Reprinted from the AMERICAN JOURNAL OF BOTANY, 20: 535–544, Oct., 1933

THE AQUATIC FLOWERS OF A TERRESTRIAL PLANT, *HELICONIA BIHAI* L.

ALEXANDER F. SKUTCH

(Received for publication November 4, 1932)

The profusion of the huge, undivided leaves of the great herbs of the genera *Heliconia* and *Calathea* constitutes one of the most striking and characteristic features of the vegetation of the humid lowlands of Central America. While scattered plants are sometimes encountered in the forest, the largest species of these genera are preëminently plants of open, sunny places. They thrive along the low banks of rivers and lagoons, in abandoned clearings of all sorts, in scrubby pastures, and some kinds in low, swampy places. It is only the smaller-leafed species that are really at home in the original forest. The foliage of some species, especially the great, oblong leaves of *Calathea lutea, C. magnifica, C. insignis,* and of *Heliconia mariae,* stands erect and stiff, and is more bizarre than handsome; but the long and comparatively slender, gently bending, light-green leaves of *Heliconia bihai* are outstanding in grace and beauty. The lamina of flowering plants of this species reaches 3 m. in length, with a width of about 30 cm. This plant occurs throughout the Caribbean lowlands of Central America, but is rather local in its distribution. In some districts it is exceedingly common, while in other intermediate regions, apparently suited to its habits, it is rather rare. Nowhere have I found it more abundant than in the province of Bocas del Toro in western Panama. By virtue of its creeping rhizomes it forms dense clumps in abandoned fields, bushy hedgerows, and along the banks of lagoons. The distinctive form and color of its leaves at once distinguish it from the other great-leaved species with which it grows.

The inflorescence of *Heliconia bihai* is to my mind the most beautiful of all its genus—at least among the Central American members, which alone I know at first hand. It stands in the midst of the leaves, at the top of the short false-stem composed of their overlapping, sheathing bases, usually from 1 to 1.5 m. above the ground (fig. 5). The strongly folded bracts of the flattened inflorescence stand in two ranks, which alternate along the length of the strong, flexuous rhachis. These bracts are highly and attractively colored, and form the chief beauty of the plant. There are from five to ten on each side, according to the size of the inflorescence. The lower bracts are about 20 cm. long, whence there is a gradual reduction in length upward to the most apical, which measures about 10 cm. Sometimes the basal bract bears a reduced but perfect green lamina at its apex, and then it is of course much longer. The central region of each outer face of the folded bract is colored with a bright but delicate shade of red, which pales outwardly to light orange

or sometimes white. This in turn is narrowly bordered with green along the margin and keel of the bract. As the bract ages, the green spreads and encroaches on the brighter color of the center.

The bract is thick and fleshy, and its central portion is occupied by a series of large lacunae similar to those found in the sheath and midrib of the foliage leaf. The free edges closely clasp the rhachis and the swollen base of the next bract above on the opposite side, forming a tight container in which rain water accumulates and remains. During the period of bloom, which on the Caribbean coast of Panama begins with the onset of the drier season in late December or early in January and continues until June, they are found to be constantly filled with water. The inflorescence of all healthy plants is strictly erect, and if for any reason the stem of the plant leans to one side or another, a geotropic curvature of the axis below the lowest bract restores it to the vertical position essential to the holding of its water supply.

The flowers are borne in two ranks along the upper side of the fleshy, somewhat conical peduncle which stands in the axil of each bract, except occasionally the lowest (fig. 1). Each flower is subtended by a large, white,

