THE SYSTEMATICS AND ANATOMY OF GONGYLOCARPUS (ONAGRACEAE)

SHERWIN CARLQUIST AND PETER H. RAVEN
Claremont Graduate School, Claremont, California, and
Division of Systematic Biology, Stanford University, Stanford, California

ABSTRACT

The unique fruiting structures of the closely related, principally Mexican, monotypic genera Gongylocarpus and Burragea (Onagraceae) compelled a detailed anatomical and cytological investigation of these plants which led to the conclusion that they should be included in a single genus, Gongylocarpus. Gongylocarpus fruticulosus (Burragea), endemic to two adjacent islands off the west coast of Baja California, is divided into two subspecies, subsp. fruticulosus and subsp. glaber. The vegetative and floral anatomy, including wood anatomy, of both species is described. The fruits of these two species grow into the stem by meristematic activity during the course of ontogeny, the ovaries in the mature flower being superficial and sessile in the leaf axil. There is no pedicel associated with the flower, but only a branch gap. Meristematic tissue at the base of the locules divides rapidly at a relatively late ontogenetic stage, the ovaries growing downward into the stem and crushing the pith. The mature, heavily sclerenchymatous fruits are located wholly within the stem, and in G. fruticulosus they are aggregated into long chains. Both species have a gametic chromosome number of n = 11, a characteristic otherwise unknown in the tribe Onagraceae but shared with other generalized groups in the family. Taken together with other features, this suggests a primitive position within the tribe for Gongylocarpus.

GONGYLOCARPUS (ONAGRACEAE) is a principally Mexican genus of two very distinctive species characterized by a unique fruiting structure. In both, as will be shown in this article, the mature capsules become deeply imbedded in the pith of the stems on which they are borne. One of these species, G. rubricaulis Schlecht. & Cham. (Fig. 3), is a weedy annual with small white flowers, widespread in mainland Mexico and adjacent Guatemala, from ca. 1200—2300 m elevation (Fig. 1). The other, G. fruticulosus (Benth.) T. S. Brandegee (Fig. 2), is a low shrub with large purple flowers, entirely confined to two adjacent islands in Bahía Magdalena, Baja California, where it occurs near sea level (Fig. 1). The latter was segregated as the genus Burragea by Smith and Rose in 1913, and this segregate genus has subsequently been accepted as distinct. The present study was undertaken to determine the degree of relationship between these two habitually very distinct species, particularly in the light of a comparative anatomical investigation; to investigate their position within the family Onagraceae; and to provide an adequate description of the ontogeny of their bizarre fruiting structures.

Gongylocarpus (Onagraceae) first came to the attention of the botanical world through collections of the weedy annual G. rubricaulis (Fig. 3) made by Schiede and Deppe from "cultus et inculitis circa Jalapam" (i.e., near Jalapa, Vera Cruz). This material was made the basis of a new genus and species by Schlechtendal and Chamisso in 1830. The species is so distinct and uniform that it has never been placed in any other genus, described under any other name, or subdivided taxonomically. Its flowers open early in the morning and the short white petals are fugacious; collections made in the middle of the day or in the afternoon often lack them completely. The anthers deposit pollen directly on the globose stigma soon after the flowers open, although the stigma may ultimately be held above the anthers. A full complement of seed is set following self-pollination. We have not seen insects at the flowers of the two populations studied in Chiapas (cited below), nor on plants cultivated in San Cristóbal las Casas, Chiapas, within the native range. This predominant autogamy may help to account for its uniformity over its rather wide range (Fig. 1). Gongylocarpus rubricaulis very often occurs as a weed in cornfields, where its lax reddish stems may be conspicuous locally; sometimes it is found on rocky slopes, particularly in disturbed ground, and sometimes in moist places. Although widespread, it is not often collected and is rather sporadic and local in occurrence.

The second species of the genus, G. fruticulosus (Fig. 2), was described by Bentham (1844, p. 15) as an aberrant species of Gaura. Bentham...
considered the imbedded fruits to be "the effect of some disease or parasite ... [and] not the healthy natural form of the plants." He considered his new species to be allied to the earlier described G. rubricaulis, the fruits of which he likewise considered diseased. Mrs. Curran (1888) found material of the Baja California species among collections made at Bahía Magdalena by Walter E. Bryant earlier the same year. Apparently in ignorance of Bentham's much earlier publication, she described it as a new species of Gongylocarpus, G. frutescens, and redefined Gongylocarpus to accommodate it. Mrs. Curran's future husband, T. S. Brandegee, visited Bahía Magdalena in January 1889 and in the report of plants he collected in Baja California made the combination Gongylocarpus fruticulosus, reducing G. frutescens to synonymy. In 1913 Smith and Rose separated G. fruticulosus as the type of a new genus which they named Burragea in honor of the commander of the steamer in which Rose had visited Baja California in 1911.

