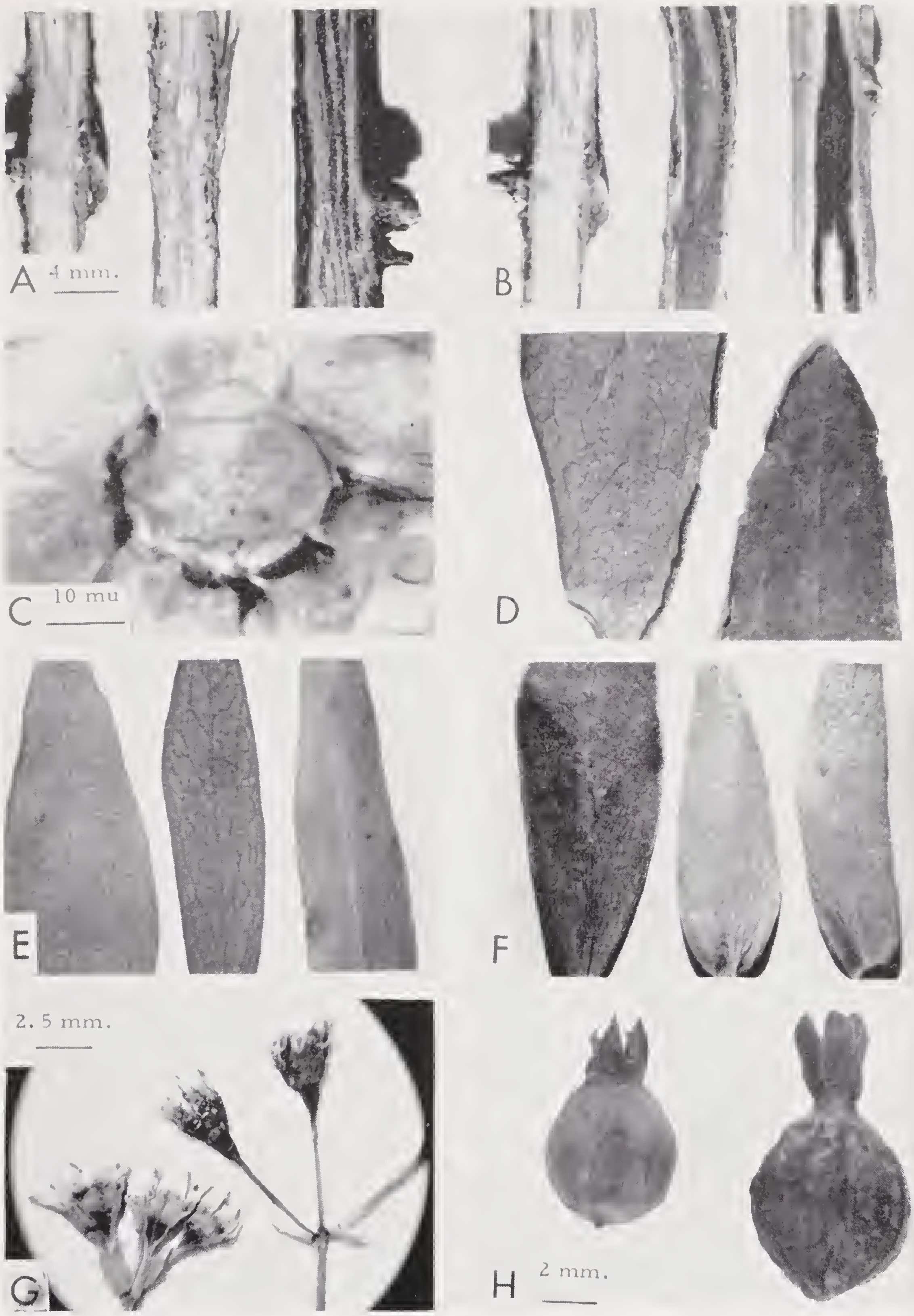

PLATE 8. Taxonomically important anatomical-morphological features. A-B. Rhizome cortical parenchyma color: (A) subsp. *umbellata* (*Piehl 58171*) compared with subsp. *elegans* (middle; *Jávorka* in 1929, BP) and subsp. *californica* (r.; *Piehl 59491*); (B) whitish in subsp. *umbellata*, blue in subsp. *pallida* (r.; *Piehl 59365*), brown in intermediate between them (middle; *Dworak* in 1912, NEB) (scale of B, D, E, and F as in A). C. Detail of blue, intercellular deposit around single rhizome cortical parenchyma cell (center) of subsp. *pallida* (*Piehl 59224*). D. Upper (r.) and lower leaf surfaces of subsp. *umbellata* (Mass., *Rand* in 1891, GH) showing curled margin, conspicuous veins, and whitened lower surface. E. Lower leaf surfaces of subsp. *umbellata* (l.; Mich., *Hermann 6790*, GH) and of intermediates between subsp. *umbellata* and subsp. *pallida* (middle; Neb., *Aughey* in 1874, NEB; r.; Neb., *Dworak* in 1912, NEB) with progressively less curling of margin, protrusion of veins, and greater leaf thickness. F. Lower leaf surfaces of subsp. *pallida* (l.; Wash., *Constance & Beetle 2745*, WTU; middle; N. M., *Piehl 59348*), plus upper surface of latter showing similarity. G. Individual cymules showing extremes in pedicel lengths: subsp. *umbellata* (l.; *Piehl 6037*) and subsp. *elegans* (*Wagner* in 1910, PRC). H. Fruits and persistent calyces of subsp. *umbellata* (*Piehl 59774*) and subsp. *pallida* (r.; *Piehl 59581*), the latter with fleshier, more oblong sepals, thicker, more roughened pericarps and larger, often less globose fruits. Floral tube constricted into a neck below calyx (r.); neck essentially lacking (l.).