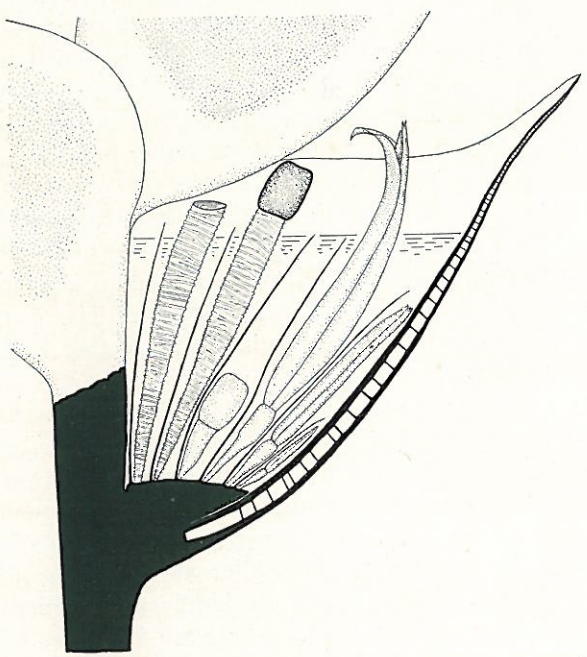

Fig. 1. Portion of the inflorescence of *H. bihai*. A side of a single bract has been cut away to expose the buds, flowers and fruits. There may be seen within this bract, from right to left, two unopened buds, a flower in anthesis, an immature fruit on a short pedicel, a mature fruit on an elongated pedicel, and an elongated pedicel from which the fruit has fallen. Each of these structures is subtended by a bractlet. The level of the water within the bract is indicated by broken lines. Each bract subtends a raceme containing many more flowers than are shown here. March 25, 1929. × 2/3.

chartaceous, ovate-deltoid bractlet, 5 to 5.5 cm. long by 2 to 3.5 cm. broad. Those of the two ranks alternate and somewhat overlap each other. The thick, clavate pedicel of the flower and immature fruit is 1 to 1.5 cm. long. The perianth tube is narrow and contracts upward, 6 to 6.5 cm. long in anthesis, in color white tipped with green. Five of the six divisions of the perianth are fused into a unit whose compound nature is indicated by the five short teeth (three interior and two exterior) at its summit. The narrow free sepal lies on the abaxial side of the flower and is free almost to its base. It fits so closely around the remaining portion of the perianth that a watertight seal is formed between the two divisions. The flower bud, enveloped by its bractlet, completes its development wholly submerged in the water which fills the concavity of the bract. The close union of its perianth parts effectively prevents the access of water to its interior. During the night before the flower opens, the tube elongates until its apex extends about 2 cm. above the level of the water, and its tip is just visible above the bract's upper margin. The filaments of the five fertile stamens are so long that the anthers are borne at the upper extremity of the tube, where they surround the capitate stigma, which terminates an equally long style. The pollen, consisting of large, perfectly smooth grains 90 to 100 μ in diameter, and intermixed with numerous acicular crystals derived from the anthers, is shed directly upon the stigma. This occurs early in the morning, as the flower opens by the bending back of the apex of the free sepal. Thus admittance to the long perianth tube is gained through a narrow aperture at its upper end. The pollen grains burst if they are touched by water, and accordingly the complete exclusion of this fluid from the developing bud is of considerable importance to the plant.

At the base of the tube of newly opened flowers is a rich accumulation of nectar secreted through three small pores at the base of the style, which are the orifices of a large, three-armed nectary situated in the axis and septa of the three-celled, three-ovuled ovary.

I have seen the flowers visited only by several kinds of humming-birds. The large, brown Hermit (*Phæthornis longirostris*), with its long, slender, curved bill, is a constant patron of the *Heliconia* flowers. I have frequently watched these humming-birds as, poised on vibrant wings, they sucked nectar from the flowers, and Carriker (1910) records that in Costa Rica this species "is fond of flowers of the wild plantain and feeds on nothing else while they are in bloom." Wild plantain is a term applied indifferently to the various species of *Heliconia* encountered in Central America. In probing the flowers, the bird hovers in a very upright position and bends its head sharply downward to insert its bill into the tube. I have also many times watched the green, ruddy-tailed Rieffer's Humming-bird (*Amazilia tzacatl tzacatl*), the commonest humming-bird in clearings throughout the Caribbean lowlands of Central America, hovering beside these flowers, often in the evening, after they had long been self-pollinated. The bill of this species, only 2.1 cm.

long, is quite inadequate to reach the store of nectar, but the tubular tongue can be extruded for a great distance and probably suffices to attain the desired prize; yet, since the whole bird measures only 9.8 cm. in length, it must require quite a stretching, if indeed it is actually able to do so. In addition to these two, I have seen a third, unidentified humming-bird, a brown Hermit of medium size, poised before the flowers.

