# Pitcher Plants and Their Moths

By

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[*Reprinted from* NATURAL HISTORY, Vol. XXI, No. 3, pp. 296-316, 1921]

THE PITCHER PLANT, *Sarracenia flava*

Though many insects are lured to their death by this plant, from whose nectar-baited pitchers they never emerge, it in turn is victimized by a moth that lives, immune, in association with it. The drooping pitchers here shown have been collapsed by the larvæ of that moth (*Exyra ridingsii*) just before pupating, the collapsed pitcher closing the tube above and giving additional protection to the helpless pupæ

# PITCHER PLANTS AND THEIR MOTHS

## THE INFLUENCE OF INSECT-TRAPPING PLANTS ON THEIR INSECT ASSOCIATES

BY

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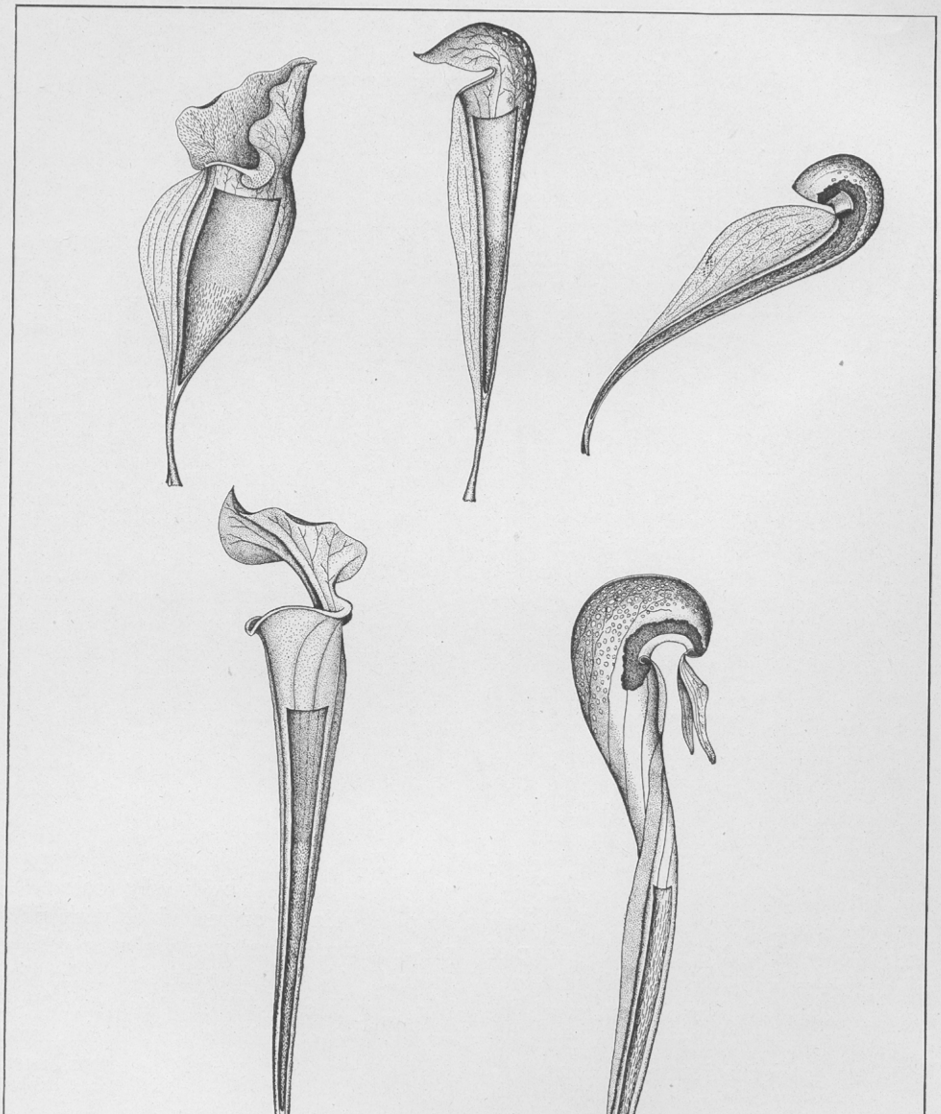
IT is most obvious that in the development of the higher plants and of the insects each has had great influence on the other. Floral colors, fragrance, nectar secretion, structure—all the complicated adjustments to secure insect pollination—are matched in the insect world with modified mouth parts, pollen-gathering and nectar-storing structures, specializations of instinct with reference to the utilization of flower products. Even more generally the food-plant relation, usually detrimental to the plant, is of obvious significance and importance to the insect. Thus, by the almost innumerable plant-insect relationships, either both plant and insect benefit or the insect benefits at the expense of the plant.

In rare instances these conditions are reversed; the plant, instead of being eaten, becomes the devourer. These insectivorous plants, representing a unique point of contact between the plant and insect worlds, show resultant complicated adjustments. If a restricted group of insectivorous plants has long been in contact with a restricted group of insects, we may with reasonable certainty expect to find the specialization of the plants as insect traps in some degree met by insect specialization to evade or even to utilize these traps. Do the insect associates of insectivorous plants exhibit any definite change of structure or of instinct resultant from their contact with these plants?

In America north of Mexico we have a number of types of insectivorous plants—notably the sundews, *Drosera*, Venus's-flytrap, *Dionæa*, and the pitcher plants, Sarraceniaceæ,[1] a purely American family containing three genera and nine species. Of the Sarraceniaceæ one genus and species, *Heliamphora nutans* Bentham, has been recorded only from Mount Roraima, on the borders of British Guiana, and in its native home has been seen only a few times by civilized man; one genus and species, *Darlingtonia* (or *Chrysamphora*) *californica* Torrey, inhabits mountain bogs of northern California and southwest Oregon; and of the typical genus, *Sarracenia*, seven species are found in the southeastern United States, only one of these seven, *purpurea*, ranging north of Virginia to Labrador.

The leaves and petioles of all the North American Sarraceniaceæ are modified into hollow structures, or "pitchers," which exhibit many specializations as insect traps. The accuracy of this interpretation of these structures has been questioned from time to time, but no other explanation of them seems to us admissible. Quite generally, by non-botanical observers, their pitchered leaves are classed as flowers. They are all more or less brilliantly colored—striped, veined, or reticulate with purple-red, sometimes on a white or yellow ground. They exhale a fruity or honey-like fragrance. All of them secrete a sweet fluid containing fruit sugar from numerous nectar glands so distributed that insects are enticed to the rims of the pitchers and thence inside. In most species inward directed hairs offer additional guidance. Once inside the pitcher, the insect steps upon the smooth "conducting surface" and is precipitated to the bottom of the tube, from which escape is barred by long, elastic, downward-directed hairs. In some species escape by flight is further discouraged by a series of translucent "windows," which stud the hood on the side farthest from the orifice of the pitcher. The pitchers of all the species, at their

[1] Macfarlane: Sarraceniaceæ, in Engler, *Das Pflanzenreich*, 34 Heft (IV. 110), Leipzig, Engelmann, 1908



THE FIVE TYPES OF PITCHERS OF NORTH AMERICAN PITCHER PLANTS

*Purpurea* *Minor* *Psittacina*
*Flava* *Darlingtonia californica*

most active period as insect traps, contain a clear fluid, which in some is purely a plant secretion but which in others, by their structure more exposed to the weather, is usually greatly diluted with rain water. In at least four species this secretion has the quality of quieting or stupefying captured insects, whose struggles usually cease within a very few seconds after capture. In six of our eight species it has been shown that the fluid contains a protein-digesting enzyme, active to extreme dilution; they also invariably contain proteolytic bacteria. The quantity of the secreted pitcher liquor is greatly increased by food stimulation, and from it both liquids and nutrient solids in solution are rapidly absorbed by the pitcher walls.[1]

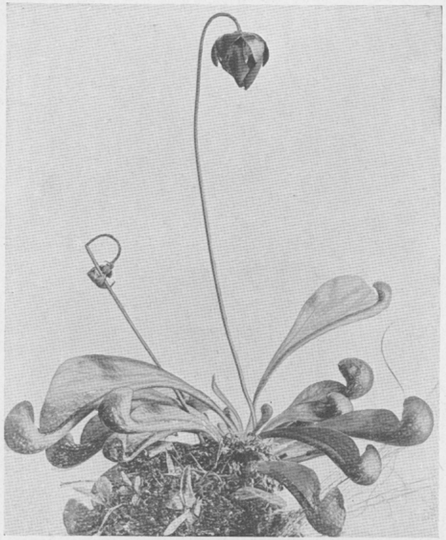
If further evidence were necessary that the pitchered leaves of the Sarraceniaceæ are specialized insect traps, their efficiency as such would seem conclusive, for especially the larger southern species often capture insects in almost incredible numbers. The bulk of these captures usually consists of Lepidoptera, Coleoptera, Hymenoptera, and Diptera; but all the principal orders of insects are represented, as well as spiders of many species, occasionally mollusks and crustaceans, and even some small vertebrates (tree frogs and lizards) whose remains occur in the mass of captures, which frequently fills the pitcher tube to the height of several inches.

