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Studies on the Parasitism of *Buckleya Quadriala*, B. et H., a Santalaceous Parasite, and on the Structure of its Haustorium.

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With one plate.

I. INTRODUCTION.

The family Santalaceæ includes, according to HIERONYMUS,[1] twenty-six genera, some of which are already known as hemiparasites.[2] But investigations on this family are far from being complete and especially those species known as hemiparasites can scarcely be said to have been adequately treated, if we except some widely distributed species belonging to the genus *Thesium*. The inadequacy of our knowledge of this family has led HIERONYMUS to remark most properly that probably other genera of the Santalaceæ should be counted among the category of the hemiparasites.[3]

1). HIERONYMUS, Santalaceæ. ENGLER und PRANTL, Die natürlichen Pflanzenfamilien, III. 1, 1889, p. 202.

2). These are *Henslowia*, *Phacellaria*, *Osyris*, *Santalum*, *Comandra*, *Thesium*, *Arjona*, and *Quinchamalium*.

3). HIERONYMUS, loc. cit. p. 203.

It must therefore be admitted that studies on the ecology and physiology of these plants, interesting and important as they are, are still wanting, whereas about the habits of hemiparasites belonging to other families we have a more or less clear knowledge, owing to the numerous investigations of KOCH,[1] PEIRCE,[2] HEINRICHER,[3] WETTSTEIN,[4] etc.[5]; for instance, the gradation of accommodation from autophytic towards parasitic nature was found to prevail among several kinds of plants in a certain family. So far as the Santalaceæ are concerned, the results obtained up to the present time are, as already indicated, very meagre, and leave much to be desired, especially on the mutual relations between the host and the parasite.

With the view of throwing some light upon this subject, I took up *Buckleya Quadriala* for study, as this plant is easily accessible to us. It will be proper to give first an account of its parasitic nature and then to proceed to the structure of its haustorium.

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1). KOCH, Ueber die directe Ausnutzung vegetabilischer Reste, etc. Ber. d. deutsch. bot. Gesellsch. Bd. V, 1887, p. 350; ——, Zur Entwickelungsgeschichte der Rhinanthaceen. I. Rhinanthus minor Ehrh. Jahrb. f. wiss. Bot. Bd. XX, 1889, p. 1 and II. Euphrasia officinalis L. Jahrb. f. wiss. Bot. Bd. XXII, 1891, p. 1.

2). PEIRCE, On the Structure of the Haustoria of some Phanerogamic Parasites. Ann. of Bot. Vol. VII, 1893, p. 291.

3). HEINRICHER, Die grünen Halbschmarotzer. I. Odontites, Euphrasia und Orthantha. Jahrb. f. wiss. Bot. Bd. XXXI, 1898, p. 77; II. Euphrasia, Alectrolophus und Odontites. Jahrb. f. wiss. Bot. Bd. XXXII, 1898, p. 389; III. Bartschia und Tozzia, etc. Jahrb. f. wiss. Bot. Bd. XXXVI, 1901, p. 665; IV. Nachträge zu Euphrasia, Odontites und Alectrolophus. Jahrb. f. wiss. Bot. Bd. XXXVII, 1902, p. 264; ——, Zur Entwickelungsgeschichte einiger grüner Halbschmarotzer, (Vorl. Mittheil.). Ber. d. deutsch. Bot. Gesellsch. Bd. XVII, 1899, p. (244); ——, Auf dem Wege vom Halbparasitismus zum absoluten Parasitismus. Sond. Abdruck aus Ber. d. naturwiss.-medicin. Vereins in Innsbruck. XXV, 1899/1900.

4). WETTSTEIN, Monographie der Gattung Euphrasia. Leipzig 1896.

5). BONNIER, G., Sur l'assimilation des plantes parasites à chlorophylle. Comptes rendus. Bd. 113, 1891; ——, Recherches physiologiques sur les plantes vertes parasites. Bull. d. l. soc. bot. d. France et d. l. Belgique 93, p. 77; CANNON, W. A., The Anatomy of Phoradendron villosum Nutt. Bull. of the Torrey Bot. Club. vol. 28, 1901, p. 374; VOLKART, A., Untersuchungen über den Parasitismus der Pedicularis-Arten. (Inaug.-Diss.). Zürich 1899; SPERLICH, A., Beiträge zur Kenntniss der Inhaltsstoffe in den Saugorganen der grünen Rhinanthaceen. Beihefte z. Bot. Centlbl. Bd. XI, 1902, p. 437.

So far as my knowledge goes, there is no literature specially concerned in the study of *Buckleya*. G. A. CHATIN, in his elaborate work, "Anatomie comparée des végétaux (Plantes parasites)," has given a study of *Buckleya distichophylla* among others, but he has given nothing about the structure of its root-system.[1] A comparative anatomy of the Santalaceæ was then made by M. BEHM,[2] who has studied all known species of *Buckleya, viz., B. distichophylla, Quadriala* and *umbellulata*; but his purpose was to find out some anatomical characters for identifying sterile specimens, so that he confined himself merely to an investigation of the structure of leaves and stems, leaving the root-system entirely out of account. It seems to me that the genus *Buckleya* has till now been considered as an autophyte; for example, it was included by CHATIN, in his above cited work, among "plantes non parasites."[3]

There is, however, good reason to think that he did not examine the root, because even a most superficial examination of the root-system should be quite sufficient to convince one of its parasitic nature.

As to the structure of the haustorium in the Santalaceæ the works of PITRA,[4] SOLMS-LAUBACH[5] and SCOTT[6] are especially instructive. PITRA studied the anatomy of the haustorium of *Thesium ramosum*; SOLMS confirmed, in *T. pratense*, the results of PITRA's

1). 2nd edition 1892, p. 372 and Pl. LXXI.