It has already been mentioned that the pollen is shed directly upon the stigma at the time the flower opens. In view of this circumstance the significance of the visits of the humming-birds is not easy to determine. Possibly the pollen brought on the bill of the bird from another plant is prepotent over the flower's own pollen, but in the absence of this the flowers are self-fertilized. In the lowlands of Guatemala, where the species is abundant, I bagged two developing inflorescences, just on the point of opening, on February 28. By the end of April no seeds had matured, but on May 15 I collected 109 seeds from the two inflorescences, and on June 11 an additional 49. More detailed studies of ornithophilous flowers are certainly much to be desired, especially since doubt has been cast upon the utility of the visits of birds to *Marcgravia,* Thomas Belt's classic example of ornithophily, by the discovery of Bailey (1922) that two species at least (*M. cuyuniensis* and *M. purpurea*) are, like *Heliconia bihai,* self-pollinated.

The style and filaments of *Heliconia bihai* continue to elongate after the pollen has been shed. These slender organs thereby become much crumpled in the tube, and finally often force the anthers and stigma to emerge from its tip, but by the time they become exserted they are almost always discolored and in early stages of decay.

The flower parts above the inferior ovary decay beneath the bractlets without abscission. Their decomposition, together with that of various kinds of foreign matter which collect in the little pools of water in bracts, causes them to become disagreeably foul. They swarm with aquatic life, conspicuous among which are the large "rat-tailed larvae" of a drone fly (*Eristalis* sp.) and numerous mosquito "wrigglers" (*Culex bihaicolus* D. & K.).[1] The former are of a genus well-known for its preference of foul water in which to deposit its eggs; and these particular larvae are able to crawl over the surface of the plant to a pool inside another bract in case their native pond is drained, which happens when the Purple Gallinule tears apart the bracts to obtain the seeds. Doubtless the protozoologist would find these little aerial pools a rich collecting ground.

The fruit develops in complete submergence. While unripe, its surface is pure white; but upon the approach of maturity it takes on a lavender tint which finally deepens into a rich cobalt blue. In shape the berry is oblong, 11 mm. long by 9 mm. in diameter; and it contains at most three elongate seeds, 11 mm. in length, with a warty, brown, horny seed coat. The thin

[1] For the determination of these larvae I am indebted to Dr. C. T. Greene of the National Museum.

flesh of the fruit is almost tasteless, but the presence of numbers of free raphid cells containing bundles of acicular crystals causes a stinging sensation in the mouth, somewhat milder than that produced by the corm of the Jack-in-the-pulpit. It contains no starch, but is rich in oil globules and is eagerly sought by birds.

At maturity the fruit is pushed above the surface of the water by the rapid elongation of the pedicel, which, because of its interesting behavior, deserves special attention. The numerous vascular bundles are closely aggregated at the center of the thick, club-shaped structure characteristic of the unripe fruit (fig. 2). The outermost of these bundles are accompanied by strands

