The Dissemination and Germination of *Arceuthobium occidentale*, Eng.¹

BY

GEORGE J. PEIRCE.

Associate Professor of Plant Physiology, Stanford University, California.

With Plates III and IV.

INTRODUCTION.

‘SO much has already been written on this genus of the Loranthaceae that many will no doubt be surprised that there should be anything new to be said on the subject.’ From this modest introduction Johnson (1888) proceeds to a description of *Arceuthobium Oxycedri*, which is the more remarkable for its excellence when one realizes the meagreness of the material at his disposal. If it were not that I have had the opportunity to study another species alive and out of doors, as well as in the laboratory, to see it disseminating its ‘seeds,’ and to observe their germination, I should have no excuse for attempting to add anything to Johnson’s paper. As it is, I hope to be able to clear up certain matters which have hitherto been obscure.

The material of *Arceuthobium occidentale*, Eng., which I have studied was on trees, young and old, of *Pinus radiata*, D. Don., the Monterey Pine², which grows wild mainly along the shore of Monterey Bay on the coast of California. It is also abundantly planted about San Francisco Bay, and elsewhere. The affected trees which I studied were either in the Arboretum of Stanford University, where *Arceuthobium* has of late suffered greatly from the general improvement of the Arboretum, or in the forest on Point Piños, one of the heads bounding Monterey Bay. This forest protects the town of Pacific Grove from the inward blowing sand which, instead of piling up as at present in fine dunes, would otherwise blow over and bury the town. The preservation of this forest is therefore important, a matter made very serious from the extraordinary number of untoward influences, natural and artificial, now operating there. A careful study of one of the enemies of this pine, therefore, may lead to practical advantages as well as to facts of some botanical interest.

¹ Read before the Botanical Section of the British Association, Cambridge, August, 1904.

² For a study of the effects of another parasite which attacks this pine see Peirce, G. J., Notes on the Monterey Pine, Botanical Gazette, vol. xxxvii, 1904.

[Annals of Botany, Vol. XIX. No. LXXIII. January, 1905.]

Some of the material used was alcoholic, but always controlled by the examination of fresh. The fresh material was studied out of doors in the Arboretum and in the forest, and in the Hopkins' Seaside Laboratory at Pacific Grove, as well as at Stanford University. I had fresh material sent to me repeatedly from Pacific Grove at times when I was unable to go there. The study of the dissemination and germination of this parasite must include the observation of the climatic conditions under which the plant lives, especially the humidity of the air. At Stanford University, which is three miles from San Francisco Bay, and cut off from the ocean winds by mountains ranging from 1,000 to nearly 3,000 feet in height, the air is much drier and the winter temperature lower than at Pacific Grove, which is on the Bay of Monterey, and is only a mile from the open sea. Though in both places the rainy season is only from October to April, the rainfall is heavier at Pacific Grove than at Stanford University. The winter temperature at Stanford University is considerably lower than on the coast, where in most places frost occurs scarcely oftener than once in a decade. There was no frost this last winter. On the other hand, the summer temperature of Stanford University is decidedly higher and the air dry, while the coast is cooler and likely to be buried in fog. Fog prevails on the coast during much of the time when the fruits are ripening, while further inland it occurs only at night. When the fruits are ripe the comparatively humid air of the coast keeps them from drying. When rain comes in addition their water content is still greater. But further discussion of the relations of climate to this plant may be deferred for the moment.

DISSEMINATION.

Arceuthobium occidentale flowers from September to January: in a year from that time the fruits are ripe. If heavy rain and high wind come at this time, all or nearly all of the fruits are shaken off; the plants may even be broken to pieces, for they are brittle, and hence the whole crop of two seasons' growth may be destroyed. In some years I have been unable to get fruits after mid-November. This current year, however, I found the fruit very abundant in the woods at Pacific Grove in the Christmas holidays (1903-4).

It is well known that the fruits of *Arceuthobium* are explosive. Before passing to a description of the anatomy and mechanics of the explosive fruit, I should like to call attention to the conditions under which the fruits were disseminating the 'seeds' at Christmas time, 1903.

The weather was showery, but whether the sky was overcast, with or without rain falling, or whether the sun was shining, the air was damp and the temperature mild. In the woods at Pacific Grove the air was still

damper than elsewhere, and dampest of all in the thickets where the pines were small and close together. It is precisely in these thickets and close stands of young pines that *Arceuthobium* is most abundant. On some of these young trees, fifteen to twenty feet high, I counted over twenty separate bunches of *Arceuthobium*. On trees farther apart, or isolated, *Arceuthobium* occurs in far less numbers, if it is to be found at all. Some young trees in the thickets were dead, from no other apparent cause than the great number of *Arceuthobium* plants which they had borne. In many cases where a branch bore a particularly large and vigorous bunch of *Arceuthobium* the branch was dead beyond the parasite, as Cannon (1901) observed on oaks attacked by *Phoradendron*.