It is now possible to specify the range of Gongylocarpus fruticulosus (usually given as "vicinity of Magdalena Bay") somewhat more closely than in the past, following our study of journals, herbarium labels, and the pertinent literature. This species is absent on the mainland, which is flat and monotonous on the plains behind Bahía Magdalena, and occurs only on the two islands forming the outer margin of the bay. Here it grows in sandy arroyos draining off the high granitic ridges and nowhere else. Populations of this species on the southern island, Isla Santa Margarita, are identical with those on the southern end of the northern island, Isla Magdalena, being separated by about 5.5 km of water. Plants in both areas are relatively narrow-leaved and pubescent, with the pubescence in some individuals consisting of short, and in others of long, unicellular trichomes. The longer trichomes differ from the shorter ones only in the length of their stalk; both have a bulbous head (Fig. 6). Thus neither is appropriately described as more "glandular" (Munz, 1960) than the other. These two pubescence forms are often obtained in mixed collections, form part of interbreeding populations, and in our opinion do not deserve the taxonomic recognition accorded them by Munz (1960), as Burragea fruticulosa var. frutescens (Curran) Munz and var. fruticulosa, respectively.

Fig. 1. Mexico and Guatemala showing distribution of Gongylocarpus. G. rubricaulis, dots; G. fruticulosus subsp. fruticulosus, filled triangle; subsp. glaber, open triangle.

Fig. 2—3.—Fig. 2. Gongylocarpus fruticulosus subsp. glaber, Moran 10804, habit of flowering and fruiting branch.—Fig. 3. G. rubricaulis, McVaugh 18937, habit of flowering and fruiting branch. Both, X 3.
The southern high ridge of the northern island, Isla Magdalena, is just over 16 km long, and from its northern end a long, narrow sand bar curves around some 24 km, forming the eastern shore of Bahía Santa María. At the north end of this bay, and still part of Isla Magdalena, a second high granitic peak reaches about 380 m in height. In the arroyos of the vicinity occurs the third major group of populations of the species. These are separated from the populations on the southern end of the island by a much larger gap of unfavorable territory than that between the two islands. In this northern area the plants are glabrous with blunt leaves mostly 4–7 (not 2–4) mm wide. The first collections here were made by Rose in 1911, and were curiously confused with Mrs. Curran’s *G. frutescens*, an error probably made because she made no mention of pubescence in her original description. Thomas (1950) recognized this error but still considered this group of populations worthy of specific rank, and described them as *Burragea glabra*. Still later Munz (1960) reduced this taxon to subspecific status, a decision with which we concur, especially in view of the geographical pattern outlined in the present paper. This necessitates the following new combination: *Gongylodocarpus fruticulosis* (Benth.) T. S. Brandegee subsp. glaber (Thomas) Carquist & Raven, comb. nov.


Munz’s choice of a lectotype for this species has been discussed by Raven (164ab).

*Gongylodocarpus fruticulosis* is a shrub up to at least 1 m tall with thick woody stems. Johansen (1930) has published a photograph of the habit of *G. fruticulosis* subsp. *fruticulosis* taken near the southern end of Bahía Santa María. The persistent rose-purple petals of *G. fruticulosis* are longer than the sepals and often exceed 1 cm in length, whereas in *G. rubricaulis* the fugacious white petals are only about 2 mm long. In *G. fruticulosis* the flowers open in mid-morning and the globose stigma is held well above and away from the anthers at anthesis. These flowers are said to be frequented by numerous insects in nature, and Dr. Reid Moran took a number of small beetles, a bee, and a moth from two different populations. Furthermore, the species is apparently self-incompatible, as determined from failure of a healthy plant of *G. fruticulosis* subsp. *glaber* (progeny of Moran 10804) cultivated at Stanford to set seed following repeated self-pollination. Most strikingly, the fruits of *G. fruticulosis* are imbedded in the stem in sausage-like swollen chains (Fig. 2), which are perhaps shorter in subsp. *glaber* than in subsp. *fruticulosis*. The fruits of the annual *G. rubricaulis* are imbedded individually (Fig. 3), although, as pointed out in the original description, they may be in loose chains. This, taken together with the thick, entire leaves of *G. fruticulosis* and the much thinner, denticulate ones of *G. rubricaulis*, renders each species very distinctive in aspect. The following pages will be devoted principally to an evaluation of the similarities and differences between them.

**Materials and Methods—** Anatomical preparations were based mostly upon specimens collected in the field and preserved in FAA or FPA. These collections included *Gongylodocarpus fruticulosis* subsp. *fruticulosis*, Man-of-War Cove, Isla Magdalena, Baja California, Moran 10810 (DS); south of Puerto Cortez, Isla Santa Margarita, Moran 10830 (DS); *G. fruticulosis* subsp. glaber, Bahía Santa Maria, Isla Magdalena, Moran 10804 (DS); *G. rubricaulis*, Toh Tik Paraje, Municipio of Chamula, Chiapas, Breedlove 7154 (DS—developmental studies of young fruits), 7860 (DS); SW side of Teopisca, Chiapas, Breedlove 7864 (DS). Dried material of *G. rubricaulis*, Sierra del Tigre, 3 mi S of Mazamitla, Jalisco, McVaugh 13937 (RSA), proved useful for anatomical study because it bore mature fruits. Liquid-preserved materials proved excellent for general anatomical purposes and for ontogenetic studies of flower and fruit. Because ovules and seeds are imbedded within the stems, special fixation techniques would be required for studies of embryoology, which could thus not be undertaken here.