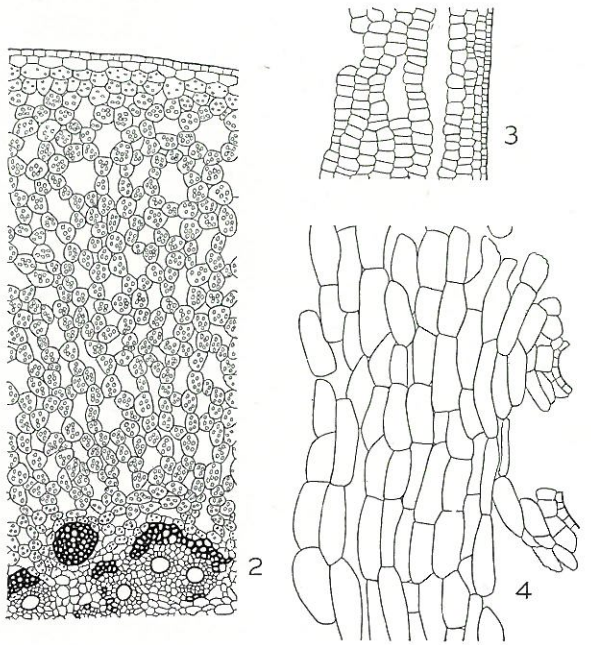

Fig. 2–4. Fig. 2. Portion of the cross-section of the unelongated pedicel of a full-grown, almost mature fruit, showing the central cylinder with its vascular bundles and fibrous strands, and the cortex with its large lacunae and thin-walled, starch-filled cells. Fig. 3. A portion of the cortex and epidermis of a similar pedicel in longitudinal section (starch grains not shown). Fig. 4. A corresponding section of a pedicel after complete elongation, showing the rupture of the epidermis and the great increase in length of the cortical cells. All figures from camera lucida drawings, × 50.

of thick-walled, lignified fibers. This central cylinder of the pedicel is surrounded by a lacunar tissue composed of short, rounded cells enclosing large air canals—a typical cortex for a submerged organ! The walls of these cells are very thin, and their cavities are filled with numerous, large starch grains. After the berry has ripened, the pedicel begins to elongate, increasing in a short time from 1 or 1.5 cm. to between 4.5 and 6 cm. in length. The elonga-

tion is effected entirely by the growth of the cells of the cortex. The central strand, with its thick-walled fibers, is incapable of stretching and pulls away from the surrounding cells. Thus the extended pedicel becomes a tube in all except its basal portion. The epidermal cells do not elongate, and the two or three subjacent layers of angular cortical cells increase very slightly in length. They are torn by the growth of the pedicel into a number of narrow, transverse rings, which continue to surround the organ and give its surface a corrugated appearance (fig. 1, 4). Those regions which do not elongate are poor or lacking in starch, in sharp contrast to the lacunar tissue.

The elongation of the pedicel is effected merely by the stretching of the walls of the cortex, unaccompanied by cell division. In the pedicel of the immature fruit, these cells measure 19 to 44 μ in length, while upon elongation they attain a length of 96 to 272 μ—an increase of about five or six times, or roughly in the same ratio as the change in length of the entire pedicel. The starch completely disappears from these cells during the process of elongation. Although no chemical tests could be made, the starch is probably converted into sugar, which increases the osmotic pressure of the cortical cells, or is otherwise used in performing the work of growth. Only the pedicels which bear fertile fruits ever elongate. This rapid stretching of the spongy tissue reminds me more of the sudden elongation of the stipe of the fungus *Mitremyces* than any kindred phenomenon among vascular plants with which I am personally familiar.

By the elongation of the pedicels the fruits are raised above the bractlets and reach the level of the edge of the bract, where their glossy, intensely blue surfaces catch the eye of passing birds. Despite their unpalatability to the human taste, they are eagerly sought by birds of several species. The Purple Gallinule (*Ionornis martinica* L.) is the bird I have most often observed eating them. I know of no more attractive picture of tropical wild life than that formed by the lovely creature as it clasps the gayly colored bracts with its long, yellow toes and pecks at them with its bright red bill. Not content to wait until the normal elongation of the pedicel brings the ripe fruit within easy reach, the bird tears apart the thick bracts to obtain the ripening but still submerged berries. The inflorescences are greatly mutilated by this activity, and great numbers of flowers and torn bractlets strew the ground beneath them (fig. 6). Perhaps, too, the bird consumes some of the larvae which the bracts harbor. The plant pays dearly in destroyed and blasted flowers and young fruits for the dispersal of its seeds by the Purple Gallinule. The Scarlet-rumped Tanager (*Ramphocelus passerinii*) also visits the inflorescences and probably feeds on the berries.

In the valley of the Rio Morjá on the boundary between Guatemala and Honduras, I frequently found the bracts of this plant torn to pieces, in much the same manner as I had seen them mutilated in Panama three years earlier. The Purple Gallinule, which despite its vast range is a bird of very local occurrence, was not met during five months of field work on the plantation

where these observations were made, and I was never fortunate enough to discover the creature responsible for these depredations on the plant. I rather suspect the White-bellied Wood Rail (*Aramides albiventris*), which is quite abundant in the region, but the matter still remains a mystery to me.