In the damp air of the thickets little water is lost by evaporation from the fruits; if rain falls, still less. The fruits seemed to me plumper and more translucent than the few which I had found in the Stanford Arboretum. Without any apparent disturbance the fruits would explode; I could hear them, I might even be struck by the flying 'seeds'; but if the wind gently shook a bunch of fruiting *Arceuthobium*, or the raindrops fell upon the fruits, or I lightly struck a branch of pine on which the fruiting parasite grew, there would be a momentary fusilade, the 'seeds' flying in all directions, and sticking to whatever they struck, provided always the speed at the time they struck were low enough to be offset by the adhesion of their gelatinous outer-coats to the object struck. That the speed with which the 'seeds' leave the parent plant is high any one knows who has been struck by the hard, pointed little bodies. The speed must be great to carry the 'seeds' far, for they are heavy. It is impossible to determine the distance to which a 'seed' may be thrown. I can only estimate this from experiments. The longest distance to which a 'seed' was thrown in the laboratory was fifteen feet. The air of the laboratory was dry, but I had kept the material, sent from Pacific Grove, in an air-tight preserve-jar in which there was a little water. In other words, the air surrounding the material was as moist as that at Pacific Grove, and the fruits were as plump and tense. I have no doubt, from the relative positions of my work-table and of the book-shelf on which the 'seed' stuck, that it could have gone at least ten feet further.

Let us turn now to the structure and mechanics of the fruit. In Fig. 1, Plate III, we see a small fruiting branch, natural size, which was growing a few years ago in the Stanford Arboretum. At Pacific Grove the fruits may be as many again on a branch. The fruits are complex. Morphologically they include the receptacle adherent to the ovary (Engler and Prantl). Skrobischewsky (1890)—only reviews of whose paper I have been able to see—describes the fruit of *A. Oxycedri* as consisting of (1) a one or two-layered epidermis, (2) underlying this four or five layers of collenchyma, (3) parenchyma with vascular bundles embedded in it, (4) the gela-

tinous seed-coat, (5) then three or four layers of tannin cells, (6) the endosperm, (7) and finally the embryo. Thus we have seven concentric layers of differentiated tissues. As *A. occidentale* is slightly different I may go into some detail as to the structure of the fruit. Figure 3 is a diagram of a longitudinal section of a fruit with the 'seed' still in it, and with a part of the stalk still attached. The diagram falls into three parts from top to bottom. The uppermost part, cut off from the rest by the oblique line *a-b*, is covered by heavily cutinized epidermis (*c. ep.*), one-layered, with the outer cell-walls much thickened, and many stomata, the guard-cells of which are depressed (see Fig. 5). Underlying this are several layers of parenchymatous cells (*c. p.*) containing chlorophyll grains in abundance, and with cellulose walls. Under this are two or three layers of somewhat elongated cells (*l.*) with lignified walls more or less spirally thickened. This conical layer is continuous nearly or quite to the top. Within this, again, are parenchymatous cells in which part of the gelatinous 'seed' is embedded. Below the line *a-b* the structure is surprisingly different. The epidermis (*ep.*) is scarcely cutinized, and has no stomata. Underlying this is a very gelatinous collenchyma (*g. c.*), the thin places in the cell-walls of which are still cellulose. This gelatinous collenchyma is several layers thick, and abuts within upon the gelatinous 'seed' coat (*g. f. c.*). This coat extends nearly around the 'seed,' is absent on the end which is to be forward when it is thrown out, and is thickest at the top, which will be the back end in flight. The 'seed' is covered all around with a sclerotic coat (*s. f. c.*) from one to three cell-layers thick. Enclosed within this is the endosperm (*end.*), in one end of which the embryo (*emb.*) lies. At the line *c-d* is the so-called abscission layer, a single row of very thin-walled cells (Fig. 6) lying between masses, above and below, of thick gelatinous-walled cells.

A cross-section of a fruit from which the seed has been expelled is shown in Fig. 4.

Passing now to the mechanics of discharge one sees at once that the top of the fruit is so made as to be able to resist considerable pressure from within the fruit, that the middle and lower parts will develop pressure whenever they can absorb enough water, and that the line of mechanical weakness is the so-called abscission layer, where the fruit is attached to the stalk. Given, then, the conditions such as I have described above—abundance of water in the soil and in the host, from which the parasite absorbs water and the gelatinous parts of the fruit take it up, and air so moist that little water is lost from the fruit by evaporation—it is inevitable that a very considerable pressure must develop in the fruit. MacDougal (1899), describing another species, says: 'During the ripening period the contents of the expulsory layer undergo such chemical changes as to give the contents a very high isotonic coefficient. The consequent osmotic

attraction of water into this layer sets up a turgescence which could not be measured, but which probably amounted to many atmospheres.' In *A. occidentale* we see that it is the imbibition of water by the material of the cell-walls rather than the osmotic activity of the cell-contents which brings in water; that the water is taken up and held by the swelling gelatine of the walls. What the resulting pressure amounts to is unknown, and may for the present remain unguessed.