Structurally our eight species exhibit five different types of pitchers. In *Sarracenia purpurea* Linn. the pitcher is wide in proportion to its height; the hood or "operculum" is vertical. The wide mouth is thus almost fully exposed to the weather, and the pitchers are usually full, or partly full, of rain water. In *Sarracenia flava* Linn., *S. sledgei* Macf., *S. drummondii* Croom, and *S. rubra* Walt., the pitchers are tall, slender, more or less tapering and trumpet-shaped; the hood is lidlike, partly overhanging the mouth, and although beating rains sometimes gain access, only the narrow, basal portions of these pitchers normally contain fluid. In *Sarracenia minor* Walt. (*variolaris* Michx.) an overarching, helmet-shaped hood practically excludes rain water. In *Sarracenia psittacina* Michx. the pitchers are recumbent, and the narrow, tubular pitcher orifice is concealed beneath the closed hood, shaped like a parrot's beak. In *Darlingtonia* the pitcher orifice opens upward into an expanded, bladder-like hood, and a cleft appendage hangs from its anterior rim.

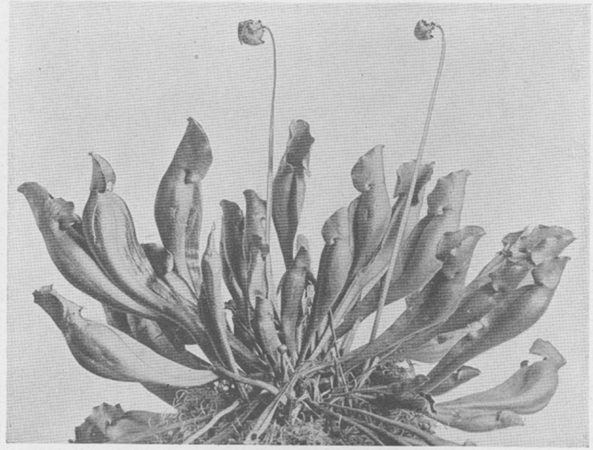
In some degree these and other structural differences are explicable as adaptations for the capture of special groups of insects. The captures of all the species, however, are most varied. These captures obviously consist not only of nectar-loving insects attracted by the bright colors, the fragrance, and the nectar bait, but also of many others whose presence cannot thus be explained: carrion-feeding species attracted by the odor of the mass of previous captures, predacious and parasitic insects whose habit it is to search every nook and crevice, insects of blundering flight—locusts and heavy-bodied beetles—which form a considerable proportion of the mass of insect remains. All of these begin to accumulate as soon as the new pitchers open in the spring.

Obviously, then, with their captures including so large a representation of the insect fauna of their habitat; with the plants themselves, sometimes occurring in almost pure stands over considerable areas, yet notably of restricted distribution and habitat; we can scarcely expect to find among their insect captures any significant adjustment to what must be for any given species an occasional and local, rather than a relatively frequent and general, source of danger. These plants, however, in addition to their insect captures have many insect associates. Their flowers exhibit intricate

[1] "The Absorption of Nutrients and Allied Phenomena in the Pitchers of the Sarraceniaceæ" by Joseph S. Hepburn, E. Quintard St. John, and Frank M. Jones in *Journal of the Franklin Institute*, Vol. 189, No. 2, February, 1920.



The low-growing, almost aquatic *Sarracenia psittacina* in times of temporary inundation captures great numbers of water beetles, whose polished bodies are gripped by the densely placed, long, elastic bristles which line its tubes



The exposed pitchers of *Sarracenia purpurea*, usually filled with rain water, often buried to their lips in the deep sphagnum in which they delight to grow, are pitfalls for ground-inhabiting insects, though their captures are by no means restricted to such species. This, the most familiar of our pitcher plants, as an insect trap is less uniformly successful than other species, though at least the narrow tubular basal portions of its pitchers are usually packed with insect remains

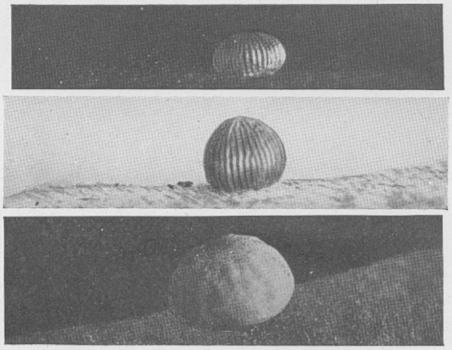
*Sarracenia minor* usually grows in a drier situation than *purpurea*. It has a baited pathway from the ground to the pitcher's rim. Its drier pitchers are often literally stuffed with the bodies of ants

The showy tops and flattened lids of *Sarracenia drummondii* (on right), *Sarracenia flava* (in center), and *Sarracenia sledgei* (on left)—fragrant, nectar-baited, conspicuously raised above the surrounding vegetation—form natural alighting places for the flying insects which largely constitute their prey. Well developed pitchers of these species usually exceed twenty inches, quite frequently thirty inches, in height. The picture of *Sarracenia sledgei* is here reproduced by courtesy of the *Journal of the Franklin Institute*

adaptation to secure insect pollination. The flower, the flower stem, the unripe and the ripe ovary, the fleshy rootstock, each forms the food of one or more insect species, which, however, do not come into frequent or necessary contact with the insect-catching devices of the plant. The pitchers themselves, like many other hollow, vegetable structures, are utilized as homes by certain nest-building Hymenoptera. The mass of insect captures in the pitchers offers too rich a supply of animal food to have been overlooked, and in seven of our eight species we find this material constituting the larval food of sundry dipterous insects—some of them exclusively pitcher-plant insects, and including representatives of the families Culicidæ, Chironomidæ, Mycetophiladæ, Phoridæ, Sarcophagidæ, and Chloropidæ.

Among these insects we find numerous examples of apparent adaptation, of both structure and instinct, to their uniquely dangerous habitat; and the degrees of adjustment to this environment, as exhibited by these insects, are most suggestive of the steps by which it has been obtained. The most unmistakable evidence, however, that the peculiar characters of these plants have been a significant factor, if not the most important factor, in determining the course of the evolution of some of their associated insects, is presented by a little group of noctuid moths belonging to the genus *Exyra* Grote, whose entire life cycle is passed in most intimate contact with these plants.

Of the three species[1] of *Exyra*,—*rolandiana* Grt., *ridingsii* Riley, and *semicrocea* Gn.,—*rolandiana* is the constant associate of *Sarracenia purpurea*, from Canada to the Gulf of Mexico; *ridingsii* Riley, of *Sarracenia flava*, from North Carolina to southeastern Alabama; and *semicrocea* Gn., the most adaptable of them all, seems equally at home in *Sarracenia rubra*, *S. minor*, *S. drummondii*, *S. sledgei*, and *S. psittacina*, its range extending from North Carolina to southern Mississippi,—probably into Texas with *sledgei*,—for the range of each species seems to be coincident with that of its associated food plant. These three insects exhibit adjustments, common to them all, which relate to the general plan of the insect trap of *Sarracenia*, indicating an association antedating the splitting of the insect group, if not the plant group, into several species; and they show further adjustments, each species to its own food plant, indicating that this process of adjustment has continued, either coincident with the development of the plant species or at least following the insect's association with these plant species. This will become apparent by considering the plant-insect relation stage by stage in the life cycle of the insects.