Sections of stems bearing flowers in various stages of development were prepared from all liquid-preserved collections. To demonstrate ontogenetic sequences many series of longitudinal sections were required. These sections were supplemented with several series of transverse sections, and both transverse and longitudinal sections of mature fruiting stems. Younger stages were sectioned at 6–10 µ, mature stages at 12–15 µ. Although all three collections of *G. fruticulosis*, representing the three main areas of this species, were studied intensively, there proved to be no appreciable anatomical differences among them. Sections were stained with a safranin–fast green technique corresponding to Northen’s modification of Foster’s tannic acid–ferric chloride method (Johansen, 1940). Sections of the dried material were prepared similarly except for expansion of the material in 2.5% aqueous NaOH prior to infiltration.

Wood was sectioned at 20–25 µ with a sliding microtome. Wood samples were liquid-preserved, a desirable procedure because of the phloem bands often present in woods of Onagraceae. The fixed material of *G. fruticulosis* had been contaminated with ferric salts owing to rusting of metal caps on jars. This iron contamination proved desirable because it pre-stained phloem bands. Thus a simple safranin stain without counterstaining proved sufficient for wood sections.
Vegetative anatomy—Ergastic substances—
Onagraceae are rich in ergastic materials. Crystals (presumably calcium oxalate), gums, and mucilages have been reported by Metcalfe and Chalk (1950). As noted by Metcalfe and Chalk, mucilage idioblasts may or may not contain crystals. In Gongylocarpus fruticulosus these and other ergastic materials are present. Some, such as those observed in wood, take the form of massive accumulations, yellowish in unstained sections and staining brightly with safranin. These appear to contain an oily or resinous component. Others, which appear granular and grayish, seem tannin-like or phlobaphene-like in character. Obviously, much remains to be learned about ergastic materials in Onagraceae. One or more of the above materials may account for reports of milky juice in Gongylocarpus rubricaulis on certain herbarium labels (Hinton 5039 and 8134, both from Pantoja, Temascaltepec, México). We have not been able to confirm this observation ourselves in living plants, however.

Trichomes—Single-celled hairs (Fig. 6) are scattered over protoderm and young epidermis of both species. The trichomes are identical in both. In the three collections of Gongylocarpus fruticulosus, these trichomes persist to various extents on the mature leaves and stems. They are not apparent on mature herbage of subsp. glaber, whereas they occur in subsp. fruticulosus. These differences occur late in ontogeny, and there is no basic difference in trichome type or occurrence among the populations of this species. The thin wall and bulbous head of trichomes suggests that they are glandular. The supporting stalk is thick-walled but not, apparently, lignified.

Leaf anatomy—Leaves of the two species differ not only in gross morphology (Fig. 2, 3) but in anatomy as well. The thick leaves of Gongylocarpus fruticulius (Fig. 4) are composed of large cells which, in addition to a photosynthetic function, probably serve for water storage. These leaves are isolateral in construction. All mesophyll parenchyma cells contain chloroplasts (not indicated in Fig. 4) in abundance. In addition, small amounts of tannins were observed in many mesophyll cells. Occasional raphide-bearing idioblasts occur in the mesophyll. Epidermal cells are quite thick-walled on both surfaces. This thickening is not cutinized. The epidermal surface is raised into a series of ridges which run predominantly parallel to the long axis of the leaf. Leaves of Gongylocarpus rubricaulis (Fig. 5), on the other hand, are thin and bifacial. A single layer of palisade is present; the remainder of the mesophyll is spongy. Occasional crystal-bearing idioblasts are present. These cells contain packets of raphide-like prismatic crystals or packets of true raphides. Epidermal cells are small, do not have notably thick outer walls, but the external surface bears a pattern of relief much like that of Gongylocarpus fruticulosus leaves.
Fig. 7-11. Wood sections.—Fig. 7-9. Gongylotropus fruticosus subsp. fruticosus, Moran 10810.—Fig. 7. Transection. Many dark-staining cells are filled with an unidentified resin-like substance. The dark band near top is composed of thin-walled cells, some of which are sieve tubes.—Fig. 8. Transection showing thick-walled gelatinous fibers.—Fig. 9. Tangential section. Rays contain tannins.—Fig. 10-11. G. rubricaudis, Breedlove 71E4.—Fig. 10. Transection, more recently formed elements above.—Fig. 11. Tangential sections. Fig. 7, 9-11, × 70. Fig. 8, × 125.
In both there are three or four layers of lamellar collenchyma beneath the epidermis. As the stem matures these collapse into a compact papery tissue which creates the smooth appearance of stems in this genus. The cortex and pith consist of thin-walled parenchyma. Scattered within this parenchyma are large ovoid idioblasts containing raphides, mucilage, or both. During secondary growth, there is no sclerenchyma formation in cortex, pith, or secondary phloem. Bark formation consists only of successive cork layers formed from consecutive cork cambia. This results in the thin sheets of exfoliating cork so characteristic of older stems of Onagraceae.