Finally, the pressure within the fruit becomes too great, under the conditions which I have described, and, with or without some jar to set it off, the fruit breaks at the base. The conical shape of the 'seed,' with the larger end at the back, gives it a cumulative impulse from the top and sides of the fruit, the sides compressing and indirectly propelling it, the top propelling it directly since, before the fruit breaks, much of the pressure has been against the tough epidermis and the lignified layer at the top, stretching these upward.

Passing now to the 'seed.' Morphologically this is a seed enclosed in the inner part of the ovary (Engler and Prantl). The greater part of it is covered with a gelatinous layer sticky enough to attach it to smooth objects as well as rough. This layer will take up still more water from damp air, swell, and so come into contact with a still more extended surface than it at first touched. Furthermore, this gelatinous material dries only very slowly even in dry air. But damp air, only moderately cool, is necessary for germination.

The structure of the 'seed' is essentially as described and figured by Johnson (1888), but as *A. occidentale* appears to differ somewhat I may give some details. The gelatinous outer layer (see Fig. 7, a 'seed' fixed in dilute Flemming's solution, and Fig. 12, a longitudinal section of an ungerminated 'seed') consists of much-elongated cells, their much-thickened walls consisting of two layers (Fig. 8), an outer of gelatinous material, an inner of cellulose spirally thickened. The cell cavity is very narrow. These long cells are attached obliquely or at right angles to cells of the sclerotic layer of the 'seed.' On the outside (as Fig. 8 shows) 'dirt' of all kinds may adhere. Figures 9 and 10 show the extent to which these gelatinized cells may expand. Figure 9 shows a cross-section of these cells near the tip, tangential to the seed, which had lain for some weeks in 95 % alcohol. Figure 10 is the outer part of the same section after it had lain for a quarter of an hour in water on the slide.

With the slow loss of water which takes place as the air dries, these long cells, attached at their tips to whatever the 'seed' has struck, and at their bases to the firm sclerotic coat, contract, shorten. Owing to the spiral thickening of the inner cellulose wall, the shortening of these cells pulls the 'seed' closer and closer, and attaches it more and more firmly, to whatever it has struck. This attachment may hold for many months, for I have seen 'seeds'

a year old still attached to the leaves on branches which they struck and on which they had failed to germinate. The attachment of the 'seed' is then very firm, and may be increasingly firm as time goes on.

So far as my observation goes, the majority of the 'seeds' strike the leaves of the pine, either of the tree on which they grew or of one near by. Owing to the various positions of the fruits, the directions in which the seeds are shot are very various. Some must go to the ground at once, others up into the air, but the majority certainly nearly horizontally, for in the close clumps of trees where *Arceuthobium* is most abundant the parasites are, most of them, on branches from four to ten feet from the ground. I have never seen the plant high up on old Monterey Pines, though it is reported on the high branches of other pines elsewhere. In the Stanford Arboretum it is not on the branches at all, but forms a more or less complete ring around the trunk of the tree two or three feet from the ground. Comparatively few of the enormous number of seeds produced where *Arceuthobium* flourishes reach places favourable for germination and for penetration into a host. The explosive fruit, therefore, is a very powerful but very wasteful means of disseminating the plant, much less efficient than the less astonishing fleshy fruits of *Viscum*, *Phoradendron*, and other Loranthaceae.

GERMINATION.

The 'seeds' of *Arceuthobium occidentale* will germinate on anything, if they will germinate at all. I have seen germinating seeds on pine-needles, dead as well as living, on dead branches, on trees and shrubs of other sorts, on a fence board, anywhere where the air was moist and warm enough. But I have not been able to grow the plants at Stanford University. The reason for this, I am sure, is the cold of winter and the drier air. Until the parasite has penetrated into the host it can get water only from the air. It is therefore very dependent upon such a degree of moisture in the air as will not rob the gelatinous coat of the seed of more water than the embryo requires for its growth and penetration into the host. The gelatinous coat is the water-reservoir of the embryo as well as the means of attaching the seed to the host—two very important functions, requiring the differentiated cell-walls above described. Germination will not be successful, however, unless the seed fall on a branch, the rough surface or the angles of leaves or branches of which oppose the gliding of the growing root over the surface. On leaves the root will continue to grow, gliding over the surface, to an astonishing length, three centimetres or even more, until no longer enough food can be taken out of the endosperm.

The embryo is a simple cylindrical structure lying in the endosperm at the upper end, that is, toward the tip of the fruit. The cotyledons are represented only by a slight notch at the lower end. The epidermis is the

only tissue differentiated. This lies at first in close contact with the endosperm, but as germination progresses it is no longer in contact. The embryo must therefore absorb dissolved food diffusing out of the endosperm into a layer of water which surrounds the embryo. Whether the embryo forms enzymes which, diffusing into the endosperm, dissolve the solid foods stored therein, or whether the endosperm cells themselves dissolve these solid foods, which thereupon diffuse outward toward the embryo, there is at present no means of telling. As all attempts at experimental germinations have hitherto failed, there is no hope for an immediate answer to the question, though an answer might throw an interesting light on the physiological chemistry of germination in exalbuminous plants. The embryos are bright green, and contain much starch, at least in the earliest stages of germination. The radicle has no cap at any time, and the tip for some distance back, even in the later stages of germination, consists of merismatic cells, with only the dermatogen at all differentiated.