Magnifications of the eggs of *rolandiana* (topmost), *semicrocea* (middle), and *ridingsii* (lowest)

These eggs are deposited by the parent moths on the inner walls of the *Sarracenia* pitchers, usually some distance below the mouths

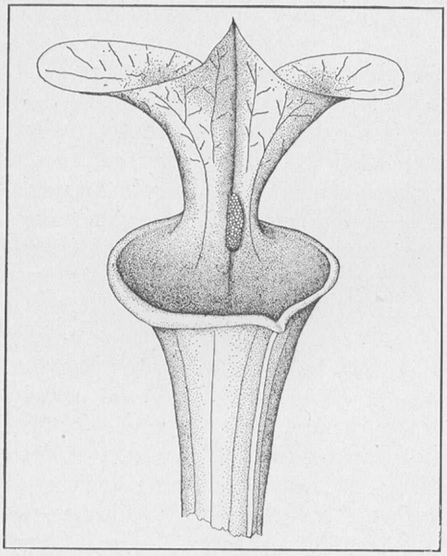
The eggs of *rolandiana* and *semicrocea* are of the usual noctuid type—yellow or yellowish green, polished in texture, dome-shaped, and vertically corrugated; that of *ridingsii* is larger, white, unpolished, much more flattened basally, and shows only faint indications

[1] Four species are recognized in the check list of Lepidoptera. In the opinion of the writer, however, *fax* Grt. and *rolandiana* Grt. are almost certainly identical. The better known name *rolandiana* is retained in this article, for it is possible, though extremely improbable, that *fax* Grt. may be found again as a rare and local species.

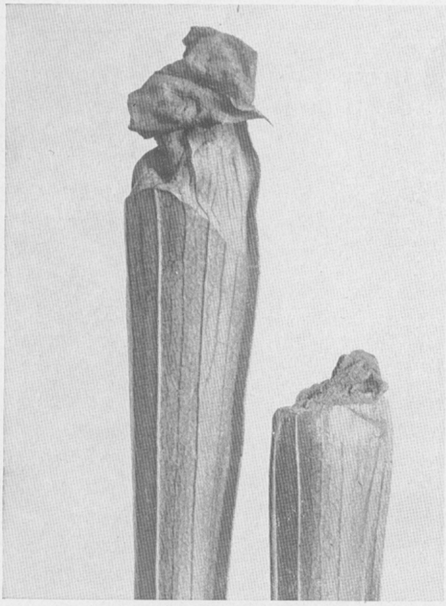
of a few broad, shallow, and less regular corrugations. Such a departure from the general type of its group and from that of its own genus would seem to have some significance. As a suggestion, and not as a theory, it may be stated that the great trumpet-shaped pitchers of *flava*, in which these eggs are deposited, in the early season exude an exceptionally abundant nectar bait, which gathers in drops on the hood and throat and runs down the walls of the pitcher, where it evaporates to dryness, leaving a white, sugary incrustation which persists for weeks; and the slightly wrinkled, dull white, flattened egg of *ridingsii* bears resemblance to one of these dried nectar drops. This resemblance can be of use only if it offers some protection. Although ants frequent the pitchers for nectar, and although spiders are often, and small acarids usually, present in the pitchers, the only observed enemy of *Exyra* eggs is a minute egg parasite, a *Chalcis*, which sometimes destroys a very considerable proportion of the eggs of *semicrocea*, but which has not yet been found in *ridingsii*. Would a female *Chalcis* in search of noctuid eggs fail to recognize an egg which departs from its type?

The eggs of *ridingsii* and *semicrocea* are deposited singly; for, as will appear, it is of vital importance that only one larva should occupy a pitcher, and when more are present, one drives out or kills the other; the eggs of *rolandiana* are deposited in groups of five or six up to as many as fifteen, to a pitcher, but only one such lot to a plant. Why? Of all the *Sarracenia* only *purpurea*, the food plant of *rolandiana*, has in its habit of growth a considerable number of pitchers in close contact—usually so close that their shape is distorted by mutual pressure; and from these short, wide pitchers growing thus in dense, interlaced masses, even very young larvæ may scatter and find their way, with a very few seconds' exposure, from pitcher to pitcher. In *flava*, *rubra*, *drummondii*, *sledgei*, and *minor*, the food plants of *ridingsii* and *semicrocea*, the pitchers are taller and much more separated in their habit of growth, so that traveling from one pitcher to another becomes a long and dangerous journey for a small larva—a journey not to be undertaken except under the compulsion of failure of food supply or at the time of pupation. In the one instance it is better for the species that the parent moth should not expose herself by too frequent flight and search for perhaps widely scattered clumps of *purpurea*, for the larvæ can readily change from leaf to leaf before their increasing size necessitates sole occupancy of a pitcher; in the other, flight from pitcher to pitcher, which though not in contact, are usually found in close proximity over wide expanses, is better than the long exposure of a young larva in a journey from one tall pitcher to another. Thus the habit of growth of the food plant determines the egg-laying habit of the associated insect.

In their larval stages these insects exhibit a succession of unmistakable adjustments to their plant habitat. The older larvæ of all three species have the common habit of protecting themselves from the attacks of parasites, spiders, and predacious insects, and to some extent from the weather, by closing the mouths of the pitchers they inhabit with closely spun, silken webs, then of feeding on the inner surface below the webs without piercing or rupturing the walls, which though thus eaten away to a thin, bladder-like condition, provide them with a closed feeding chamber, with perfect concealment and comparative security against intrusion from without. They exhibit but slight diversity of method in spinning the ceiling web. With *rolandiana* in *purpurea*, *ridingsii* in *flava*, *semicrocea* in *rubra*, *sledgei*, and *drummondii*, the fine, close, almost transparent web is spun horizontally across the throat of the pitcher, at



*Flava* is characterized by a deeply incised groove in the throat of the pitcher. The newly hatched larva of *ridingsii* creeps to this groove and constructs over a portion of it a cradle-shaped or hammock-like shelter of silk and corky frass particles, beneath which it lives for a few days, feeding on the portion of the pitcher thus covered and the immediately adjacent parts. No other *Exyra* constructs such a shelter



Pitchers of *sledgei* which young larvæ of *semicrocea* have converted into closed feeding chambers by girdling.

or slightly below the lips. Accidental tears and punctures of the pitcher walls are also ceiled, broken webs are replaced, and a larva placed in a cut section of a pitcher promptly ceils both ends. In the hooded leaf of *minor*, *semicrocea* sometimes follows the same method, but often curves the web upward and forward into the apex of the hood, or more rarely connects the lateral margins of the hood and the lips with an almost vertical web. In *psittacina*, *semicrocea* simply ceils the small, hidden leaf orifice, thus providing a closed feeding chamber with the least possible expenditure of silk. All these departures from the usual method, made possible in each case by the structural peculiarities of the food plant in which they occur, result in securing a larger leaf area for feeding under the protection of the silken web and in lessening the chance that a failure of food might necessitate a change to another pitcher.