PLATE 9. General morphology and variation. A. Pollen grain in optical section (polar view); minute striations are faintly visible within the wall. B. Pollen in equatorial surface view showing reticulate exine. C. Successive stages of germination from hypocotyl (r.) to epicotyl stages in subsp. *pallida* (C-19). D. Seedlings of subspecies *pallida* (l.), *californica* (middle), and *umbellata* (age varies slightly; center pot diameter = 12 cm.). E. Distinctly 3 ranked leaves of sterile shoot (E-H from Cheboygan Co. Mich.). F. Vigorous clone partly excavated to show invading rhizomes. G. Part of a clone with much-branched shoots. H. Part of a clone with many, ascending (not wilted) leaves from same locality as G.

Plate 10. Phenology, habit variation, and parasitism. A. Aerial stem bases in winter showing enlargement of several axillary buds (upper), single bud (lower; subsurface bud also visible on rhizome), and lack of enlarged buds (middle). B. Axillary buds showing early bud expansion in spring. C. Spring flushing showing stem tips enveloped by large leaves, producing a swollen aspect (approximate stage of meiosis in anthers). D. Later spring aspect with flower buds, now white, visible. Several shoots have arisen from one caudex. E. Habit of specimens grown in uniform culture (l. to r.): subsp. *umbellata* from New Jersey (C-90) and West Virginia (C-85); intermediate between subsp. *pallida* and subsp. *californica* from Arizona (C-76); and subsp. *pallida* from New Mexico (C-18). F. Numerous shoots from single decumbent aerial stem which overwintered. G. Large haustoria firmly attached to *Populus grandidentata* root. Much smaller haustorium at pointer. *Comandra* rhizome parallels host root below. H. Vertical section of haustorium which has penetrated xylem and pith of *Poa* root (in transection at r.). A portion of curved xylem strand visible through center of haustorium.