It may be of some systematic value to record that, though quite by chance, I found two embryos in one 'seed,' as shown by Fig. 14. These two embryos are of unequal size, and only one could possibly have developed into a new plant. Johnson (1888) records having always found only one embryo, but remarks (p. 158) that 'the general result of the investigation tends to show that in the possibility of the formation of two embryos and in habit the affinity of *Arceuthobium* to *Viscum album* is closer than was generally supposed.' I cannot consider the habit of this species of *Arceuthobium* at all like *Viscum* or the allied genus *Phoradendron*, as will appear later on.

The root does not appear to be geotropic, but as in other Loranthaceae (Pfeffer II. 575, 1900) it is negatively phototropic in marked degree, growing always away from the light, down a needle or along a branch toward the central and darker part of the tree (see Figures 15, 16, 17). I have never seen a root-tip pointing in any other direction than away from the light, and often it was necessary for the root to make a turn of over 90° to do this (Fig. 16). I have seen roots turned 180°, but in these the curve was always a spiral, downward as well as backward. We may have here the influence of gravity supplementing that of light, but as the light reaction is so marked and the geotropic reaction so slight, we may doubt, until experiment furnishes evidence, whether these roots are geotropic at all. In this respect they are like *Viscum*, the roots of which are not geotropic.

The roots do not appear to be very sensitive to contact. They grow generally in fairly close contact with the surface of pine-needles or branches, but they do not stop growing and form holdfasts on the needles, though the contact with the surface of the needle may be long continued. The root may even grow for some distance over the comparatively rough surface

of the bark of the Monterey Pine. Until its further growth is opposed by some obstacle—a slight elevation of the surface or the base of a bunch of leaves or of a branch (Figs. 17, 18, 19, 21)—the root grows on, always toward the trunk of the tree. In colour it is usually more or less claret-red.

When the further growth in length is blocked, the root forms a thick holdfast. This is shown in Figs. 13, 17, 18, 19, 21. The holdfast consists at first of an undifferentiated mass of dividing and growing parenchymatous cells covered by a single layer of dermatogen cells which above differentiate into ordinary epidermis cells, and below, where the cells are in contact with the bark, elongate somewhat and firmly attach the holdfast to the bark, much as is the case in *Cuscuta* (Peirce, 1893) and other haustoria-forming parasites. Into this growing foot the material in the upper (cotyledonary) end of the embryo or seedling is transferred. In consequence this upper end shrinks as the lower grows, the 'seed' coats become loosened and may blow away, and the seedling becomes mainly a foot with a small and shrivelled prolongation (see Figs. 18, 19). In this foot (shown in section in Fig. 13) differentiation begins, vascular tissues form, and then the central part of the foot grows out into the bark. That both pressure and chemical action co-operate in the penetration of the haustorium into the host is highly probable, to judge from other cases (Peirce, 1893, 1894), but the effects of pressure are far from evident. Instead, appearances all point to the much more important action of substances excreted by the cells of the haustorium, enzymes which dissolve the walls of opposing cells and hence permit the easy and rapid penetration of the haustorium through the dead outer bark into the living cortical parenchyma of the host. The haustorium has no cap, the cells at the tip elongate and spread out as in *Cuscuta* (Peirce, 1894), forming strands of infecting-cells which grow in various directions toward the medullary rays of the host, grow through these to and through the cambium, dissolving the opposing cells as they grow. Finally, the haustorial cells effect a direct attachment with the young cells of the wood of the pine branch. These last haustorial cells and those above them differentiate into tracheids, some of the cross-walls may disappear, and a direct connexion by conducting tissue is established between the wood of the host and the mass of *Arceuthobium* cells in the cortex of the host.

It is to be noted that, while the cells at the tip of the haustorium are growing out and forming infection strands which penetrate the medullary rays of the host, the main part of the haustorium is increasing in size, forming a mass of parasitic cells in the cortex of the host (Fig. 22). Morphologically this mass is a part of the haustorium, itself a special outgrowth of the tip of the radicle of the seedling. This mass presently differentiates into conducting and parenchymatous tissues, buds form which develop into branches which grow out through the bark into the air (Figs.

20, 21). These branches are pale green, later they become much greener. They at first vegetate and later flower. We have here an instance of regeneration without wounding, amputation, or other pathological stimulus. The small part of the seedling which penetrates the host forms and develops stem and leaves, a small part of one organ—the root—develops into a complete plant by forming the missing members.