Secondary xylem anatomy—Basal portions of Gongylocarpus fruticulosus stems accumulate a woody cylinder 8 cm or more in thickness, whereas G. rubricaulis stems have a woody cylinder about 1 cm in diameter. Wood anatomy of the former (Fig. 7–9) differs markedly from that of the latter (Fig. 10, 11) in certain conspicuous features, but basically they share the same pattern. The similarities and differences are best summarized in formal descriptions:

Gongylocarpus fruticulosus: Secondary xylem containing included (intraxylary) phloem in tangential bands of various lengths, rarely around the entire stem circumference. Vessels solitary, in radial chains, or pore multiples (average number of vessels per group: 1.97). Vessel diameter 20–102 (average 53 μ); vessel-element length 122–428 μ (average: 226 μ). Vessels with simple perforation plates. Intervascular pitting alternate, pits circular to elliptical in shape, about 5 μ long, vestured. Apertures of pits adjacent in a helix interconnected by continuous grooves. Tracheids and fiber-tracheids absent. Libriform fibers thin walled (2 μ) or thick walled (up to 8 μ), the latter with prominently gelatinous walls. Libriform fibers average 20 μ wide at widest point, average length 400 μ. Axial parenchyma vasicentric, scanty. Mucilage-bearing idioblasts present within phloem bands. Ray tissue heterocellular; procumbent cells restricted to multiseriate portions of multiseriate rays. Ray cells with lignified secondary walls. Multiseriate rays 2–3 cells wide at widest point, with long uniseriate rays. Multiseriate rays average 0.39 mm in height, uniseriate rays average 0.14 mm in height. Prismatic crystals present in some ray cells. Tannin-like or resin-like substances forming massive deposits in ray cells and, to a lesser extent, vessels, libriform fibers, and axial parenchyma.

Gongylocarpus rubricaulis: Secondary xylem without growth rings or included phloem. Vessels solitary, in radial chains, or pore multiples (average number of vessels per group: 1.88). Vessel diameter 24–110 μ (average: 63 μ); vessel-element length 143–551 μ (average: 361 μ). Vessel elements often caudate. Vessels with simple perforation plates (one scalariform-like multi-perforate plate seen). Vessel pitting chiefly scalariform, some alternate and opposite pitting present. Pits varied in length. Pit apertures wide. Vesturing vestigial or absent. Tracheids and fiber-tracheids absent. Libriform fibers thin-walled (2 μ). Libriform fibers average 36 μ at widest point, average length 490 μ. Axial parenchyma vasicentric, scanty. Ray tissue heterocellular; procumbent cells restricted to multiseriate portions of multiseriate rays. Ray cells with lignified secondary walls. Multiseriate rays 2, infrequently 3 cells wide at widest point, with long uniseriate rays. Multiseriate rays average 0.48 mm in height, uniseriate rays average 0.12 mm in height. Ergastic materials (including crystals) absent from all cell types.

Differences between wood of G. fruticulosus and that of G. rubricaulis seem largely related to habit. Because G. rubricaulis is a short-lived annual, its wood is more highly juvenilistic than that of G. fruticulosus. The presence of longer vessel elements and vessel pitting composed largely of scalariform pits with gaping apertures in the annual species are conditions related to paedomorphosis (Carlquist, 1962) and do not denote that its wood is more primitive than that of G. fruticulosus. Gongylocarpus rubricaulis may lack intraxylary phloem because of its limited accumulation of wood. The two genera differ conspicuously with regard to accumulation of ergastic materials.

The woods offer few features which have not been reported previously for Onagraceae (e.g., Metcalfe and Chalk, 1950). The scalariform pitting in G. rubricaulis is one of these. The presence of grooves on vessel walls of G. fruticulosus is also apparently reported for the first time in the family, but it is probably related to xeromorphy. Such grooves are common, for example, in Compositae of arid situations (Carlquist, 1985). The habitat of G. fruticulosus—segments of the Baja California littoral—seems clearly xeric.

FLOWER AND FRUIT ANATOMY—The unique habit of bearing fruits within the stem in Gongylocarpus compels study of this phenomenon not only from a descriptive standpoint but with regard to ontogeny as well. The question of how this habit is achieved ontogenetically is much easier to answer than what is perhaps a more significant question: how was this mode of fruiting achieved phylogenetically?