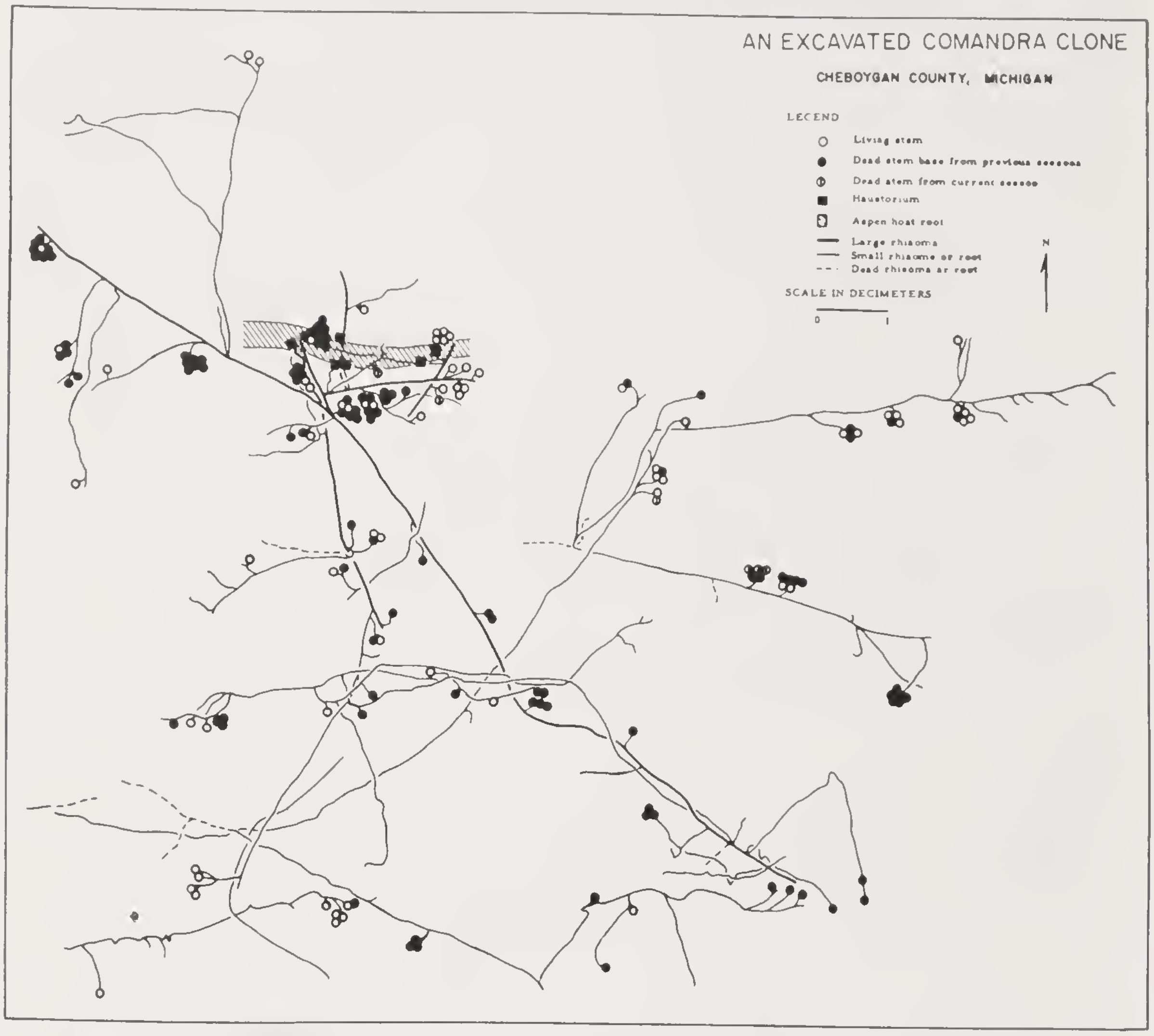

Plate 11. Map of an excavated clone. A small clone which had haustorial attachments to a single *Populus grandidentata* root, and which lacked vigor as evidenced by dead rhizomes and aerial stems, and little or no rhizome invasion. Mapped in August 1958, a few parts of the clone were still alive in 1962, and some haustorial connections intact.

PLATE 12. *Comandra* habitats. A. Subsp. *umbellata* grew in back of (to right) and along crest of berm; fruits dispersed lakeward. First seedling from nature found here in 1960 (Lake Michigan shore, Sturgeon Bay, Emmet Co., Michigan). B. Subsp. *umbellata* was collected near sea level along this road and in open woods (Atlantic Co., New Jersey). C. Subsp. *umbellata* was collected from this dry, rocky roadbank in the Appalachian region (ca. 2,100 ft.; Fulton Co., Pennsylvania). D. Subsp. *pallida* was found near rim of caprock (foreground) (Garza Co., Texas). E. Subsp. *pallida* occurred abundantly in interdunal flat and less frequently in loose gypsum sand of dune (White Sands, Otero Co., New Mexico). F. Subsp. *californica* grew in very dry soil among shrubs (*Arctostaphylos* largely) and conifers (Tuolumne Co., California). G. Specimens intergradient between subspecies *californica* and *pallida* occurred about the bases of oaks at the crest of a roadcut (Santa Catalina Mts., Pima Co., Arizona). H. Much-branched, linear-leaved specimens of subsp. *pallida* growing with *Opuntia* in gypsum soil (Custer Co., Oklahoma).

PLATE 13. Selected herbarium specimens. A. Subsp. *elegans* showing development of lateral shoots from caudex which in upper specimen was decumbent (*Zitti & Forstner 1671*, BP). B. Variation in habit and leaf width of subsp. *elegans* (*Borbás* in 1873, BP (r.); *Borbás* in 1891, PRC (upper l.); *Wagner* in 1911, PR (lower l.)). The small shoot at the upper left shows lateral shoots from a short, erect caudex. C. Subsp. *umbellata* showing tall shoots with paniculate inflorescence (Conn., *Eames* in 1893, 1895, GH). D. Subsp. *umbellata* (Newfoundland, *Pease & Long 28110*, GH) displaying shorter habit, corymbose inflorescences, and short caudices.

PLATE 14. Selected herbarium specimens. A. Subsp. *californica* showing long caudex with many lateral branches and strongly floriferous aspect often found in this subspecies (Calif., *Heller 13013*, WTU). B. Exceptionally tall specimen of subsp. *californica* with long caudex from which 9 shoots have arisen; 2 mature fruits are still attached (Ariz., *Piehl 59453*). C. Unusually tall specimen of subsp. *pallida* with long, attenuate leaves and large flowers (B. C., *Calder & Savile 7977*, DAO). D. Subsp. *pallida* with linear leaves on lateral branches and elliptic to ovate leaves on main axis; caudex is lacking as aerial stem dies back completely (Okla., *Stevens 298*, GH).

PLATE 15. Distribution of *Comandra* in the Balkan States. (Map reprinted with permission from John Wiley & Sons, Inc.)

Plate 16. Distribution of *Comandra* in North America. As in Plate 15, the distribution shown here is inclusive; *Comandra* is, of course, actually absent from many local (sometimes sizeable) areas. Inset at lower left shows details of Arizona distributions (large circles show localities for subsp. *californica*; shading as in legend). Map reprinted with permission from John Wiley & Sons, Inc.

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