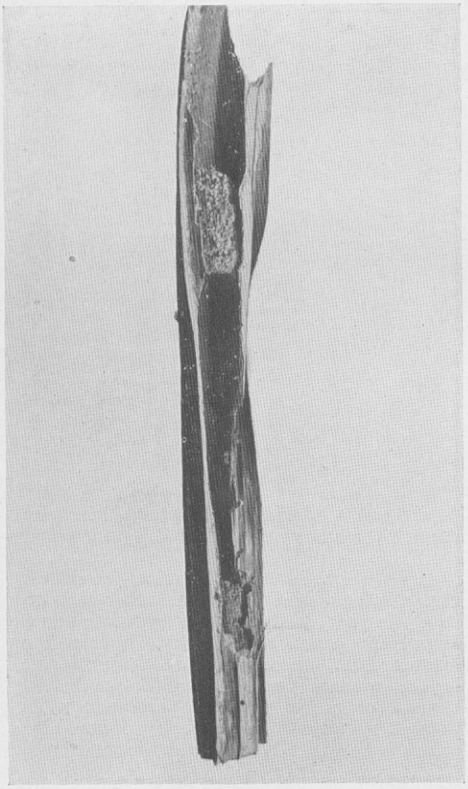
It is beyond the power of a minute, newly hatched *Exyra* larva, however, to ceil the mouth of a large pitcher with silk. The first-stage larvæ of *ridingsii* (the largest species) are, for example, about 2.6 mm. ($\frac{1}{10}$ of an inch) in length, and the flaring mouth of the pitcher of *flava* in which they hatch may be 75 mm. (3 inches) across. At this early age, translucent, almost colorless, half buried in the plant tissue and surrounded by the refuse of their feeding, they are extremely inconspicuous, and within the pitchers they must possess some degree of immunity from the usual enemies of young caterpillars. Where the age and structure of the pitcher permit, however, they adopt further means of defense, as indicated in the illustration above.

The spring generation of *semicrocea* emerges from the egg when many of the pitchers of its food plants are tender and immature—hermetically sealed, spear-shaped tubes, pushing their way up to their full height before the lips of the pitchers open and they begin to function as insect traps. The young larva finding a pitcher in this condition, ensures the continuance of a closed feeding chamber as follows: below the yet unopened lips of the pitcher, on the inside, it cuts one or more narrow encircling grooves—the groove cut by the newly hatched larva is so narrow and thread-like that it can be detected only by holding the leaf to the light. If the leaf be sufficiently tender, the portion above the groove quickly dies, contracts, and hardens, forming a tough, unbroken cap or lid to the still growing and expanding pitcher; and as this cap includes the pitcher's mouth area, a closed feeding chamber is thus created and maintained, providing the insect with food and protection through its most defenseless period; for having fed for some days in the closed chamber thus created, it is then large enough to effect a rapid change, if necessary, to an older and larger pitcher, which it quickly ceils with a silken web. This groove-ceiling is sometimes attempted in pitchers too old to respond, in which case the larva, as soon as may be, resorts to the web-ceiling method, expanded pitchers with ineffective grooves and typical ceiling webs being of common occurrence. The young larvæ of *semicrocea* employ this groove-ceiling method of maintaining a closed feeding chamber, whenever the pitcher conditions permit, in all five of their food plants.

Pitchers of *Sarracenia purpurea* the one normal, the other groove-girdled by the larva of *Exyra rolandiana*. The enclosure thus formed, which in the springtime would be utilized as a closed feeding chamber soon to be destroyed by the rapidly growing larva, in winter constitutes a dry, bladder-like hibernaculum, where the semilethargic larva, in the warmer periods, may do a limited amount of nibbling at the thickened walls without destroying the efficiency of its more or less water-proof compartment

*Sarracenia purpurea*, probably to a greater extent than any other species, produces new, and consequently unopened, pitchers more or less throughout its growing season, though more abundantly in the spring and late summer; and in these pitchers the young larvæ of *rolandiana* follow identical methods; but with this species the groove-ceiling operation serves for defense through two very different periods of the life cycle. All three *Exyra* pass the winter as larvæ in the pitchers of *Sarracenia;* but as the structure and winter condition of the different pitcher plants are so varied, to ensure shelter and safety through this period of helplessness and enforced inactivity requires very different preparation on the part of the larvæ, and accordingly we find widely different methods in the construction of their hibernacula.

The wide, open-mouthed pitcher of *purpurea*, throughout much of its geographical distribution subject to winter conditions severe enough to convert the water filling its pitchers into solid cores of ice, its low growth and almost aquatic habitat often subjecting it to partial or complete submergence, offers to the hibernating larva of *rolandiana* an apparently difficult problem; but when, in the late summer, a young larva of this species groove-ceils a *purpurea* pitcher and then, preliminary to hibernation, ceases to feed and grow (for the winter is passed as a third-stage larva or younger), the pitcher walls, unmutilated by feeding, thicken and toughen to a



Low in the narrow, tubular, basal portion of the *flava* leaf the hibernating larva of *ridingsii* constructs its winter quarters. In this chamber the larva is well insulated against cold and excessive moisture

leathery consistence and serves as a hibernaculum.

Not all the hibernating larvæ of *rolandiana* find pitchers suitable for the girdling process. Any time from November to May, if we burrow with our fingers into the moss in which *purpurea* is growing, and lift the plants out bodily, in addition to the old and mature pitchers radiating from the apex of the rootstock, we may find one or several small, succulent, pinkish white, unopened leaves, too short to have yet pushed their way up through the surrounding sphagnum; and the slightly nibbled top of one of these immature leaves, with a flimsy, silken web flecked with bits of reddish brown frass closing the tube, is a usual indication of the presence of a hibernating larva. If no leaf suitable for either of these methods be available, the larva descends to the very bottom of an old, dry pitcher, and with silk and refuse partitions off a little, conical chamber in this narrow, lower extremity of the tube.

*Ridingsii* in *flava* is confronted by a problem quite different. Though taller and more erect, and usually growing in a drier habitat than *purpurea*, the pitchers of *flava* die to the ground in winter, and their flaring upper portions, dry and brittle, are almost sure to be split and shredded by the winter winds. In *flava*, in the late summer, no tender, unopened leaves are available for groove-ceiling, and there are no immature pitchers at the base of the plant. A different method of preparation for hibernation is necessitated by these conditions. The larva of *ridingsii*, feeding freely in the upper part of a *flava* pitcher, fills the lower portion for several inches with fine, corky débris and frass. In this material it constructs an arched chamber often several inches in length—the floor of compacted refuse, for walls the tough, dry, thickened basal portion of the pitcher, the roof a smoothly arched, compacted mass of corky frass and fine refuse strengthened with silk, above which the packed frass may extend for several inches.