The development of the flower is, in fact, quite uncomplicated. As shown in Fig. 12, a floral primordium is first apparent as a flattish emergence within the axil of a leaf primordium. This emergence is flattish rather than dome-shaped because at a very early stage the periphery gives rise to a ring-like primordium of the floral tube. This floral tube, the tips of which become calyx lobes, develops rapidly (Fig. 13). The tips of the future calyx lobes fold inward over what is now
a cup-like primordium. Primordia for corolla lobes and stamens appear within this cup (Fig. 14). They are followed in quick succession by emergence of primordia of the eight stamens and the two style branches (Fig. 15, 16, 17). The pair of style branches are formed laterally with reference to the stem, that is, along a tangent to the stem (Fig. 16). Simultaneously with appearance of petal primordia, a cavity develops in the center of the flower (Fig. 15). The base of this cavity will become the locules of the ovary, and the upper portions will become the narrow cavity which penetrates the floral tube. As the young flower grows (Fig. 15), this cavity becomes markedly elongate, an event which is due not so much to invaginating growth as to the elongation of the floral tube itself. Shortly after the formation of the cavity, meristematic areas subdivide the basal
portion into two locules. These meristematic areas (Fig. 17) take the form of two bands which grow toward each other, meeting, fusing, and forming a septum which is oriented along a radius of the stem bearing the flower. Simultaneously, the two style primordia grow toward each other at right angles to the septum primordia below (Fig. 16). The pair of style primordia fuse, except for the space which penetrates the floral tube, a space which in the mature flower is lined by stigmatoid tissue. Later developments (Fig. 18) include elongation of the floral tube, innervation of all primordia with procambium, and formation of a mound-shaped nectary at the base of the style. In the ovary region a pair of ovule primordia appear, one on each side of the septum (Fig. 19, 20). From the time of their appearance the ovule primordia grow downwards. One, then two integuments are initiated in succession around the nucellus primordium.

Notable at this stage is the fact that the ovary and its contained ovules are within the leaf axil but not yet imbedded within the stem, contrary to all earlier descriptions. Invasion of the pith region is achieved in later stages (Fig. 18, 21). This invasion is accomplished not by submergence of the ovary, but by pronounced growth of its lower portions. The base of the ovary locule at stages such as those of Fig. 19 and 22 is highly meristematic and stains deeply. Divisions in this region lengthen the loculi markedly. These divisions (Fig. 22) form packets of cells which resemble those produced by rib-meristem activity somewhat, although the files may be variously oriented.

The venation of the floral tube and ovary at anthesis is shown in Fig. 23. The flower is seen to be sessile within the axil of a leaf. The leaf at this node is unilacunar, supplied by a single unbranched trace. Despite the departure of only a single trace, the leaf gap is rather wide. There are four major and four minor veins within the floral tube. These are supplied by branches from the edges of the gap. The lowest pair forms, by fusion, the abaxial of the major traces. The middle pair forms the lateral pair of major traces. The upper pair forms by fusion upward the adaxial of the major floral-tube traces. Note should be taken of the fact that the adaxial floral-tube bundle is inverted in orientation compared with stem bundles. There is, in fact, a shift and inversion of xylem-phloem orientation where these bundles depart from the gap and fuse in their upward extent in the floral tube. Minor bundles branch from the major ones in symmetrical patterns indicated in Fig. 23. The septum is provided with a commissural vein between the adaxial and abaxial major floral-tube veins, and from this commissural vein the two ovule traces branch and extend downwards. A few strands of phloem (Fig. 21, lower right) may extend downward to the bottom of the locules. There is no xylem which penetrates into the pith as the fruit enters the pith.

The venation of flowers of the two species is alike in all essentials. Three locules per ovary often form in Gongylocarpus rubricaulis, whereas two are almost invariably present in G. fruticulosus. No exceptions were seen in either species to the presence of only a single ovule per locule.

At maturity the fruits of both species appear wholly imbedded within the pith of stems (Fig. 2, 3, 24–27). The floral tube is persistent in Gongylocarpus rubricaulis (Fig. 27), less so in G. fruticulosus (Fig. 24). The vascular cylinder is greatly widened by invasion of ovary tissues and ovules (Fig. 25, 26). This widening takes the form of lateral stretching of pith-ray parenchyma and cortical parenchyma; the bundles do not appear distorted; their rigidity is suggested by the presence of libriform fibers which result from secondary growth in the bundles. In G. fruticulosus pit cells are short lived and collapse even before the growth of ovary and ovules into the pith region.

The mature fruit wall in the two species is sclerenchymatous, but histologically, their fruit wall structure differs. In G. fruticulosus, the locules of the ovary are surrounded by a mass of sclerenchyma which is irregular in shape.