Although *Heliconia bihai* is decidedly a terrestrial plant, its flowers and fruits develop in an aquatic medium, in little private pools which collect in the concavity of each cupped bract. One at once seeks resemblances to the flowers of truly aquatic plants. In many of these, as in *Heliconia,* the buds

Fig. 5–7. Fig. 5. A group of inflorescences of *Heliconia bihai* L. Almirante, Panama, January 8, 1929. Fig. 6. An old inflorescence of *H. bihai,* showing the work of the Purple Gallinule in tearing apart the bracts. April 27, 1929. Fig. 7. The pendent inflorescence of *Heliconia mariae.* Almirante, Panama, January 8, 1929.

develop in complete submergence, and water is excluded from their interior by the close-fitting perianth parts. Except in certain sections of the family Potamogetonaceae, the pollination of the flowers of most aquatic plants occurs above the surface of the water. One is reminded of the long perianth tube of the pistillate flower of *Elodea,* which bears the stigma just above the surface of the pond, while the ovary remains submerged. It is a peculiarity of the flower of *Heliconia* that, although its pollination is subaerial, the birds which visit it must stick their tongues well below the surface of the water to reach the nectar which attracts them. In the ripening of its fruits in complete submergence, *Heliconia* agrees with a large number of aquatic plants

which, like it, are specialized for subaerial pollination; it is necessary to mention only *Elodea, Valisneria, Peltandra,* and *Heteranthera,* among many others.

The fact that the flowers of a species of *Heliconia* (called *bihai* but judging from the illustration apparently not this species) develop beneath the water which collects in the bracts was observed by Schimper (1903), who describes also the similar situation which prevails in *Nidularium* and certain other bromeliads, where the entire inflorescences develop submerged in the water which collects between the leaves of these tank epiphytes. In *Mendozia velloziana,* one of the Acanthaceae, the fused bracts form water-filled cups in which the flower buds develop. A phenomenon somewhat kindred to these is found in the so-called water-buds of a number of tropical plants, of which *Spathodea,* described by Treub (1890), is perhaps the classic example. But the situation in these is really quite different, since the flower buds of these species develop in the air, although their calyces are turgid with water secreted into them by internal glands, and bathed in this the corolla, stamens, and pistils develop. In *Heliconia bihai* and a few related species the water is held outside instead of inside the calyx. In either case it may prevent the access of destructive insects or their larvae to the essential organs, if this is really the function of these peculiar arrangements.

What advantage this aquatic habit of its flowers may be to *Heliconia bihai* is a matter of pure conjecture. Many related species, as *H. mariae,* produce pendent inflorescences in which, of course, standing water cannot collect. The spaces beneath the bracts of these plants, as is the case also with the close-bracted inflorescences of many species of *Calathea, Costus, Renealmia,* and other Scitamineae, often swarm with ants, cockroaches, and other insects which, added to the slime and the decaying vegetable matter which also are found there, make them very unpleasant to handle. The creatures which they harbor doubtless inflict a certain amount of injury to the flowers; yet these do succeed in setting a sufficient number of viable seeds to propagate the species. Ants and most other mature insects are held aloof from the developing flower buds, the ovaries, and the immature fruits of *Heliconia bihai* by the aquatic medium with which they are bathed, and the larvae which develop there apparently do not harm them.

A comparison of the inflorescence of *Heliconia bihai* with that of *H. mariae* Hooker reveals certain interesting peculiarities in the former which appear to be correlated with the aquatic environment of its flowers. *H. mariae* is the largest and most abundant representative of its genus in Bocas del Toro province, and is widespread throughout the Central American lowlands. It grows on rather dry hillsides, well-drained banks of lagoons, and in second-growth thickets in level areas, provided the ground is not marshy. Plants favorably situated attain a total height of 9 m., and produce heavy, pendent, flattened inflorescences which sometimes reach a length of 120 cm. (fig. 7). The closely overlapping, two-ranked bracts are of a lurid, dull-red