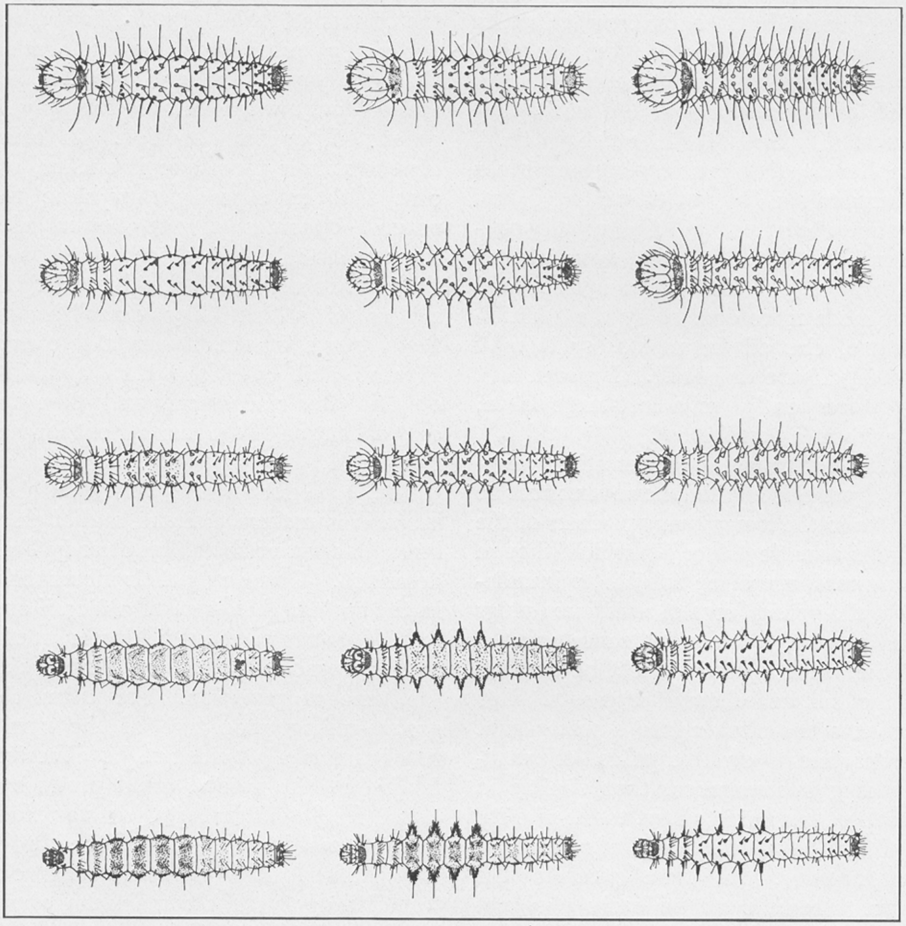
With *semicrocea* the problem of winter survival changes again. In *rubra*, *minor*, *drummondii*, and *sledgei* the pitchers are erect. They usually grow in drier situations than *purpurea* and are thus not so subject to inundation; their leaves are comparatively free from rain water; and some of them remain green and unwithered, or partly so, throughout the winter, thus providing springtime food for the hibernating larvæ, suitable quarters for pupation, and even shelter for the emerging moths long before the spring growth of *flava* is available for *ridingsii*, which, remaining in its hibernaculum until the growth of new pitchers in the spring provides it with fresh food, is thus a month later in completing its transformations; that is, the seasonal history of the food plant determines the time of appearance of the associated insect. In these erect, green pitchers the larva of *semicrocea* prepares its hibernaculum by spinning a dense, opaque web across the tube, usually considerably below the throat, even halfway down; the web is sometimes thickened and made more opaque by the addition of fine, chewed fragments, or it may consist of pure white silk. Beneath this, most frequently as a last-stage larva, *semicrocea* hibernates.

One significant and interesting variation from this method, however, must be noted: in the low-growing pitchers of the almost aquatic *psittacina*, which, though rain-proof, are often subject to inundation, the young larva of *semicrocea* plugs the narrow, tubular entrance of the pitcher with a tough, thick, button-like wad of silk and chewed fragments. This converts the pitcher into a water-tight compartment even capable of withstanding submergence, thus similar in function, but not in origin, to the girdled, bladder-like hibernaculum of *rolandiana* in *purpurea*. In these pitchers the larvæ hibernate at an early age, not later than the third instar. Thus in *semicrocea* the age at hibernation, as well as the character of the hibernaculum, seems to be influenced by the food plant.

The flower buds of *Sarracenia*, formed in the late summer or early fall, are all ready to push their way upward at the approach of spring, with, or even before, the spring leaves, and they shoot up rapidly, sometimes at the rate of an inch a day. The same warmth which starts the flower buds racing upward also arouses the *Exyra* caterpillars in their hibernacula, for the green, succulent buds and expanding blossoms are the favorite spring food of these larvæ. Creeping up the stem, they bore into the globular flower bud, and the overlapping layers of expanding sepals and petals soon hide the entrance hole. In feeding, they avoid the outer layers, web together accidental apertures, and desert these shelters only when the food supply is exhausted, or for pupation. In older blossoms their procedure is similar, except that on entering they close the natural openings of the flower with silken webs or else block off a portion of the interior with such a web, under the shelter of which they demolish the fleshy parts of the flower and ovary. Flowers and buds are thus available only in the springtime, and then for only a fraction of the number of hibernating larvæ.

The behavior of the newly hatched larvæ in immature pitchers, and of older larvæ in open pitchers, has already been described. On leaving their hibernacula in the spring, the larvæ of *ridingsii* and *rolandiana* are of the third instar, ready to feed voraciously and grow rapidly to the time of pupation. For them the groove-ceiling procedure of the newly hatched larvæ would not be effective, for before the groove could produce a closed feeding chamber their voracious feeding would have wrecked the top of the pitcher. *Ridingsii*, creeping out from its dry-stem hibernaculum about April 20 (in South Carolina), finds its food plant, *flava*, in full bloom. If it finds an unoccupied bud or blossom, this provides it with sufficient food to complete its larval growth without further change. At this date the new pitchers of *flava* are slender tubes, pointed and entirely closed at the top, pushing their way up through the dead, dry leaves of the previous season. The larva of *ridingsii*, not readily finding a bud or blossom, creeps up one of these immature, tubular pitchers, and eating a hole just large enough for entrance, creeps inside. This process occupies only a few minutes.

Once inside, spinning a ladder of silk as it climbs the vertical walls, the larva creeps up into the closed peak of the hood, where its first feeding on the inner surface from the apex downward re-



Larval stages, from the egg to maturity, of the three species of *Exyra*, with special reference to the divergent development of *rolandiana* (left row) on the one hand, and *semicrocea* (middle row) and *ridingsii* (right row) on the other. Note in the two species last mentioned the development in the successive molts of the "lappet tubercle," Kappa (IV), and the absence of this character in *rolandiana*. These "lappets" keep their possessors from too intimate contact with the pitcher walls

sults in the drying up and toppling over of the whole upper portion, effectually preventing the pitcher's mouth from opening and ensuring a permanently closed tube which may be maintained in this condition with a minimum expenditure of silk in webbing over accidental openings. *Rolandiana* adopts a similar method in the tender new leaves of *purpurea;* and all intergrades between wide open, older pitchers ceiled with horizontal webs and tender, new pitchers ceiled by feeding and patching may be found.

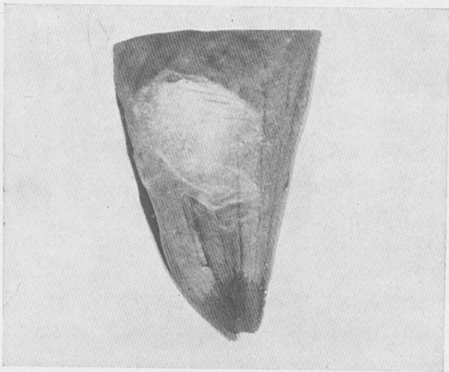
The larvæ of *Exyra* present some unusual characters for noctuid larvæ, which, excepting the flower-feeding ones and other brightly-colored, exposed-feeding types supposed to exhibit warning coloration, are usually of dull colors, brown or gray, and without horns, prominent tubercles, or a hairy coating. *Exyra* larvæ vary individually from brown to more usually purplish red or even to bright wine-red, and are white between the segments; consequently their colors to a considerable degree match the red veins and mottlings of their food plants. They are all more or less pubescent—*rolandiana* the most, *ridingsii* the least—and they all have the habit, when disturbed, of retreating down the pitcher wall or of releasing their hold and falling to the bottom. If in its descent *rolandiana* is precipitated into the water-filled pitcher of *purpurea*, it is able to support itself on the surface film and wriggle its way to safety; and actual experience with *semicrocea* larvæ in *psittacina* has shown them capable of swimming from plant to plant. Both color and vestiture seem to have been modified, with an intelligible relation between these modifications and the characters of their food plants and the plant habitat.