Goebel (1900) says, 'Als Organe "sui generis" dürfen wir auch betrachten die Haustorien der Parasiten.' He supports this assertion *first* by saying that in *Cuscuta*, where the haustoria most closely resemble lateral roots, there is no positive proof of their being roots though they arise endogenously, and in the *second* place by the haustoria of the Rhinanthaceae, Orobanchaceae, and Balanophoreae, which are certainly not root-like in appearance. In *Arceuthobium* the haustorium almost immediately ceases to be root-like in appearance, yet it is plainly a modified root-tip. The same is the case in *Pharadendron* and *Viscum*. The single root of the seedling grows into the host, and in the tissues of the host the tip becomes a mass of cells, at first parenchymatous, later including prosenchymatous cells, and sends out strands which penetrate the medullary rays and form a direct connexion with the tracheids of the host. The primary haustorium of *Arceuthobium* is evidently the primary root of the seedling; the succeeding haustoria are branches of this primary root. In *Cuscuta*, on the other hand, the haustoria arise in the stem of the parasite from that layer of cells which in other and similar stems gives rise to lateral roots. It is not merely the endogenous origin of the haustoria of *Cuscuta*, but their origin from that cell-layer which ordinarily gives rise to lateral roots, which causes one to believe them to be lateral roots (Peirce, 1893). Similarly the lateral roots and the root-tubercles of leguminous plants originate endogenously, but it is only when one sees that the root-tubercles originate from the same layer exactly as lateral roots, and in their earliest stages are indistinguishable from lateral roots except by the presence of the infecting strands of bacteria in the cells, that one can believe them to be morphologically the same (Peirce, 1902). When one realizes the marvellous plasticity, adaptability, of root, stem, and leaf, the idea of organs *sui generis* becomes unnecessary.

After the parasite has once formed a foot or holdfast on a pine branch the succeeding stages above described are passed through very rapidly. The vegetative branches emerge much sooner than one would naturally expect. There is very little evidence of pressure being exerted by these branches in emerging from the bark, probably because they arise as buds on the outer part of the mass of parasitic cells in the cortex and are covered mainly by the dead and weathering tissues of the outer bark of the host. Later, however, as these branches increase in diameter they plainly push back the host cells by which they are surrounded.

When one compares Figs. 1 and 2 with figures of *Viscum* and

Phoradendron one sees at once that the habit of *A. occidentale* at least is entirely different from that of members of the other two genera. In *A. occidentale* the stem is composed of very evident segments, rectangular or square at the base, and cylindrical at the top of each segment. The colour is much lighter, the abundant chlorophyll being masked by a brownish pigment in the walls of the epidermal cells. The brittle stem breaks into pieces much more readily near the nodes than near the middle of the internodes, in this respect resembling the grasses and other 'jointed' plants. The stem branches profusely, the stems of *Viscum* and *Phoradendron* comparatively sparingly. The leaves are reduced to scales subtending the chlorophyll-containing branches.

In the reduction of the leaf surface, the thickening of the outer walls of the epidermis, the sinking of the guard-cells of the stomata below the surface (described by Cannon in *Phoradendron* also), the screening of the chlorophyll by another pigment or pigments (see also Cannon), we have very decided differences from the *Viscum album* of northern and moister Europe, and very evident protective adaptations to conditions which, at certain seasons of the year at least, approach much more nearly those of the desert than those of Europe. Certain species of *Arceuthobium* are found in the Sierra Nevada Mountains, where evaporation into the dry air is very rapid in summer, and in parts of Arizona and New Mexico, which are really semi-desert. While *A. occidentale* is actively vegetating, in the spring, the air may be comparatively moist, and from its host it can absorb water in plenty as the soil under the pines is full of moisture, at least below the surface. But in the summer, when no rain falls and the air is very dry, except when fogs sweep in from the ocean, the parasite must retain as much water as possible lest it perish. There is a very decided contrast, therefore, between summer and winter conditions. While the conditions for germination are those of a mild and humid climate, those of vegetation and fruiting are those of a dry and warm climate. To these two sets of conditions the parasite has adapted itself. In this respect it is like *Phoradendron villosum*, but it has carried its adaptation to the summer conditions further than has *Phoradendron*. The conditions for germination are probably the same in both plants, for only once have I succeeded in germinating seeds of *Phoradendron villosum*, and then the young plants soon perished, though I have tried at least five years.