2). BEHM, Beiträge zur anatomischen Charakteristik der Santalaceen. Bot. Centlbl., Bd. LXII, 1895, p. 65.

3). CHATIN, loc. cit. p. 372.

4). PITRA, Ueber die Anheftungsweise einiger Phanerogamen Parasiten an ihre Nährpflanzen. Reprinted from Bot. Ztg. Bd. XIX. 1861, p. 66.

5). H. GRAF z. SOLMS-LAUBACH, Ueber den Bau und die Entwicklung der Ernährungsorgane parasitischer Phanerogamen. Jahrb. f. wiss. Bot. Bd. VI, 1867–68, p. 509.

6). J. SCOTT, Untersuchungen über einige indische Loranthusarten und über den Parasitismus von Santalum album. Bot. Ztg. Bd. XXXII, 1874, p. 129, (Uebersetzt von SOLMS-LAUBACH).

investigation. SOLMS also studied the structure of the haustoria of *Osyris alba,* but he did not examine, it seems to me, a sufficient number of them. SCOTT, who was the first discoverer of the parasitic nature of *Santalum album,* made a thorough investigation of the external morphology of its haustorium, while on the other hand, our knowledge on the internal structure is still far from being complete.[1)]

II. PARASITISM OF BUCKLEYA.

Buckleya Quadriala is a diœceous shrub widely distributed in the central part of Japan. It has lanceolate or oval, opposite leaves and very inconspicuous greenish flowers on the tip of the shoot. Old stems and branches are furnished with a grayish soft corky layer, which may be stripped off in irregular thin sheets. It is well known to common people on account of its wide occurence and especially of its edible fruit, which is crowned with four narrow leafy bracts, thus closely resembling our shuttle-cock. The seeds are oval and enclose fatty substance around the small cylindrical embryo. As the plant is generally periodically cut down, so a very old stem was inaccessible to me, but at the age of nearly 40 years it measures about 3 meters in height and 9 centimeters in diameter. Formerly it was thought that this shrub could not be successfully transplanted; and the fact was well known to gardeners that, though its seeds easily give rise to seedlings, yet these soon cease to grow and sooner or later perish. The reason of this fact seems, however, to have remained unknown. Recently the interesting fact of the parasitic nature

1). SOLMS studied the structure of the haustorium of *Santalum album* on a specimen sent to him by SCOTT. See the foot note of SCOTT's paper (loc. cit. p. 148).

of this plant was first announced by Professor SHIRAI in his book on plant diseases written in Japanese.[1] This discovery led me to make somewhat detailed studies of this plant. First of all, I intended to determine its hosts by means of a close examination of its roots, while I was obtaining numerous haustoria for anatomical study. The plants thus determined as hosts till now are as follows:—*Cryptomeria japonica, Abies firma, Chamæcyparis obtusa, Quercus glandulifera, Carpinus japonica, C. yedoensis, Fagus japonica, Rhododendron sinense, Alnus firma, Fraxinus longicuspis, Lespedeza Buergeri, Ilex macropoda* and *Stachyurus præcox.*

Besides I was struck with the remarkable phenomenon that the plant seems to be able to select its host, for in a certain region where several kinds of conifers grow side by side, I have always failed to find any *Buckleya* where pine-trees grow, while on the other hand it is found abundantly and in a flourishing condition where other conifers as such *Cryptomeria, Abies,* or *Chamæcyparis* stand. Even where foliage trees and *Abies* grow mingled together, *Buckleya* is found most abundantly near the latter and in such cases a close examination always shows that *Buckleya* is parasitic on the *Abies.* My culture experiments with the seed of *Buckleya* showed that all the plants used were capable of being hosts, as, for instance, all the seedlings of *Buckleya* developed haustoria as soon as their young roots came in contact with those of other plants such as *Quercus glauca, Podocarpus sinensis, Torreya nucifera,* etc., and even with those of *Pinus Thunbergii,* though this fact seems to be contradictory to what had been observed in nature.

The development of the parasite in the cases of various hosts,

1). SHIRAI, Plant Diseases 1894 (In Japanese).

however, seems to display a certain unmistakable inequality of degrees, noticeable already at the end of the first growing period: the most vigorous development is undoubtedly attained by seedlings feeding on *Abies* and *Cryptomeria*. As the cultivation is yet at its beginning, it is not possible to decide conclusively whether all these hosts are really able to maintain *Buckleya* for any great length of time. However, from the mode of development of the parasite, both in nature and in my experiments, it seems possible to conclude that *Buckleya* prefers *Abies* and *Cryptomeria* as its host.

III. DESCRIPTION OF THE HAUSTORIUM.

If we examine a young *Buckleya*, one year old, we see that the whole system of the root from the hypocotyl to the fine rootlets is provided with numerous small haustoria firmly adhering to the fine rootlets of the host (Fig. 1), but in the older parasite the axial main part of the root is free from haustoria, while they are present on the lateral roots and mostly on the distal portions. The form and size of the haustorium vary within wide limits. The form seems to depend mainly upon the size of the host and especially upon the stage of development of the haustorium itself. The young haustorium is generally roundish especially when it attacks slender roots; but that fully grown is elliptical in surface view, the major axis running across the long axis of the host-root (Fig. 3), and dome-shaped in side view (Fig. 5. *c*.). Its external form may partly depend upon its internal structure, which in its turn differs according to the age, so that the form had better be considered in a later chapter which treats of its structure. Its size also depends in a certain degree upon its age,

but exceptionally even a young one is enormously large; for example, I found on *Cryptomeria* a haustorium, only one year old, which measured 8 mm. in diameter (Fig. 2 *b*), while, generally, haustoria of such age measure only 3–4 mm. On the other hand the largest haustorium which I have ever obtained was found on *Abies:* it had attained 14 mm. in diameter, at an age of perhaps more than twenty years.[1)]

The surface of the haustorium is smooth when young (Fig. 5 *a*), but becomes gradually coarser, owing partly to the development of the corky layer and its splitting off in scaly sheets as in the epidermis of stem and root, and partly to the formation of concentric stripes around the haustorium, which become more numerous as the latter becomes older.