Fig. 12–23. Development of flower in Gongylocarpus fruticulosus.—Fig. 12. Apical meristem, showing primordium of flower in axil of leaf, left.—Fig. 13. Young flower, showing incurving calyx-lobes primordia.—Fig. 14. Young flower. Origin of corolla-lobes and stamen primordia and ovarian cavity are shown in this stage.—Fig. 15. Young flower, showing origin of style-branch primordia; floral-tube cavity is well formed at this stage.—Fig. 16–17. Transections of the stage shown in Fig. 15. Subtending leaf would be at left of these sections. Meristematic areas are shown stippled.—Fig. 16. Section at top of floral tube; the two style-branch primordia are seen, center, surrounded by petal and stamen primordia.—Fig. 17. Section at base of floral tube, in future ovary region. Origin of ovary septum is indicated by arrows: primordia from above and below meet and fuse.—Fig. 18–20. Sections from flower prior to anthesis. At this stage, origin of ovules upon septum is shown. Stippled area indicates meristematic zone at base of locules; broken lines represent procambium strands.—Fig. 18. Flower from radial section of a stem.—Fig. 19. From tangential section of a stem, base of ovary corresponding to that of Fig. 18, but sectioned at right angles to it, showing septum and origin of ovules.—Fig. 20. Transection of ovary region and base of subtending leaf.—Fig. 21. Section of flower shortly before anthesis, showing base of floral tube and ovary. The ovule and funiculus, center, are elongating rapidly downward into the rapidly growing locule base (stippled) which is invading the pith region. Xylem of bundles shown in black, phloem left clear.—Fig. 22. Packets of meristematic tissue from base of locule; epidermis of locule above.—Fig. 23. Three-dimensional reconstruction of node and auxiliary flower, showing venation. Brackets in figures = 100 μ except for Fig. 18–21, in which a 1-mm bracket with a 100 μ segment marked off is shown.
Facing the locule is a thin-walled epidermis (Fig. 28); underlying it is a hypodermis composed of small cuboidal thin-walled sclereids densely filled with rhomboidal crystals. Interior to the hypodermis are many layers of libriform cells. These are gelatinous fibers which result directly from the packets seen in Fig. 22. The lumina of these fibers are completely filled with an un-

![Diagram of stem sections containing fruits.](image)

Fig. 24–27. Sections of stem containing fruits. All are oriented with leaf or leaf scar at left. Portion patterned by vertical lines is sclerenchyma. Xylem of bundles is shown in black, phloem left clear.—Fig. 24–25. Gongylotus fruticosus subsp. fruticosus, Moran 10810.—Fig. 24. Portion of radial section of stem. Only left two-thirds of stem shown; this portion applies to the flower, the floral tube scar of which is seen, above left. The pith has been almost completely obliterated by expansion of fruits. Seed is shown attached to funiculus, which contains a vascular bundle.—Fig. 25. Transection of fruting stem. Median section of fruit with two seeds is shown, left.—Fig. 26–27. G. fruticosus, McVaugh 12887.—Fig. 26. Transection, showing three-loculate fruit in median section; trace of leaf which relates to this fruit is shown, left.—Fig. 27. Radial section of node in fruit, showing portions of three seeds. Septa, which run vertically, are not shown in perfectly longitudinal section. Scale shown by bracket = 1 mm, with 100 μ segment marked off.
identified substance which stains brightly and uniformly with safranin. Outside of the gelatinous fibers, which form the bulk of the sclerenchyma shown in Fig. 24 and 25, are pockets of large, thin-walled sclereids, isodiametric in shape. These sclereids are provided with a few inconspicuous pits and may contain a few rhomboidal crystals (Fig. 28, right). Outside of the area designated as sclerenchyma in Fig. 24 and 25 are thin-walled parenchyma cells. Although these might look like pith parenchyma cells, they are in fact developed from the meristematic areas at the ovary base, not from the pith itself.

In Gongylocarpus rubricaulis the sclerenchyma surrounding mature seeds forms a discrete spheroid (Fig. 26, 27). This sclerenchyma (Fig. 29) consists of isodiametric thin-walled sclereids which contain rhomboidal crystals. Walls of these sclereids contain numerous simple pits, round in outline, and the cells resemble tracheid-like transfusion cells. The epidermis facing the locules consists of small thin-walled cells filled with the dense, amorphous, bright-staining substance. These sclereids contain numerous rhomboidal crystals. Underlying the hypodermis are several layers of prosenchymatous cells superficially resembling small, spirally thickened, primary-xylem tracheids. The thickenings do not have borders and are gelatinous in nature. Underlying the layers of tracheid-like cells are one or two layers of thin-walled prosenchymatous cells filled with the dense amorphous compound.

In Gongylocarpus rubricaulis the pattern of seed-coat histology is entirely different (Fig. 31). The epidermis and hypodermis consist of squarish cells filled with the bright-staining amorphous substance. Interior to the hypodermis are two layers of cells without contents; the inner layer is composed of cells which are elongate but not prosenchymatous. The fifth cell layer contains scattered droplets of the bright-staining material.