Something more should now be said of the anatomical relations of parasite and host, and of the effects of the parasite upon the host. Figure 2 shows the direct connexion of a branch of *Arceuthobium* with the wood of the host. In Fig. 22 we have a diagram showing two masses (parts of one) of *Arceuthobium* cells in part of a cross-section of a pine branch. The tissues of the parasite are shaded, those of the host white. In this figure we see that strands of cells of the parasite run from the main mass in the

cortex into the medullary rays of the host, traversing the cambium and passing into the wood. In Fig. 23, a diagram of part of a cross-section of an infected pine branch, we see that from a vascular bundle of the parasite (shaded) in the cortex of the host (unshaded) a vascular bundle occupies the middle of the branch of the parasite which has penetrated into the wood of the host through a medullary ray. Figure 24 represents a tangential section of an infected pine branch through the wood, and shows the direct contact of a tracheid of the parasite (shaded) with a tracheid of the host. Figure 25 is also a tangential section of a branch of pine, but through younger wood, and shows, in the centre, the strand of tracheids and vessels connecting with the older wood, and at the sides the direct connexion of younger *Arceuthobium* cells with the young tracheids of the host. At *a* in this figure we see how thin is the membrane through which the young *Arceuthobium* cell absorbs water from the pine tracheid. By preserving these thin places in the walls, the transfer of water from the cells of the host to the adjacent cells of the parasite is made as easy probably as the transfer of water from tracheid to tracheid through the wood of the host. I have seen no cases in which no membrane at all intervened between the tracheids of host and parasite, though there may be such places.

In this perfect connexion of the xylem-tissues of parasite and host we have nothing uncommon. A more interesting question is as to the relations of the phloem-tissues of the two. In tangential and other sections through the bark I have sought vainly for anything more than contact between the cells of *Arceuthobium* and the sieve-tubes of pine. Fig. 26 at *a* and *b* shows *Arceuthobium* cells (shaded) in direct contact with sieve-tubes of pine. This tangential section was so thin that under an oil-immersion objective I could plainly see the sieve-plates in actual section, but I could never find any place where the pine formed a sieve-plate on the side of the tube toward an adjacent *Arceuthobium* cell. There may be such places, but I have searched long and carefully enough to doubt it. In this respect, therefore, *Arceuthobium* resembles other chlorophyll-containing parasites, e. g. *Viscum*, *Phoradendron* (Peirce, 1893). But from the anatomical fact of the absence of sieve-plates in the walls between the sieve-tubes of the host and the living cells of the parasite the inference is not justified that the parasite absorbs only food-materials, not elaborated foods, from the host (Pfeffer i. 355; Peirce, 1903). In fact Fig. 26 shows plainly that osmotic transfer must take place through the thin walls separating the sieve-tubes of the host from the cells of the parasite whenever the physical conditions make osmotic movement through the thin walls in either direction necessary. The presence in either host sieve-tube or parasitic cell of a greater proportion of dissolved substance, food or other, will inevitably entail the movement of that substance to the cell that contains less.

The life-history of this perennial parasite supports this view. The branches at first vegetate in the air, and later flower and fruit. After their crop of 'seeds' has been discharged they die and fall away. At this time no part of the parasite may be visible outside the body of the host. The persisting part of the parasite, embedded and concealed in the host, contains no chlorophyll. It corresponds with *Rafflesia*, *Balanophora*, &c., and at this stage is altogether different from *Viscum* and *Phoradendron*. When *Arceuthobium* becomes active again, as it does in the spring, forming buds and developing these into branches, it must do this work either at the cost of foods elaborated by itself and stored in the mass of parenchymatous cells of its own in the cortex and medullary rays of the host, or at the cost of foods drawn from the host, or both. As I saw no evidence of any great accumulation of foods in the parasitic tissues embedded in the host, I am inclined to believe that, though its aerial parts contain chlorophyll, *Arceuthobium* is a much more complete parasite than *Viscum* and *Phoradendron*, and, in spite of having no sieve-plate connexions with the sieve-tubes of its host, that it absorbs and uses foods elaborated by the pine. The perennial part of *Arceuthobium* is probably completely parasitic so long as it has no aerial branches. During the many months when it has aerial branches it may not be a complete parasite, and may be merely a 'water-parasite.'

Arceuthobium, therefore, shows a distinct advance over *Viscum* and *Phoradendron* toward complete parasitism, and is an interesting link in the chain connecting independent plants and completely parasitic forms.

Owing to the presence in the host of a perennial part of *Arceuthobium*, it is out of the question to exterminate the parasite by merely removing the aerial branches. The spread of *Arceuthobium* in a forest can, however, be prevented by removing the fruiting branches before the fruits are ripe. If this were done every two years through a series of years, and the infected trees gradually thinned out, the parasite could be exterminated. Thinning the forest, thus exposing the parasite to greater dryness during the summer and greater cold during the winter, would tend to keep it in check. In a natural forest of thick growth combatting the parasite is not likely to be successful. In a planted forest, carefully watched, there should be no danger of any great damage from this source. When we learn in America to take as intelligent and skilful care of our forests as we now do of our gardens the phanerogamic parasites will do little damage to the trees.