In respect to their position on the mother-root, we can distinguish two kinds of haustoria—the *lateral* and the *terminal.* The lateral haustoria occur most frequently and in the young plant the haustoria seem to be exclusively of this kind, looking like the nodules on the roots of Leguminosæ (Fig. 1). However, the haustoria in the older part of the root are generally terminal and they make an appearance as if the root tips of the parasite were penetrating directly into the host-root (Figs. 2 *b*, *c*; 3 *t*; 4; etc.). This difference in the position of haustoria leads us to inquire their origin, their manner of formation and their morphological nature. The occurence of a terminal haustorium in a perennial parasite has been already noticed by HEINRICHER who regarded this position in *Lathræa* as being caused by the breaking off of a part of the mother-root and added: "Ja, ich glaube auf Grund eingehender Beobachtung sagen zu können, dass die Wurzel-

1). The largest haustorium among Santalaceæ was mentioned by SCOTT in the *Santalum album*, as being 8 Linie (18 mm.) in diameter. SCOTT, loc. cit., p. 148.

spitze sich nie zum Haustorium umbildet, sicher aber geschieht das nur selten."[1)]

The terminal position of the haustoria of *Buckleya* may be ascribed to the same cause, and this may be most clearly proved by a comparison of the various stages of their development, which display an apparent transition from the lateral to the terminal position. Considering at first a young haustorium, which lies laterally to the mother-root, we frequently find that the part of the mother-root beyond the point where the haustorium is emitted is retarded in growth (Fig. 5. *a*, *pr*), and this difference of development beyond and behind that point becomes more obvious as the root advances in age. That portion of the mother-root which lies beyond the haustorium and is retarded in growth, comes to obliterate gradually until at last it is cast away, leaving behind merely a small process or a scar at a certain point of the haustorium (Fig. 5. *b*, *c*). But in an old, vigorously grown haustorium, even such a scar becomes indistinguishable and thus the haustorium becomes apparently terminal (Figs. 2 *b*, *c*; 3 *t*; 4). The above stated facts regarding the position of the haustorium are not difficult to understand, if we examine its anatomical construction. The fact of the modification of the root-tip to the haustorium seems questionable to me, though HEINRICHER, as above cited, stated that this takes place in some rare cases, because the young root of *Buckleya* is provided, as usual, with a root-cap as well as with root-hairs.

Sometimes it is not easy to mark off exactly the connecting part of the haustorium from the mother-root, in the case of the

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1). HEINRICHER, Biologische Studien an der Gettung Lathræa. Ber. d. deutsch. bot. Gesellsch. Bd. XI, 1893, p. 9. ——, Ueber Lathræa Squamaria. Sep.-Abdrk. aus d. Ber. d. naturwiss.-medic. Vereins in Innsbruck, XXI 1892/93.

terminal one. Such is the case when the axis both of the haustorium[1] and the mother-root run in the same direction, while the mother-root grows in thickness together with the haustorium, the thickening taking place gradually towards the haustorium (Fig. 4. *b*). The root thus thickened looks as if its tip, in the course of its longitudinal growth penetrated into another root, or as if its tip expands after it has come in contact with the root. Even where the haustorium is terminal, the exact limit between it and the mother-root is clearly distinguishable, if the mother-root be slender and the haustorium greatly developed, or if the direction of the axis of the mother-root be at a right angle or nearly so to that of the haustorium, as it should be if the haustorium were originally in a lateral position (Figs. 3; 5. *c*).

IV. ANATOMY OF THE HAUSTORIUM.

Let us now turn to the discussion of the inner structure of the haustorium. This is in general so similar to that of the Santalaceæ already investigated that it seems scarcely worth while to enter into details. But as the structure varies within certain limits according to age, it deserves special attention as to its modification. For the sake of convenience I shall discuss the structure of the young and old specimens separately. I shall first take up the young stage in order to show how closely the structure of the haustorium in this stage resembles that of other Santalaceæ in the main, endeavouring at the same time to make intelligible its later modification as well as the nature of some of its tissues, which have hitherto been misunderstood.

1). By the axis of the haustorium is meant that line which connects its point of origin and the front of the haustorium.

A haustorium is made up of the outer *cortical* and the inner *axial* parts. The cortical part, or briefly the cortex, is composed throughout of parenchymatous cells: those lying at the periphery are larger than the inner ones, roundish or tangentially stretched and loosely connected together, leaving numerous intercellular spaces between them, while those lying in the inner part arrange themselves regularly, are rich in plasm and are elongated in the longitudinal direction[1] (Fig. 8 *co.*). In the median region of the cortical parenchyma along the lateral sides of the haustorium,[2] some layers of cells, extending from the apex to the base,[3] collapse, lose their contents, and their wall becomes pressed together into a *striated band,* one on each side[4] (Figs. 7, 8, *st*). The band and those cells, which surround it and are soon to undergo the same fate, are clearly distinguishable by the absence of any trace of reserve starch-material, from the surrounding parenchyma, which are gorged with it at this period.

On the apex of the haustorium the cortical part goes into the formation of the *attaching-folds,* which overlap the host-root and lie in pairs on both sides of the haustorium itself, the younger folds being formed successively one after another inside the older (Fig. 7 *at, at'*). The development of these folds seems to depend upon the size of the host: for instance, when the latter is comparatively young and slender, generally a large thick fold is de-

1). *i. e.*, in the direction of the axis of the haustorium.

2). As the lateral side we designate each half of the haustorium divided by the plane which passes through the axis both of the haustorium and the host-root.