The larvæ of all three species are strongly constricted between the segments; and two of the three species, *semicrocea* and *ridingsii*, beginning with their first larval molt, develop structures probably unique in this group of insects. These are greatly enlarged, spiny, lateral tubercles—"lappets," they have been called (see illustration p. 308)

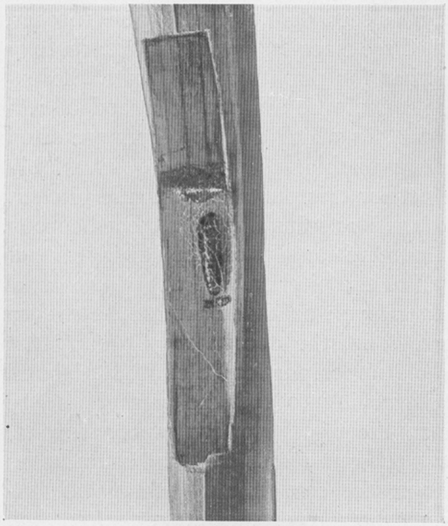
What is the office of these "lappets," and why are they possessed by the two species, *ridingsii* and *semicrocea*, but not by the third, *rolandiana?* Undoubtedly they serve to keep their possessors from too intimate contact with the pitcher walls, the portion of the plant's insect trap against which these larvæ are in essential need of protection, for under like circumstances caterpillars of other species frequently become too tightly wedged in ever to escape, and these *Exyra* larvæ have the habit of penetrating to the lowest possible portions of their dangerous homes. It is still more significant that of the three, *rolandiana* only fails to develop these bristly "lappets" or "elbows," for this species, inhabiting the wide, squat pitchers of *purpurea*, has ample room between the walls, in that portion of the pitcher which it habitually occupies.

Whether the last larval food has been an unopened bud, a blossom, an immature, closed leaf, or an open pitcher, all three species of *Exyra* resort to a pitcher for pupation; and with the exception of the hibernated brood of *ridingsii*, for which open pitchers are often not available, they almost invariably select for this purpose a mature pitcher. *Rolandiana* spins a thin, flattened cocoon of pure white silk on the concave inner wall of the pitcher, well above the usual water level; or if the pitcher be a very small one, the cocoon may occupy the whole upper portion, a close, horizontal web serving to ceil the pitcher and to form the upper portion of the cocoon; or else, in an old leaf that contains no water, the cocoon may occupy the extreme bottom of the pitcher, often well hidden under an accumulation of insect remains, frass, and vegetable débris, in a small chamber partitioned off by the silken wall of the cocoon. If any reason for choice among these methods is discernible, it would seem that the first is more prevalent in large, roomy, well-developed pitchers, the latter in small, crowded, distorted, or mutilated ones.

Like *rolandiana*, *semicrocea*, preparing for pupation in any of its five food plants, usually enters a pitcher that has not been mutilated by feeding. A single, significant variation in *semicrocea's* pre-



Before spinning its cocoon of pure white silk (shown above) the larva of *rolandiana* usually crawls to a pitcher of *Sarracenia purpurea* that has not been mutilated by feeding and which shows no outward indication of the larva's presence



Before pupating the *semicrocea* larva closes the pitcher selected, often a considerable distance below the lips, with a ceiling web of denser and more opaque construction than that beneath which it has fed. Just under this web it constructs a filmy, silken cocoon. The tube is often slightly ceiled below the cocoon as well

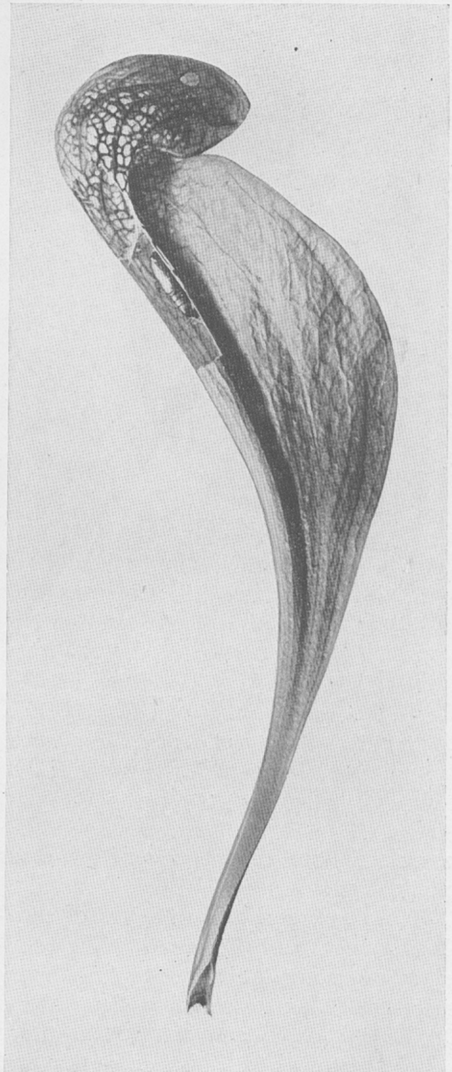
paration for pupation as pictured above occurs in *psittacina*, whose pitcher has a concealed leaf orifice, small and tubular, hence offering greater difficulty for the escape of the emerging moth. In this plant the larva, before spinning the ceiling web or constructing its cocoon, cuts a large emergence hole in the peak of the hood; that is, *semicrocea* in its four food plants with wide-mouthed pitchers makes no provision for the escape of the moth, and in *psittacina* with its narrow orifice makes provision for that event.

In a mature leaf of *flava*, *ridingsii* preparing for pupation, resorts to entirely different methods: instead of changing to a new pitcher showing no external signs of its presence, it burrows down into the corky refuse of its own feeding, which fills the lower portions of the tube; in and of this material, with little or no apparent admixture of silk, it constructs an evenly rounded, oval cell in contact with the leaf wall on one side, within which it changes to a pupa. It does not ceil the pitcher above, with silk, for usually the top has already been eaten to a thin membrane and is in a more or less collapsed condition, which the larva frequently accentuates, as a preliminary to pupation, by girdling it above the frass level with a deeply cut, encircling groove, causing the whole upper portion of the pitcher to topple over and thus more effectually closing the tube. That is, the groove-cutting habit, employed by very young larvæ of *semicrocea* to produce a closed feeding chamber, and by *rolandiana* of like age for the same purpose, but of perhaps greater importance, to ensure a water-tight compartment for hibernation, reappears in *ridingsii*, a species otherwise barred from the use of this device by the seasonal history of its food plant, as a means of obtaining protection to the pupal chamber.

The hibernating larvæ of *ridingsii* are often ready for pupation before the pitchers of *flava* are open at the top, so that many larvæ of this brood are compelled to pupate in immature, unopened pitchers, and under these conditions they exhibit some habits not always apparent in the later broods. As a result of the larva's having entered and fed upon one of these pitchers, as already described, there has collected in the lower part of the tube a sufficient accumulation of corky frass in which to construct a cocoon. The collapsed and toppled-over upper portion effectually closes the tube above. Below the collapsed portion, but well up in the tube, the larva cuts an emergence hole, large enough for the moth, its wings still moist and flexible, to creep out; lower in the tube it cuts a much smaller hole to ensure drainage if in the pitcher's damaged condition rain water should gain access; just above the drainage hole it closes the tube with an open-meshed web, which permits water to drain through, but serves to exclude unwelcome insects from below; above the drainage hole and below the emergence hole the larva then constructs its usual oval cell of corky frass and changes to a chrysalis.

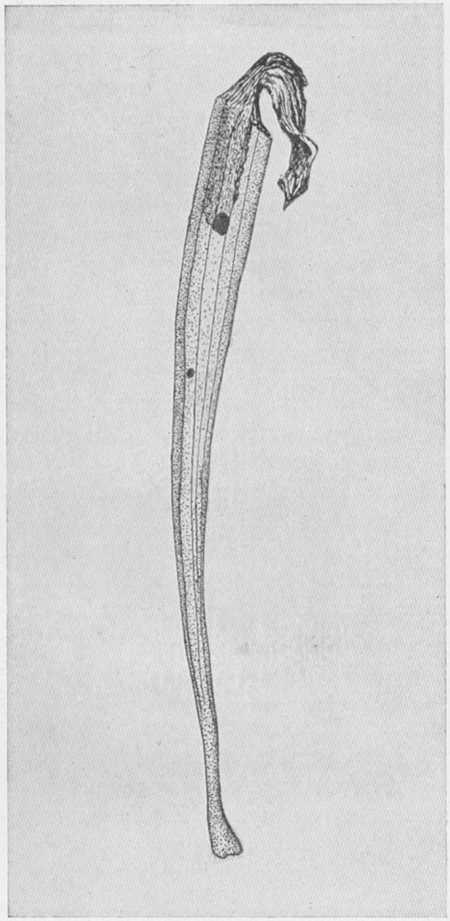
The presence of these two holes is an infallible indication of the occupancy of the young pitcher of *flava* by the pupa of *ridingsii*. On the pitcher-plant meadows around Summerville, South Carolina, for example, in early May, hundreds of these pitchers may be thus identified, picked, and gathered, each containing a pupa ensconced between the two holes. These outward signs are recognized, too, by a bird—probably a partridge, but not positively identified—which splits the tube between the emergence and drainage holes and extracts the pupa. As was noted long ago by a botanical observer, the pitchers of *minor* are also habitually split open by birds for the insects contained therein; but *semicrocea*, the *Exyra* more frequently occupying these pitchers, by its habitual choice of unmutilated pitchers for pupation, avoids giving outward indication of its presence and is thus to some degree protected against this enemy. *Ridingsii*, constructing its cocoon from the refuse of its own feeding, is debarred from this defense.