The ontogeny of flowers and fruits in Gongylocarpus presents several noteworthy features. First, at the time of anthesis the flower could be said to be “normal.” The ovary is sessile in the leaf axil but not sunken into the stem. Penetration of fruits into the stem thus takes place at a relatively late ontogenetic stage. Second, the position of the fruits is a matter of differential growth. The base of the locules is like a concave apical meristem. The products of this meristematic action are incorporated within the stem rather
than outside because of the nature and location of this meristematic zone. If the ovary had a meristem at the level of the leaf axil, the products would be forced outside the stem. Third, there is no question of discovering limits of the fruit within the stem. The tissues of the fruit are derived from the locule base, not from the pith which is crushed. A feature worthy of mention in this regard is that there is no pedicel subtending the flower, merely a branch gap (Fig. 23). This sets the stage for entry of fruit tissues into the pith. Those who expect ontogeny to demonstrate phylogenetic stages will be disappointed, for the flower and fruit ontogeny of the genus is unique and does not reveal phylogenetic stages by which the internal positioning of the fruit has been achieved. Although ontogeny of flowers in angiosperms occasionally does give some hints about phylogenetic sequences, it cannot be expected to retain or reflect any large bulk of phylogenetic history of particular flowers. Any ontogenetic series may be expected to be either the most efficient means of reaching a final product beginning with a meristem or in the process of developing toward it. This efficiency, in general, tolerates few stages capable of being interpreted in terms of phylogenetic history, and it is certainly true of the inferior ovary. In dicotyledons at large which have inferior ovaries, ontogeny does not feature fusion of primordia resembling the appendicular fusions supposed to have occurred in phylogenetic derivation of the inferior ovary. Rather, the inferior ovary is ontogenetically the product of shift in meristematic activity: so-called “toral growth” forms a floral tube at the base of appendage primordia. This is well illustrated by Onagraceae.

The consequences of the above considerations are that direct histological comparison of the internal fruits of Gongyllocarpus with the normal external ones in other genera of Onagraceae does not seem feasible. In addition, fruit histology is so closely geared to dispersal mechanism that comparisons are of doubtful value phylogenetically.

The fruiting stems of Gongyllocarpus fruticulosus contain much thin-walled parenchyma in addition to sclerenchyma. This thin-walled parenchyma, when dry, may account for floatability of the fruiting stems in this species. Such fruiting stems have a corky texture when dry, reminding one of sea-water-dispersed fruits such as those of Cakile. The fruiting stems of G. fruticulosus have no special dehiscence mechanism; they may fray slightly at maturity but break irregularly, suggesting the possibility of sea-water dispersal. In fact, this species always grows close to the seacoast. The dispersal of G. rubricaulis fruits would require another explanation since this species grows in interior stations. Consumption of fruiting stems by herbivores offers a possible explanation. We have been able to obtain germination from broken sections of the stem of G. fruticulosus but G. rubricaulis has not germinated. Mr. D. E. Breedlove has suggested that the common occurrence of the latter species in nitapas may in part be caused by the seasonal burning which helps to break down the materials adhering to the seeds and allows germination. Certainly a period of disintegration appears to be a necessary prelude to germination in both species.

**Pollen Morphology**—Pollen of Gongyllocarpus (Burragea) fruticulosus has been described and figured by Erdtman (1952). Our material confirms Erdtman’s data except for the polar axis dimension, which seems to be about 70 µ in well-formed grains. To Erdtman’s descriptions may be added the notation of thick intine around the germ pores and the abundance of ellipsoidal starch grains contained in the pollen grains. Pollen grains of G. rubricaulis are closely similar but somewhat smaller (average: 83 µ × 60 µ). Pollen grains of the two species are distinctive in the fact that pore areas are not accompanied by helmet-like protrusions, as is true of most Onagraceae.

**Chromosome Numbers**—Cytological materials were obtained from some of the same populations that were studied anatomically and fixed in a mixture of 3 parts absolute ethanol : 1 part glacial acetic acid. For the study of meiosis in microsporocytes, it was necessary first to hydrolyze the buds for about 15 min in a mixture of 1 part 95% ethanol : 1 part concentrated HCl, this dissolving the abundant carbohydrate granules. The anthers were then stained in acetocarmine and examined with a phase-contrast microscope. Three plants of Gongyllocarpus rubricaulis (Breedlove 7154) had 11 pairs of chromosomes at meiotic metaphase I. Two plants of G. fruticulosus subsp. glaber (Moran 10804) had n = 11, and the one of these in which pairing was observed formed two rings of four and seven pairs at meiotic metaphase I (Fig. 32). In both species the chromosomes were conspicuously heterochromatic near the median centromeres and had long, faintly staining euchromatic “tails” distally. These are the first reports of chromosome numbers in either species, although the number of G. fruticulosus has been mentioned indirectly (Raven, 1964a). The chromosome number of G. fruticulosus subsp. fruticulosus remains unknown but is very probably n = 11 also.

**Discussion and Conclusions**—In order to discuss the relationships of the two species of Gongyllocarpus in a meaningful way, it is first necessary to outline the evidence for their inclusion in the tribe Onagraceae (Raven, 1964a). Four of the six tribes of the family—Fuchsieae, Lopezieae, Circeaeae, and Jussiaeae—have stipules, as does the genus Hauya (Onagraceae). Many Jussiaeae and Epilobeae, which almost all occur in wet places, as well as Camissonia sect. Lapathera (Onagraceae) shed their pollen in tetrads. Fuchsieae have a berry and Lopezieae and Circeaeae are characterized by the reduction of the androecium to two
stamens. Thus the absence of stipules, lack of tetrads, eight stamens, capsular fruits, and occurrence in dry habitats of Gongyllocarpus make its placement in Onagraceae almost certain.