3). The end of the haustorium which adheres to the mother-root is called the base and the other end which terminates in the host the apex or the front of the haustorium.

4). CHATIN (loc. cit.) and PITTRA (loc. cit. p. 15) incorrectly regarded such striation in *Thesium* as being composed of the prosenchymatous cells, but that the striation is really presented by the stretched cell-walls of parenchyma was afterwards shown by SOLMS (loc. cit. p. 559). In *Buckleya* it is composed of a very thin and delicate cell-wall presenting a fine cellulose reaction with chloroiodide of zinc.

veloped overlapping a greater part of the periphery of the host-root. The folds, in the majority of cases, are in two or three pairs, among which the inner ones are always smaller, appearing, in cross-section, like a pointed process frequently directed toward the interior of the haustorium (Fig. 7 *at'*). In *Thesium* PITRA[1] and SOLMS[2] mentioned the occurence of numerous folds in the case in which it had attacked some monocotyledonous roots, but only a single pair in the case of dicotyledonous roots. The latter author regards this difference in the number of the folds in monocotyledonous and dicotyledonous roots, to be the results of differences in the resistances exerted by the host-roots for the penetration of the haustorium and of difference in the degree of its development. He observed that the fold-formation ceases as soon as the apex of the haustorium has applied itself to the endodermis of the host, though many folds may, up to that time, have been formed successively.[3] He observed also that, in dicotyledonous roots, the penetration of the haustorium and its connection with the wood of the host are very easily accomplished, the differentiation of the tissue in the haustorium being early finished before the formation of any fold other than the primary one has taken place; while in monocotyledonous roots, as the resistance is greater, the haustorium is allowed to produce numerous folds till its tissue is completely differentiated.[4] So he regarded a certain cell-mass in the corner of the adult sucker in a dicotyledonous root as the rudiment of a secondary fold.[5] I have not yet obtained any haustorium of *Buckleya* on a monocotyledonous

1). loc. cit.
2). loc. cit.
3). loc. cit. p. 554.
4). loc. cit. p. 555.
5). loc. cit. Taf. XXXIII, Fig. 2 *m*.

root and so am unable here to compare the formation of the fold in the two kinds of roots. I can state only that in *Buckleya*, though numerous folds develope even on dicotyledonous and coniferous roots, they differ in certain respects from those of *Thesium* formed on monocotyledonous roots, for we find in the former that the outermost fold is always the thickest and the largest, adheres to the host-root even after the younger one is formed within, while on the other hand, in the case of *Thesium* it is generally the youngest fold which is the thickest and the largest, the older folds being lifted away from the host-root.[1] The cells constituting the folds differ a little from those which are found in the remaining part of the cortex. Here the outermost cells are arranged compactly and at right angles to the surface and are somewhat elongated in this direction, while the remaining cells do not keep up any definite form or size, being mostly round with wide intercellular spaces between them. Along the median region of all folds the cells seem to go into the formation of the striated bands which unite directly with the similar bands in the cortex (Fig. 7).

The surface of the cortical part, as has been stated above, is covered with corky layers (Fig. 8 *ck*). The thin and thick walled layers are formed alternately and the older part can be easily stripped off layer by layer. The layer extends not only to the exposed surface of the cortical part but also even further to that of the innermost folds, which adhere to the still active cortical tissue of the host, thus leaving only a small portion of the surface in contact with the host uncovered (Fig. 7). By this development of the cork on the contact surface, the passage of

1). PITRA, loc. cit. Fig. 12 and SOLMS-LAUBACH, loc. cit. Taf. XXXII, Fig. 4 and XXXIII, Fig. 3.

nutrient substance between the host and the parasite must be to a certain degree impeded.

Next let us consider the axial part of the haustorium. The axial part is that portion, which is composed mainly of vessels united into two strands with the parenchyma between them.[1] If we make a cross-section through the median region of the haustorium we will find a pair of semilunar *vascular strands* facing each other and running in the direction of the axis of the host (Fig. 8 *va*). The central parenchyma, which I propose to call by the name of *pith*, is composed of small polygonal or slightly elongated cells with large nuclei and rich plasm, almost all being of equal size. The pith after passing through certain places of the vascular strands goes up gradually into the cortex, there being no sharp line of demarkation between them (Fig. 8).[2]

In the strands we find also a few parenchymatous cells which are found irregularly scattered in the inner portion, while in the peripheral portion they constitute somewhat regular rows. The characters and functions of these cells will be discussed later on.

The longitudinal section of the axial part is similar in its form to a flask with rounded base and wide mouth opened at the apex of the haustorium, the strands then corresponding, as it were, to the sides of the flask, and the pith to its contents (Fig. 7 *ax*). The vessels are generally reticulated, rarely pitted. At the bottom of the flask as well as on the inner surface of its sides, the form and arrangement of the vessels appear very

1). The reader is requested to notice that the designation of this part of the haustoria of Santalaceæ as given by previous authors is such as to iuclude the innermost tissue of my cortical part with their inner part of the haustoria, which is called by PITRA "Mittere Theil" (loc. cit. p. 14) and by SOLMS-LAUBACH "Kern" (loc. cit. p. 543).

2). PITRA considered, in *Thesium*, the parenchyma between the two strands to be of the same nature as that which surrounds strands, and so he called them "Cambialgewebe." loc. cit. p. 14.

irregular; besides they are short and have an oblique terminal wall. Otherwise the vessels are regular, much elongated and have slightly oblique terminal walls. The center of the bottom of the vascular strand or properly of the axial part being composed mainly, besides vessels, of parenchyma does not look so dense as in the other parts (Fig. 19 *c, d*). When the frontal extremity of the strand bends much towards its lateral side (Fig. 10), evidently on account of the pressure exerted by the host-root, the arrangement of the elements at that part will be greatly disturbed, the vessels being much shortened into a rhombic form (the same change takes place at the same time in the cortical elements, which directly surround the strand). In general, at the frontal end of the strand the vessels are divided into numerous bundles, of which only a few vessels abut directly on the wood of the host, while others seem to disappear among the parenchyma (Figs. 7, 19). It should be noticed that the ends of these bundles of vessels are directed mostly towards the lateral side in order to abut on the radial wall of the woody elements of the host, which have been produced since the haustorium attached to the woody part of the former.