Emergence of the moths usually takes place in the daytime. From closed pitchers the moths creep out while their wings are still moist and soft; in open pitchers they rest upon the inner wall of the leaf, above their cocoons, until ready for flight; and their first flight, in fact all their flights, seem to be simply from one pitcher to another. With no apparent structural adaptation by which to overcome the trap structures of the pitchers, their entrance and safe exit seem to depend simply on knowing how. In entering, they alight on the outside and run in over the rim; in leaving the pitcher, they climb the wall, half walking, half flying, and take flight from the rim or from the wide upper portion where there is room for the free operation of their wings. The pitchers are their habitual resting places. Here they sit on the inner walls, heads upward, backing farther down when alarmed or disturbed, flying immediately to another pitcher when driven out, and refusing to leave these shelters when the pitchers are plucked or even roughly handled and carried away. The moths of *Exyra* have been observed to feed upon the



The fact that the pitcher of *psittacina* has no adequate orifice through which the moth of *semicrocea* can escape when it emerges, makes it necessary for the larva before pupating to cut for the purpose a large hole in the peak of the hood nectar secretion of the pitchers, but they do not seem ever to enter the flowers—in fact, *flava* and *purpurea* have practically ceased blooming before the *Exyra* associates of these plants, *ridingsii* and *rolandiana*, have reached the winged stage; so that these insects cannot be supposed to confer upon their plant

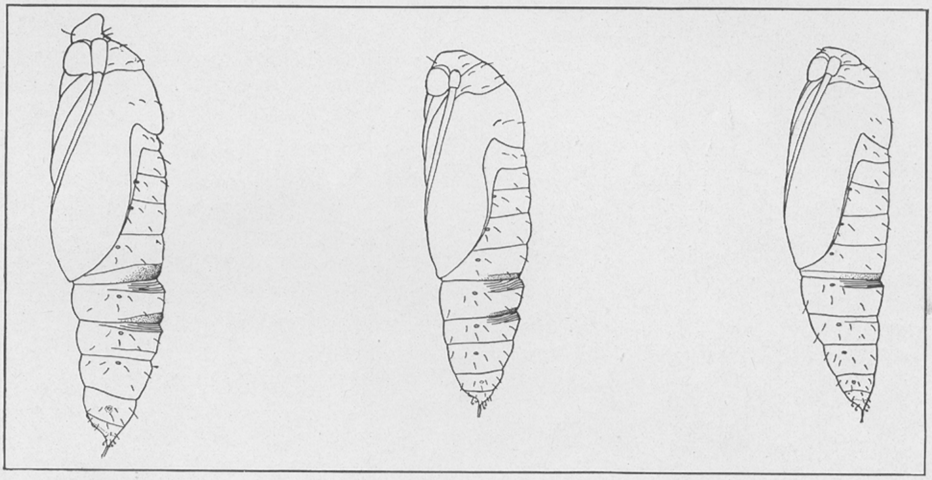
The larva of *ridingsii*, when about to pupate, constructs a cell in the corky refuse of its own feeding. When the cocoon is spun in mature pitchers, emergence and drainage holes, such as are shown in the companion picture, are often omitted.



The exterior of a young pitcher of *flava* with the two orifices made by *ridingsii*, the emergence hole through which the moth will later make its exit above, the drainage hole below. *Courtesy of Entomological News, XXIII, 1907*

associates the return benefit of cross pollination.

The black and yellow colors of *semicrocea* and *ridingsii* and their conspicuous color patterns are probably ancestral, for this coloration seems to bear little if any relation to their association with the pitcher plants, and the very remarkable range of color variation exhibited by these insects does not seem to bear any imaginable relation to their plant habitat, though it may be a direct response to climatic and food-plant conditions. Hibernating larvæ of *ridingsii*, having an abundant supply of tender, juicy food, produce moths materially larger and much more heavily marked, even to the complete obliteration of the yellow areas of their wings, than those of the later broods feeding in dry, parchment-like pitchers in their sun-baked, midsummer condition. A similar range of variation in *semicrocea*, however, is *not* seasonal, and perhaps only the experimental production of these forms, if that be possible, will satisfactorily determine their significance; in *semicrocea* there is, however, a direct food-plant effect on the *size* of the imago (the adult insect), probably resultant from the larval habit of refusing to change from pitcher to pitcher except under absolute compulsion through failure of the food supply; those from the small pitchers of *psittacina* and *rubra*, constantly average smaller than those from *minor* and *sledgei*, and these in turn, smaller than *drummondii*-bred moths.