Perhaps the strongest evidence, however, is cytological. Only members of Onagraceae tolerate hydrolysis of the pollen mother cells for more than 10 min; in members of all other tribes the chromosomes are destroyed by such drastic treatment. Only Onagraceae have reciprocal translocations as a regular part of the adaptive system in natural populations, as does Gongyllocarpus fruticulosus. Finally, only Onagraceae have large chromosomes with a conspicuous area of heterochromatin near the usually median centromere and long euchromatic “tails” (Kurabayashi, Lewis, and Raven, 1962). In short, there seems no doubt that Gongyllocarpus is allied closely to the other genera of Onagraceae and that its segregation as a separate tribe (Gongyllocarpeae (Smith and Rose, 1913) is undesirable.

What can we say about the relationships between the two species we group here as Gongyllocarpus? The unique, complicated, and virtually identical pattern of ovarian development and intrusion into the pith of the mature stems appears to make a close relationship between them certain. The fusion of the hypanthial tube a short distance below its summit and its adnation to the style below this point are characters unknown in the tribe Onagraceae. The thickened, ring-like nectary at the summit of the hypanthium and the gametic chromosome number \( n = 11 \) are otherwise unknown in the tribe Onagraceae. In addition to these major points, there are numerous detailed points of resemblance between the species: the capitate stigma; the entire petals; the four long episepalous and four short epipetalous stamens; the narrow sepals; the short, erect (but versatile, as always in Onagraceae), introrsely dehiscent anthers; and the anatomy of the secondary xylem are but a few of these. The prominent differences between the two species, on the other hand, relate to habit; degree of outcrossing (flower size, color, and persistence of petals, as well as chromosomal heterozygosity); habitat (leaf structure and probably aggregation of fruits in the xeromorphic \( G. \) fruticulosus); and capsule and testa histology. In addition, the leaves are opposite at the lower nodes in \( G. \) rubricaulis and spirally arranged, even in seedlings, in \( G. \) fruticulosus. Despite the lack of intermediate species at the present time, these differences appear far less impressive to us than do the similarities, and we believe that their relationships can best be displayed in relation to the family as a whole by including them in a single genus, as proposed first by Curran (1888). The resulting genus is not as diverse as \( Fuchsia, \) \( Ludwigia, \) or \( Camissonia, \) to mention three examples within the same family. Within the ditypic Gongyllocarpus it would be possible to recognize two sections, using the sort of standards that have been applied in other genera of Onagraceae, but this does not appear useful in such a small group.

Gongyllocarpus, thus constituted, occupies a very interesting phylogenetic position in Onagraceae. Of the six tribes recognized by Raven (1964a), the group comprising Fuchsieae, Lopezieae, and Circaeeae is obviously closely related and most generalized. Jussieaeae and Epilobeaeae, characterized by their occurrence in moist habitats, common occurrence of pollen tetrads, and tiny, almost entirely heterochromatic chromosomes which persist as chromatic dots through interphase (Kurabayashi et al., 1962), may be somewhat more closely related to one another than either is to Onagraceae; but neither appears more closely related to Onagraceae than to the group mentioned above. A consideration of trends in morphology (Raven, unpubl.) and chromosome structure (Kurabayashi et al., 1962) in the family as a whole suggests that Fuchsieae, Lopezieae, and Circaeeae are closest to the ancestral group from which Onagraceae, Epilobeaeae, and Jussieaeae have been derived, probably independently. This evolutionary model clearly indicates that \( n = 11 \) was the original basic chromosome number for the family, as it is the only basic number known in Fuchsieae and Circaeeae, and doubtless it was also the original basic number in Lopezieae (Raven, unpubl.). Gongyllocarpus is the only genus outside of these three generalized tribes which retains this original basic number. It is likewise one of the only two genera of Onagraceae which, like all members of these three tribes, have opposite leaves at the basal nodes. In \( G. \) rubricaulis. Some individuals of the otherwise quite specialized genus Gayophytum (Onagraceae) likewise have opposite leaves at the basal nodes.
western United States) and unique fruit morphology, strongly suggest that it is a relatively ancient offshoot probably arising during the early stages of evolution of Onagraceae. Perhaps owing in part to historical accident, this evolutionary line persists today as a large-flowered shrub known only from two adjacent islands off the west coast of Baja California and an autogamous annual of disturbed ground, widespread on the mainland of Mexico and in Guatemala. Although neither existing species can be said to be particularly generalized with respect to the other, the woody habit, self-incompatibility and large, insect-pollinated flowers of Gongyllocarpus fruticulosus certainly appear more so than the annual habit and small, autogamous flowers of G. rubricaulis. The unique fruit morphology of Gongyllocarpus effectively rules out any possibility of its participating directly in the ancestry of any other genus.

LITERATURE CITED