In order to obtain a more definite idea of the form of the axial part and of the structure of the vascular strands, it is advisable to consult serial cross-sections passing through several points of a haustorium, as shown in Fig. 19. At first, the section through the bottom of the flask (*c*) shows that the axial part is roundish and that vessels are densely arranged at its periphery but scattered in its center. At a little higher level the section is similar in form with a similar arrangement of vessels, but it is somewhat laterally compressed (*d*). It is thus clearly seen from these two figures that the basal portion of the vascular

strand is composed of a complete ring of vessels. But in a section passing through the median portion of the haustorium, we see that the vessels are divided into two opposing masses (*e*), giving an elliptical outline to the axial part. We find here some notches in its contour which becomes deeper as we go down to the next section. Each vascular strand dissolves away finally into a certain number of vessel-groups (*f*), and in the cross-section passing through the apical region of the haustorium we will observe that these vessel-groups are represented in longitudinal section with their ends frayed into brushes, indicating thereby that they run transversally in this region (*g*).

Occasionally we find in the pith strands of vessels or in other cases numerous strings of isolated vessels (Fig. 19 *iv*), traversing it longitudinally. Sometimes in their course they unite with the main strand and sometimes disappear amidst the pith.

At the front of the haustorium the central part is distinguished from the surrounding attaching-folds by its projecting into the host, and is therefore to be called the *sucker* as in the haustoria of other Santalaceæ. The sucker consists mainly of the axial part with a few layers of cortical parenchyma around it. There are no other particular characteristics to be noted, except that the constituent cells are somewhat elongated. It suffices to state here that the apical layer of parenchyma in the sucker, which, being free from coating of the corky layer, can be in direct contact with the host, exhibits the structure of the so-called absorbing tissue, *i. e.*, it is palisade-like, rich in granular plasm, and is furnished with a very thin wall and large round nuclei.

When we take into consideration this histological similarity of the sucker to the main part of the haustorium, and again

when we study the structure of the old haustoria, which will be described later on, the conclusion seems to be justified that *the sucker of the haustorium is nothing but a portion of its apex temporarily imbedded within the tissue of the host.*[1]

V. SECONDARY GROWTH OF THE HAUSTORIUM.

1. The Cambium.

In the foregoing pages we have described the general structure of the young haustorium, but it does not remain unaltered throughout: on the other hand, this primary structure undergoes secondary changes on account of the formation of new additional elements. Therefore in studying the secondary growth of the haustorium we must here fully treat of this tissue.[2] Notwithstanding the remarkable similarity of the structure of haustoria of all Santalaceæ to that of the same organ of *Buckleya*, yet the cambium

1). The sucker of *Thesium* was described by SOLMS-LAUBACH as follows (loc. cit. p. 545): "Der Saugfortsatz schliesst sich in seinem Bau so eng an den Haustorialkern an, dass eine davon gesonderte Betrachtung desselben nur aus Gründen grösserer Uebersichtlichkeit gerechtfertigt sein dürfte. Er besteht aus den directen Fortsetzungen aller im Obigen für den Kern des Haustorium betrachteten Gewebe. Dieselben haben jedoch hier sämmtlich in sofern eine Modification erlitten, als ihre Elemente bei weitem stärker in der Richtung der Längsachse des Haustorium gedehnt sind....."

2). On the meristem which occurs in the haustorium of *Pedicularis* VORKART says (loc. cit. p. 36): "Den Tracheidenstrang umschliesst ein embryonales Gewebe aus kleineren Zellen mit grossem Zellkern und starkem Protoplasmabelag der Wandungen." Heinricher also points out in Lathræa (loc. cit. p. 331): "Eine ebenfalls zweckdienliche Einrichtung im Aufbau des Haustoriums ist ferner die Ausgestaltung einer Meristemzone an beiden Längsseiten der Tracheidenplatte. Durch dieselbe ist dafür gesorgt, dass, wie die peripherischen Zellen des Fortsatzes im Wirthsgewebe neuen Raum gewinnen und hierdurch eine grössere Ausbreitung des Fortsatzgewebes ermöglichen, so auch eine Vermehrung der Elemente der Haustorialplatte, oder des sie umgebenden Parenchyms, vor sich gehen kann, wobei entsprechend einer vermehrten Leistung der aufnehmenden Zellen gewissermassen auch Vermehrung der leitenden gewährleisten wird. Uebrigens scheint dieses Meristem nur begrenzte Zeite hindurch thätig zu sein."

has ever been clearly mentioned in none of these. PITRA[1] has given a cambium-like tissue in *Thesium*, but in very ambiguous terms: "Zwischen diesen Gefässbogen den ganzen Raum einnehmend, ferner auf ihren äusseren Seiten, also die Gefässbündel rundherum umgebend, liegt ein Gewebe aus dünnwandigen, mit trüber Flüssigkeit erfüllten Zellen, welches die Gefässbündel in das Gewebe der Nährpflanze begleitet; es kann als Cambialgewebe der Saugwarze und der Saugwurzel betrachtet werden, ..." Thus judging merely from its structure, he regarded the central parenchyma which I call here the pith as being similar to the parenchyma outside the vascular strand, but he did not mention whether the function of these two parenchymas is idential or not. SOLMS-LAUBACH[2] observed on the outermost parenchymatous cells of the axis (Kern) in *Thesium*, "die gestreckter, dünnwandiger Zellen, wie sie in Weichbast und Cambium vorkommen." HIERONYMUS[3] also considered that parenchyma as the "an Cambium erinnernden Gewebe." Even in the case of haustorium of *Santalum* and *Osyris*, of which the secondary growth is more than probable, no particular attention has ever been paid to this feature. From my study in *Buckleya*, however, it is clear that the parenchyma immediately bordering the vascular strand is the *cambium* and it is almost certain that if the secondary growth occurs in the haustoria in other Santalaceæ it should be performed by means of this meristem interposed between the axial part and the cortex.[4] It must be understood then that this parenchyma should properly be separated from the