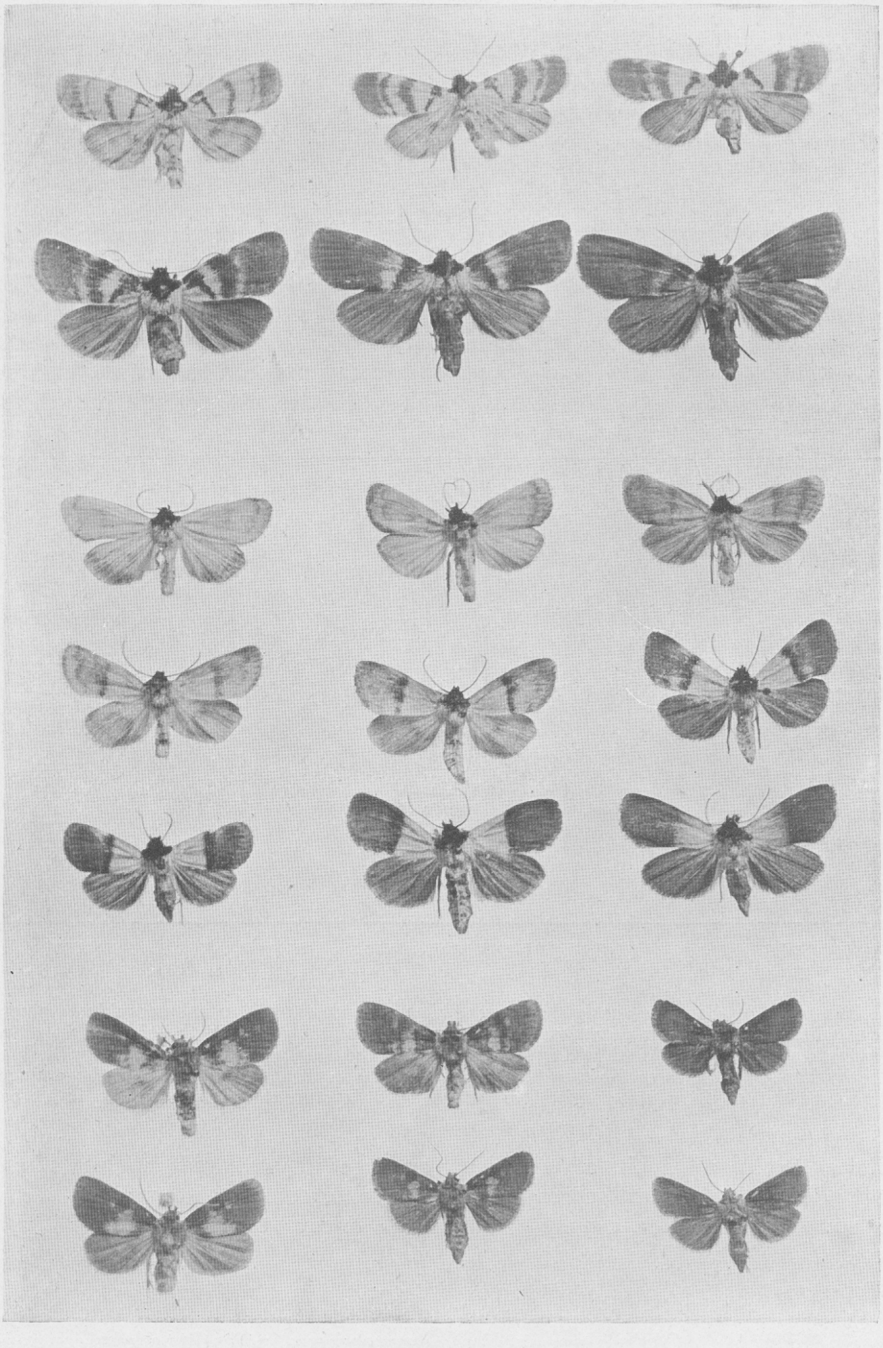
PUPÆ OF EXYRA

*Ridingsii* *Semicrocea* *Rolandiana*

The pupæ of the three species are very similar and present the usual noctuid characters, varying individually from pale amber to dark brown, almost black. Of the three species two, *rolandiana* and *semicrocea*, occupy fllmy, silken cocoons; the third, *ridingsii*, a densely packed cell of corky frass. Of the three the pupa of *ridingsii* only has its front strongly and acutely produced over the head, the office of this pointed structure being to puncture the impacted wall of its cocoon

*Rolandiana*, too, exhibits a very wide range of variation, in part geographical, the southern examples usually being smaller and darker than the northern, thus giving rise, apparently, to the extreme form furnishing the types of Grote's *Exyra fax*. Of the three species *rolandiana* only, living in the one pitcher plant, *purpurea*, whose interior is not more or less concealed by an overhanging hood and whose wide pitchers are thus open to view from above, has acquired the purple-red, yellowish red, and blackish purple tones of its food plant. The departure from the typical coloration of the genus occurs in the one species where this change is intelligible as an adjustment to its food-plant environment.

In a study of this kind there is abundant opportunity for a misinterpretation of some of the observed facts. When we endeavor to translate a document in an unknown cipher, we may easily be mistaken in the individual word; but when we spell out an intelligible and consistent message, we have reasonable assurance of the correctness of our work. As we thus review the activities of *Exyra*, we find that some of the characters common to the three species are obviously related to their pitcher-plant environment, indicating a long continued and ancestral association with these plants; but more significantly, that many if not most of their specific differences, both of structure and instinct, are made up of adjustments or adaptations to their respective food plants. Is it not,



THE VARIABLE EXYRA MOTHS

The three species of the genus *Exyra* exhibit a wide range of variation—individual. seasonal, geographic. The two topmost rows are *ridingsii*, the three middle rows *semicrocea*, the two lowest *rolandiana*. *Rolandiana*, which in contrast to the other two species lives in exposed pitchers, is afforded partial concealment through its protective coloration therefore, an inevitable conclusion that food-plant environment has determined the direction and course of their specific evolution?

If it is a "commonplace of evolutionary knowledge" that "among the best known illustrations of divergent evolution are the animals of oceanic islands, . . . . undoubtedly descended from common ancestors, yet having become distinct through changes which isolation prevented from being ground down to a common level by inter-crossing," then even the present distribution of *Sarracenia* gives further suggestion of the part of the food plant in the differentiation of *Exyra*. The geographical distribution of *Sarracenia purpurea*, from Labrador to the Gulf of Mexico, with no other plants of the genus occurring north of Virginia, places *rolandiana* out of contact with other *Exyra* for perhaps three fourths of its present extreme range. The plant is not generally distributed throughout this territory, but occurs in colonies often widely separated. *Exyra* in its winged stage—its only period of probable distribution—is short-lived, rather sluggish in habit, and weak of flight. These conditions, therefore, permanently separate a great majority of the colonies of *rolandiana* from direct contact with others of the genus and exhibit the conditions which would permit its origin in some food-plant "island" of *purpurea*, where group isolation would be as truly operative as in an oceanic island of the geographer; and of the three species only *rolandiana* exhibits a well marked geographical variation.

Although each species of *Exyra* is associated with certain *Sarracenia* species, usually to the exclusion of all others, any *Exyra* may be bred to maturity in any *Sarracenia;* and in the field, when pressed by failure of the food supply, any *Sarracenia* is recognized by any *Exyra* as a possible food plant. *Darlingtonia*, then, the only North American plant of the family with no *Exyra* associate, in its widely removed habitat suggests a food-plant "island" whose shores no *Exyra* has ever reached.

Food-plant "islands" may overlap or coincide geographically, and yet tend to separate their insect associates. At Summerville, South Carolina, where *ridingsii* is very abundant in *flava* and *semicrocea* in *minor*—these plants growing intermingled—*semicrocea*, hibernating as a last stage larva, finds its early spring food in the green, winter leaves of *minor*, and the moths appear in numbers about April 20; *ridingsii*, hibernating as an early stage larva in dry, dead leaves of *flava*, cannot complete its transformations until the spring growth of its food plant provides it with larval food. It does not leave its hibernaculum until about April 20, and the moths do not appear in numbers until May 20. Thus the spring broods of *semicrocea* and of *ridingsii*, in their mating stage, are separated by about four weeks—that is, the seasonal history of their respective food plants compels the partial isolation of one closely related species from another.

Even within the species we see something of this in process. In southern Mississippi, *semicrocea*, hibernating in *sledgei* as a last stage larva, completes its transformations and appears as a moth in early April. According to observations made in 1910, the spring emergence reached its height about April 10. In the same bog very young larvæ of this species, occupying their water-tight hibernacula in the pitchers of *psittacina*, were observed to awake from their winter lethargy in mid-April, and the first moth was noted in early May. Thus approximately a month intervenes between the appearances of moths of the same species from larvæ hibernating in the two food plants. When first found, especial attention was paid to these *psittacina*-feeding larvæ, for they were so different in age and habit from their fellows hibernating in *sledgei* that another species was confidently expected. The following is a literal transcript of field notes made at the time:

"North side of Biloxi Bay, March 9, 1910. Opened 275 leaves of *psittacina*, gathered at random from plants growing in a very s'oppy place, often partly under water or imbedded in wet sand; found three living *Exyra* larvæ, $\frac{1}{8}$ to $\frac{3}{8}$ inch long, in each instance the entrance to leaf strongly plugged by a water-tight partition, the larva low down in the narrow tube; several plugged leaves contained dead (drowned) larvæ."

As far as it is safe to judge by one season's observation, here seems to be in progress a selective process—a rigorous weeding out of all older larvæ, which had weakened their hibernacula by feeding, and of those which had not ceiled their pitchers exceptionally well—essential group-isolation enforced by food-plant characters, and a considerable degree of adjustment to those characters and to habitat.

We have tried to demonstrate, with reference to *Exyra* and *Sarracenia*, that the insects throughout their life cycle exhibit a remarkable degree of plasticity, of adaptability to varying conditions; that food-plant distribution, structure, and seasonal history, encourage or even compel group-isolation among the associated insects, creating conditions favorable to the preservation of divergent characters; that many, if not most, of the specific differences of the insects of this genus find their intelligible explanation as adjustments to food-plant characters; and since so large a proportion of these specific differences do consist of adjustments, specializations, to food-plant environment, how can we avoid the further conclusion, that on these food-plant "islands" there has been a selective process as well, by which advantageous divergences have been preserved to the exclusion of those of doubtful or of negative utility?

*Courtesy of W. R. Taylor*

A growth of *Purpurea* near Tom's River, New Jersey