color which earns for the species the appropriate, if unflattering, name "Beefsteak Heliconia." The flowers are essentially similar in structure to those of *H. bihai,* but the perianth tube is shorter, in anthesis only 4 cm. long, white at the base and deepening to red at the apex. They develop beneath closely overlapping bractlets which resemble those of its congener. In anthesis the tip of the flower protrudes about a centimeter beyond the bracts. The blossoms are much visited by humming-birds of several species; but, as with *H. bihai,* the stigma, at the beginning of anthesis in the early morning, is found to be laden with pollen from the anthers which surround it in the tip of the perianth tube. I have seen eel-worms writhing in the pollen mass! The bractlets gradually decay after the anthesis of the flower they subtend, and there is no proper abscission of the perianths, which rot away between the bracts, adding to the foulness which prevails there. The decay of these tissues is hastened by the moisture which collects abundantly among the closely packed organs, although the pendent position of the inflorescence prevents the accumulation of standing water. The entire arrangement seems a great and foul extravagance of a riotous tropical nature, and is as forbidding as it is bizarre.

One of the marked differences between the two species is found in the structure of their floral pedicels. In anthesis, that of *H. mariae* is only slightly the shorter, and is about 1.1 cm. long. The vascular bundles are collected in its center, but are more scattered than in *H. bihai* and devoid of heavily thickened mechanical elements. The cortex contains air spaces, but these are fewer and smaller than in the submerged pedicels of the other. Its component cells, as well as those in the ground tissue between the vascular bundles, are collenchymatously thickened, while those of *bihai* are thin-walled. There is a small amount of starch in the cells surrounding the vascular bundles in the pedicels of ripening fruits, and scattered small grains occur in the inner part of the cortical tissue, but the total amount is very slight when compared with that of its congener at a corresponding stage. Both the central region, with the vascular bundles, and the epidermis elongate harmoniously with the remainder of the pedicel, which accordingly remains solid and continues to be covered with the epidermis to the end. The total elongation is less than that of the pedicel of *bihai,* and a final length of 3 to 4 (rarely 5) cm. is sufficient to expose the cobalt-blue fruit beyond the bract. It is interesting that in this species the pedicel elongates, whether or not it supports a seed-bearing fruit, and the process of elongation is much more gradual. The berries are so similar in appearance and taste to those of *H. bihai* that doubtless they are equally acceptable to birds, although I do not recall actually having seen them eaten. Sometimes the seeds are viviparous and germinate while still held between the bracts. In my experience it is somewhat easier to obtain good seeds of *bihai* than of *mariae;* yet on any basis of comparison the number of seeds produced by a *Heliconia,* in return for a tremendous expenditure of material in creating the ponderous inflorescence, would seem immoderately extravagant in a plant of the temperate zones.

SUMMARY

The fleshy bracts of the erect inflorescence of *Heliconia bihai* form cups in which water collects and remains during the period of flowering. The flower buds develop in complete submergence in these little aerial pools, while the close-fitting parts of the perianth prevent access of water to the interior. At the time of flowering the perianth tube elongates until its apex, in which the stigma and anthers are borne, protrudes above the surface of the pool. The flowers are visited by humming-birds; yet at the beginning of anthesis the pollen is shed directly upon the stigma, and seeds are set freely in bagged inflorescences. The fruit develops completely submerged in the pools, but upon maturity is carried above the level of the water by the rapid elongation of the pedicel. The epidermis and central cylinder do not participate in this elongation, which is effected by the stretching, without division, of the cells of the lacunar cortex. The bright-blue berries are sought by several kinds of birds, which often inflict great injury to the inflorescence in their eagerness to reach them before they are duly exposed by the elongation of the pedicel. A comparison of *H. bihai* with *H. mariae,* a species with a pendent inflorescence, indicates several interesting modifications in the structure of the pedicels of the former, apparently associated with their aquatic environment.

SIERRA "SANTA ELENA,"
TECPAM, GUATEMALA

LITERATURE CITED

Bailey, I. W. 1922. The pollination of *Marcgravia:* A classical example of ornithophily? Amer. Jour. Bot. **9**: 370–384.

Carriker, M. A., Jr. 1910. Annotated list of the birds of Costa Rica. Ann. Carnegie Mus. Pittsburgh **6**(4): 314–915.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. English ed. Oxford.

Treub, M. 1890. Les bourgeons floraux du *Spathodea campanulata* Beauv. Ann. Jard. Bot. Buitenzorg **8**: 38–46.