1). loc. cit. p. 14.
2). loc. cit. p. 543.
3). loc. cit. p. 205.
4). In fact SOLM-LAUBACH's figure of *Osyris* (Taf. XXXII, Fig. 7 and 8) shows that the haustorium is in at least its second year, for the sucker is imbedded in the wood of the host as in the case of an old haustoria of *Buckleya*.

axial part, though the previous writers included this tissue in that part of the haustorium (Figs. 8, 14, 16 *ca*).

The function of this cambium is of course to add the wood inside and the cortex outside. In order that the growth in thickness of the haustorium may go hand in hand with that of the mother-root to which it belongs, the cambium layer extends to the base of the haustorium and unites with that of the mother-root, as the branch does to the stem.

Besides, at the apex of the haustorium we find the union of the cambium with that of the host which, we think, is the most necessary and indispensable process. For, when two tissues of quite different plants like *Buckleya* and its host come into intimate contact and when it is necessary that a physiological communication should be maintained between them, an increase of the elements for enlarging the contact surface must take place at the corresponding places in both contact surfaces in order that the danger of their slipping from each other may be avoided. Accordingly if we make a longitudinal section of the haustorium, which at the same time cuts the host-root crosswise, we see that the cambium of the haustorium joins that of the host directly (Figs. 7, 9, 10, 11 *ca*). In this way we can obtain in section a dumb-bell shaped circuit of the cambium ring through the host, the haustorium and the mother-root, whereby the elements of the haustorium are so placed, as to be in the best possible position for uniting with the corresponding elements in the host- and mother-root (Figs. 7, 9, 10).

As the cambium above mentioned serves only for the growth in thickness of the haustorium we must next inquire into the means of its longitudinal growth. In the primary growth we have seen that the apical cells of the sucker, like all the other haustoria, grow further and further in the longitudinal direction

dividing themselves transversely, and after penetrating the cortex of the host, come into contact with the wood tissue. The primary growth of the haustorium seems generally to be arrested, when its apex thus reaches the lignified cells of the wood, since, they are so hard and so thick that they can resist against the penetration of the young thin-walled apical cells of the sucker. Only rarely some few apical cells can penetrate further into the wood tissue of the host, compressing in their course the lignified cells of less resistance, as, for instance, the medullary rays. But this local and limited prolongation is not to be considered as a longitudinal growth of the whole sucker.

Again we have ascertained very frequently that when the haustorium occurs on a young host-root in the first year of its development, the penetration and longitudinal growth of the sucker do not cease at the cambium zone of the host, but on the other hand as the tissue at this stage is still soft and thin walled the sucker easily makes its way further in.

Manifestly the parenchyma will be least resistent against the pressure exerted by the forward growth of the haustorium as well as the chemical action of the same.[1] So the sucker grows in this direction, dissolving and pushing aside and exending itself to the pith.

As the apical cells of the sucker, after the primary growth, become the permanent tissue, the occurence of the secondary growth will become impossible.

2. The Vascular Strands.

Having determined the occurence of the cambium layer and its distribution, we shall now study the vessels derived from it.

1). The action of the haustorium upon the host is worthy a special treatment which will be given in future.

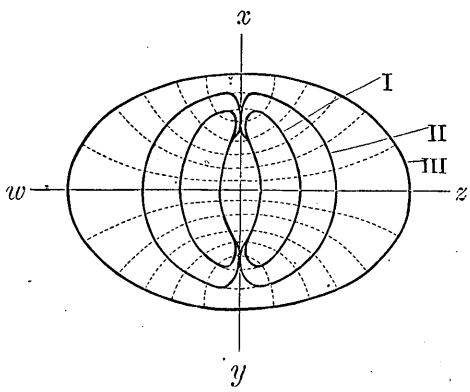
It has already been noticed that, on either transverse or longitudinal sections, vessels are arranged irregularly at the base as well as the inner region of the strand, and are short and irregular in form, while in the remaining part each succeeding prismatic vessel is so placed that the result is a radial row. It seems beyond doubt that the irregularity of the arrangement of the innermost vessels is due to their origin from the procambial cell-groups, directly differentiated in their own form just as we see in the formation of the primary wood in the fibro-vascular bundle. But immediately after the complete formation of the cambium ring, secondary elements being derived from the latter by its tangential division will be arranged in radial rows.

At the earlier period of growth, rows of vessels are directed laterally, being all approximately parallel, even at the extremities of both strands (Fig. 8). But as the activity of the cambium is greater laterally (*i. e.* in the direction of *wz*, Woodcut 1) than in the direction perpendicular to it (*i. e.* in the direction of *xy*), the diameter of the axial part increases greatly in the former direction and the rows of vessels derived henceforth begin to diverge from one another, and when the cambium becomes circular, they become radially arranged. The formation of vessels from the cambium being always strongest in the lateral direction, the vascular strand which has once become circular will then become longer laterally and take in section an elliptical shape with its minor axis placed in the direction of the major axis of the primary ellipse.[1)]

The diagram here given will demonstrate the modification of the form of the axial part during its secondary growth (Woodcut 1). It indicates three types of form in cross-section, which the

1). As far as my observation goes pretty old haustoria mostly keep this form.