As a result of the presence of *Arceuthobium* in the pine, the trunk and branches, especially the latter, exhibit considerable distortions. At a point where there is a bunch of *Arceuthobium* of considerable size, the diameter of the branch may be three or even four times greater than just below. The infecting strands of the parasite do not grow for any distance upward and downward through the cortex of the host. Instead they penetrate the

medullary rays and grow in length only as the diameter of the branch increases from year to year, exactly as do the 'sinkers' of *Viscum* and *Phoradendron*. On the other hand, the infecting strands increase greatly in width, becoming sometimes many times as broad as the medullary rays which they once penetrated and absorbed. Thus in Fig. 27 we see a tangential section of a pine branch one centimetre below a bunch of *Arceuthobium*. Here the medullary rays are only one cell broad and a few cells deep. In Fig. 28 we have a tangential section of the same branch, but in the part infected by *Arceuthobium*. The infected medullary rays have been completely displaced by absorption, and the tracheids of the host have been pressed apart, upward and downward but mainly laterally, by the strand of parasitic tissue. It is by this means that the distortions arise. When such distortions occur in the trunks of pine trees the timber is useless as lumber, and has only an inferior value as fuel. However, as pointed out above, such distortions rarely occur in the trunks of Monterey Pines, and these pines have only local use for any other purpose than fuel. The Monterey Pine is not a good timber tree.

BIBLIOGRAPHY.

- BONNIER, G.: Assimilation du gui comparée à celle du pommier. Actes du Congrès de 1889 de la Soc. Bot. de France: Bull. Soc. Bot. de France, 1890. Sur l'assimilation des plantes parasites à chlorophyll. Comptes rendus, cxiii.
- CANNON, W. A.: The anatomy of *Phoradendron villosum*. Bull. Torrey Bot. Club, xxviii, 1901.
- ENGLER AND PRANTL: Die natürlichen Pflanzenfamilien: Loranthaceen, 1894.
- GOEBEL, K. Organographie der Pflanzen. Bd. II, pp. 433-4, 1900.
- JOHNSON, T.: On *Arceuthobium Oxycedri*. Annals of Botany, ii, 1888.
- MACDOUGAL, D. T.: Seed dissemination and distribution of *Razoumowskia robusta* (Engelm.), Kuntze. Minn. Bot. Studies, xii, 1899.
- PEIRCE, G. J.: On the structure of the haustoria of some phanerogamic parasites. Annals of Botany, vii, 1893.
- : A contribution to the physiology of the genus *Cuscuta*. Annals of Botany, viii, 1894.
- : Textbook of plant physiology. New York, 1903.
- : The root-tubercles of Bur-Clover. Proc. Cal. Acad. Sci. Bot., vol. ii, 1902.
- PFEFFER, W.: Handbuch der Pflanzenphysiologie. 2te Aufl., I und II, 1897-1904.
- SKROBISCHEWSKY, W.: Morphologische und embryologische Untersuchungen der Schmarotzerpflanze *Arceuthobium Oxycedri* D. C. Riga, 1890. Review in Famintzin's Übers d. Leistungen a. d. Gebiete d. Botanik in Russland, 1890. St. Petersburg, 1892. Also Just's Jahresbericht, xix, p. 609, 1894.
- SOLMS-LAUBACH, H., Graf zu: Über den Bau und die Entwicklung einiger parasitischen Phanerogamen. Jahrb. f. wiss. Bot., vi, 1867-8.

EXPLANATION OF FIGURES IN PLATES III AND IV.

Illustrating Dr. Peirce's paper on *Arceuthobium*.

The figures were drawn either free-hand or with a Zeiss drawing-prism.

PLATE III.

Fig. 1. Fruiting branch of *Arceuthobium occidentale*. Nat. size.

Fig. 2. Section of branch of *Pinus radiata*, showing part of mass of *Arceuthobium* tissue in the bark, the connexion of this with the wood of the pine and the aerial branch of the parasite. Nat. size.

Fig. 3. Diagrammatic sketch of a longitudinal section of a fruit of *Arceuthobium*. *a-b*, the line above which the epidermis is heavily cutinized. *c-d*, the abscission layer. *c. ep.*, cutinized epidermis with many stomata. *c. p.* parenchyma cells with cellulose walls and chlorophyll grains. *l.*, the layer of cells with lignified walls. *e. p.*, epidermis scarcely if at all cutinized, with no stomata. *g. c.*, gelatinous collenchyma. *g. f. c.*, gelatinous fruit coat. *s. f. c.*, sclerotic fruit coat. *end.*, endosperm. *emb.*, embryo, with radicle up. $\times 10$.

Fig. 4. Cross-section near middle of fruit from which the 'seed' has been discharged. Large-celled thin-walled parenchyma with small but many chlorophyll grains and some yellow oil-drops. *v. b.*, the vascular bundles. $\times 29$.

Fig. 5. Epidermis from upper part of fruit, showing heavily cutinized and thick outer walls, and depressed guard-cells. $\times 300$.

Fig. 6. Part of a longitudinal section through a fruit, at the base, showing very thin-walled abscission layer between thick-walled tissues. $\times 300$.

Fig. 7. Wet 'seed' much swollen, showing markings on the gelatinous surface and the small hard ungelatinized end of the 'seed' whence the radicle will emerge. $\times 24$.