Woodcut 1.



haustorium takes in its youngest (I), middle (II), and oldest stages (III) respectively. An example of the quite similar mode of the secondary growth has already been given by SACHS[1] with a similar diagram of the wood of *Aristolochia Sipho*,[2] where the inner annual rings are at first elliptical in cross-section, then circular and finally oval. He concluded thereupon that the directions of the medullary rays are the orthogonal trajectories of those of annual rings, so in our case the latter and the rows of vessels stand to each other in similar relations.

These morphological changes of the axial part during the secondary growth take place also in its frontal part which lies in the so-called sucker. The fact that the sucker, as has been before stated, is primarily elliptically compressed along the axis of the host, might be explained as the most suitable arrangement for splitting the cortex of the host in order to make its way easily into the wood[3] (Fig. 5. *b*, *suc.*).

The vigorous increment of elements only in the lateral direction during the secondary growth must also be considered as

1). SACHS, Ueber Zellenanordnung und Wachsthum. Arb. d. Bot. Inst. in Wurzburg. Bd. II, 1882, p. 192.

2). loc. cit. Fig. 3.

3). If we take off the young haustoria from the host spindle-shaped scars will be seen on the central part of the contact surface. HEINRICHER is of the same opinion as to the reason why the tracheal plate in the sucker of *Lathræa* is placed longitudinally (Anatomischer Bau und Leistung der Saugorgane der Schuppenwurz-Arten. Cohn's Beitr. z. Biol. d. Pflz. Bd. VII, 1896, p. 331).

being very serviceable for the function of the haustorium. For in order to assume an intimate union of the elements between the host and the haustorium, it is evident that the growth in thickness of the latter must go on parallel with that of the host (*i. e.* in the direction of *wz*, Woodcut 1). But as no secondary longitudinal growth occurs in the host, there is needed in the haustorium no remarkable growth in the direction of the axis of the host (Woodcut 1, *xy*).

The natural consequence of such secondary growth in thickness especially in a lateral direction, unaccompanied by longitudinal growth, is that the axial part is reduced to a disc with various outlines, according to its age as well as to the proportion of its height to its breadth. In all haustoria, especially in old ones, the vascular strand has the concave bottom (Figs. 9, 10) and also in some vigorously growing haustoria, as, for instance, those which feed on *Abies*, the frontal portion of the strand is likewise concave (Fig. 9). So, if the haustorium is pretty old the axial part will take the form of a biconcave lens, or if it is somewhat younger it will assume the form of an amphicœlous vertebral bone (Fig. 9). In a less vigorous haustorium the front, being overlapped by the tissue of the host on account of the very vigorous growth of the latter, becomes convex and then the axial part assumes the form of an opistocœlous vertebral bone (Fig. 10). Not only are all these forms to be seen in sections, but also not infrequently they may be found even on the dead haustoria still resting upon the host; in this case, however, the cortical parenchyma having already decayed, only the hard lignified axis with concave base is barely exposed (Fig. 6 *hv.*).

3. The Cortical Part.

In the cortex there are no such remarkable changes as are seen in the axial part. The increment of elements here is exceedingly slight and at the same time as the older part of the cortex is gradually torn off by the formation of corky successive layers beneath, any noticeable increase in thickness is not observed.

The parenchymatous cells, which are the only elements of the secondary as well as of the primary cortex are regular both in form and arrangement. No differentiation whatever occurs in the same stage of development, all being similar in size, form and inner structure. Compared with the cortical elements of the mother-root, they are rather short.[1]

In the following lines I will discuss somewhat more minutely the nature of the cortical part in order to make clear its functions.

At first we will inquire whether the sieve-tube is present or not. The investigation of the haustorium of various parasites in this respect has cleared up their parasitic nature. PEIRCE[2] has studied the structure of the haustoria of some phanerogamic parasites and established the fact that sieve-tubes are present in the haustorium of the Convolvulaceæ, Rafflesiaceæ and Balanophoraceæ, while in *Viscum album*, a green parasite, they are wanting. He then drew conclusion that the former kinds of parasites must depend absolutely upon their host for food, *i. e.*, that they obtain raw materials through the tracheid or tracheæ

1). The cortex of the root of *Buckleya* consists principally of parenchyma, sieve-tubes, companion-cells and a few bast-fibres.

2). PEIRCE, On the Structure of the haustoria of some Phanerogamic Parasites. Ann. of Bot. Vol. VII, 1893, p. 291.

and elaborated materials through sieve-tubes; while in *Viscum* the absorption of food from the host is limited to crude materials in aqueous solution. Quite recently CANNON[1] has ascertained also the absence of sieve-tubes in the haustorium of *Phoradendron villosum*, a green parasite. Of course we can not establish the physiology of nourishment merely from the structure of the elements; experiments are always necessary.[2] But as this investigation is beyond the scope of the present paper I will here confine my remarks as to *Buckleya* to a description of the histological structure of the cortical part. I have examined with great care to ascertain whether the walls of any parenchymatous cells are furnished with callus, which would prove them to be sieve-tubes. After the process of PEIRCE I have stained the sections from the haustoria, collected in various periods, with an aqueous solution of anilin-blue and examined them in glyceline after washing with water. A part of the bast of the mother-root was treated in the same manner for the purpose of control. The presence of callus was evidently proved in the mother-root, but never in the haustorium. The following facts are also in the favour of the view that there are no sieve-tubes in the cortical part of the haustorium:—

1). Throughout their life, the parenchymatous cells of the cortex retain their nuclei, which are large and round or oval when young but spindle-shaped when old.

2). In these cells the slightly granular plasm accumulates around the nuclei and forms plasmic strings, while, on the contrary, in the sieve-tubes the plasm with granular contents is to be found only adhering to the cell-wall.