Fig. 8. Section through gelatinous outer coat of the 'seed,' showing long cells with narrow cavities, outer part of walls gelatinized, inner cellulose (spirally thickened). Long cells attached to thick sclerotic cells forming continuous coat around the 'seed.' $\times 300$.

Fig. 9. Tangential section of gelatinous coat of a 'seed.' In 95 % alcohol. $\times 334$.

Fig. 10. Part of the same section after lying in water fifteen minutes on the slide. The swelling of the gelatinous outer portion of the cell is very marked. $\times 334$.

Fig. 11. 'Seed' germinating on a pine-needle. $\times 3-4$.

Fig. 12. Longitudinal section of 'seed,' showing gelatinous outer coat, the sclerotic inner coat, the endosperm with the undifferentiated embryo at one end. The radicle is up, the cotyledons down and indicated only by the slight notch. $\times 20$.

Fig. 13. 'Foot' or holdfast formed by the tip of the root when it catches on rough bark. Longitudinal section. From the centre the infecting haustorium will penetrate the host. $\times 29$.

PLATE IV.

Fig. 14. Longitudinal section of 'seed' showing two embryos of very unequal size. $\times 20$.

Fig. 15. Germinating 'seed' on branch of pine, showing root already bent away from the light (negative phototropism) toward centre of the tree. $\times 8$.

Fig. 16. Somewhat older germinating seed with root growing away from the light. $\times 8$.

Fig. 17. Seedling still older, with root forming foot attaching it to the bark. $\times 6$.

Fig. 18. Showing the growth of the foot at the expense of food in the upper part of the seedling from which the coats have already fallen away. $\times 6$.

Fig. 19. Still older and larger foot; the upper part of the seedling much shrivelled and nearly empty. $\times 6$.

Fig. 20. Aerial branches already emerging after recent infection of the branch. $\times 6$.

Fig. 21. Young bunch of *Arceuthobium* branches. Note that the 'seed' has not yet fallen away and that the pine-branch is already enlarged. $\times 2$.

Fig. 22. Cross-section of pine branch showing mass of *Arceuthobium* cells (shaded) in the

cortex (unshaded) and the branches from this mass growing where medullary ray cells were before infection took place. *m. r.*, unabsorbed group of medullary ray cells surrounded by the parasite (shaded). *ph.*, phloem part of a vascular bundle of the pine. *xyl.*, xylem part. *c.*, cambium ring traversed by branches of the parasite growing into the wood. $\times 50$.

Fig. 23. Diagrammatic cross-section of a part of infected pine branch, showing continuous strand of tracheids (and vessels) from the wood of the host (unshaded) to a part of the parasite (shaded) in the cortex. *c.p.*, cortex. Other letters as above. $\times 300$.

Fig. 24. Tangential section of wood of pine showing direct contact of *Arceuthobium* tracheids (shaded) with those of pine (unshaded). $\times 416$.

Fig. 25. Similar tangential section, but in younger wood, showing (*a*) that young and forming *Arceuthobium* tracheids thicken their walls at places that correspond with the thicker parts of the walls of the pine-tracheids. $\times 450$.

Fig. 26. Cross-section of pine, showing sieve-plates in section in the walls of the sieve-tubes of pine, but no sieve-plates in the walls of the *Arceuthobium* cells directly in contact. $\times 900$.

Fig. 27. Tangential section through wood (*xyl.*), cambium (*c.*), and phloem (*ph.*) of pine branch 1 cm. below a branch of *Arceuthobium*. Note the comparatively small size of the medullary rays. $\times 84$.

Fig. 28. Tangential section in same branch in the bunch of *Arceuthobium*. Note the great increase in size of the infected medullary rays the cells of which have been entirely displaced and absorbed by *Arceuthobium* cells. $\times 84$.

Fig. 1.

Fig. 4.

Fig. 10.

Fig. 9.

Fig. 7.

G.J.P. del.

Fig. 8.

Fig. 2.

Fig. 3.

Fig. 6.

Fig. 5.

Fig. 11.

Fig. 13.

Fig. 12.

Huth lith. et imp.

Fig. 14.

Fig. 22.

Fig. 27.

Fig. 21.

Fig. 2.

Fig. 28.

Fig. 15.

Fig. 16.

G.J.P. del.

Fig. 24.

Fig. 25.

Fig. 17.

Fig. 18.

Fig. 19.

Fig. 20.

Fig. 26.

Fig. 14.

Fig. 22.

Fig. 27.

Fig. 21.

Fig. 23.

Fig. 28.

Fig. 15.

Fig. 16.

Fig. 17.

Fig. 20.

Fig. 24.

Fig. 25.

Fig. 18.

Fig. 19.

Fig. 26.

Peirce, George James. 1905. "The dissemination and germination of *Arceuthobium occidentale*, Eng." *Annals of botany* 19, 99–113.

<https://doi.org/10.1093/oxfordjournals.aob.a088995>.

View This Item Online: <https://www.biodiversitylibrary.org/item/233541>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a088995>

Permalink: <https://www.biodiversitylibrary.org/partpdf/318787>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.