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1). CANNON, loc. cit.

2). See PFEFFER's remark in his Pflanzenphysiologie 1897, Bd. I, 2 Aufl. p. 355.

3). They store up starch during the resting season in the same way as other parenchymatous cells.

4). The apical cell of the cortical part does not differ at all from that of the axial part, both being nucleated and rich in plasm (Fig. 11).

These facts led me to conclude that no elements for the translocation of the plastic substances, at least in the form of sieve-tubes, exist in the cortical part of the haustorium of *Buckleya*.

4. The Medullary Rays.

So far as I know, we are not yet aware that medullary rays occur in the haustorium of any parasite. In *Buckleya*, in which the vascular strands grow to a considerable thickness, the development of such tissue is to be expected, when we consider its physiological importance in stems and roots. It originates very early, when the vessel begins to be differentiated from among the procambial cells. Then we notice that some cells retain their parenchymatous nature, while others develop into vessels; but since the arrangement of the former at this early stage is very irregular, it can not yet be decided whether they have the property to differentiate into medullary rays or not (Fig. 14). (*Cf.* p. 13). Indeed SOLMS-LAUBACH[1] observed also parenchymatous cells in the vascular strand of *Thesium*, but about these he recorded merely that they are of the same kind as those of the cortex bordering the axial part. It is only after the full development of vessels, that the arrangement of these cells into definite *medullary rays*, which pass through the vascular strands

1). loc. cit. p. 544.

radially, is completed. The cells of the medullary rays are usually rectangularly prismatic, often with rounded corners, somewhat comparable to bricks, for they chiefly elongate in one direction and lie with their greatest diameter directed horizontally and radially. The form of rays can be learned from the sections of the haustorium in its transverse, longitudinal and tangential directions: they are flat bands, like ordinary rays, composed of many layers of cells transversely, but only a few layers thick (Fig. 16). They occur pretty abundantly; some originate from the pith and traverse the thick bundle of vessels, while others take their start in the bundle itself and proceed toward the cortical part. Even in older haustoria the wall of the cells remains *unlignified*, delicate, and capable of yielding to pressure and tension,[1] so that they are often laterally compressed, sometimes with abundant reserve starch (Fig. 16. *a*).

We may ask then how the medullary rays behave themselves when they enter the cortical part. When they penetrate the cambium layer and run among the cortical parenchyma, they are difficult to be distinguished, their structure being similar to that of the crrtical parenchyma. Their outer form and the direction of their longer axis alone serve for their distinction (Fig. 15). Not infrequently does it happen that in cross-section both elements are so similar in their form that they are hardly distinguishable from each other, but in radial section the medullary rays can always be plainly recognized as such by their horizontal course, the axis being elongated in this direction, while the cortical parenchyma runs longitudinally.

Having thus ascertained the existence and distribution of the

1). For the sake of comparison I have examined the medullary rays in the wood of the mother-root. The cell-wall is lignified and thickened, having numerous pits.

medullary rays in the cortical and axial parts, their function as the reservoir, and also as the way of conduction, of nutritive substance (mainly carbohydrate) at certain times, becomes quite evident.

5. The Annual Rings and the Formation of the Duramen.

In the stem as well as in the root of *Buckleya* we can distinguish the annual rings very clearly, though in the latter they are somewhat irregular and sometimes somewhat obscure.[1] As regards the haustorium the arrangement and structure of elements do not go so far as to make clear the difference of spring and autumn wood. Yet we can faintly recognize alternate zones of denser and less dense regions; a demarkation between the two is scarcely observable under the microscope of high power, but is visible to the naked eye as an obscure line (Fig. 20).

Of these zones, the denser are formed of vessels with lumen which is radially narrower than that of vessels of the other zone; while between the vessels of both zones there is no noticeable difference in the thickness of the cell-wall, as is usually the case.

When the haustorium attains a sufficient thickness, we can observe in the successive zones of growth or annual rings, the differentiation into the *alburnum* (younger rings) and the *duramen* (older rings). Externally the two parts are distinguished by their

1). SOLMS-LAUBACH (loc. cit. p. 539) has given as a general remark on the structure of the Santalaceous plants, "Seine (Holz) Jahrringe sind äusserst undeutlich." CHATIN (loc. cit.) however has already shown clearly the annual rings in the stem of *B. distichophylla.*

colour and density as in the stem of many trees (Fig. 21). As is well known, the duramen of the stem is characterized, not by any modification in the original structure and thickness of the cell-wall, but merely by changes of the material properties of the wall, as well as of the contents. The original physiological work (the purely mechanical function is not here considered) of the cells is rendered impossible by the accumulation of deposits of some infiltrating bodies or by the formation of thyloses within the vessels and cell-lumina. The change into duramen in the haustorium is in most respects similar to that in the stem, but here it is accompanied by a process of disorganization.

The cell-walls of the pith as well as of the medullary rays in the haustorium under consideration become lignified, and at the same time they swell up to a considerable thickness (Fig. 18), until at last they come to fuse together into a yellowish mass. The walls of the vessels are also disorganized into a yellowish substance, which fills up the lumen of the vessels and so makes the performance of their functions impossible (Fig. 17). The further essential change, which takes place during the formation of the duramen, consists in the disappearance of starch which characterises the living cell. Thus the essential physiological functions of this part, which consist in translocating and storing up the nutrient substances, become entirely impossible to be performed.

It is noticeable here that the formation of the duramen in the haustorium stands in close connection with the condition of the tissue of the host-root, with which the duramen of the haustorium is connected. For, in the cases investigated, I have found that, in the cross-section of the host (*Abies*), just under

the haustorium provided with the duramen, certain changes occur in the wood in front of the sucker. For instance, here the medullary rays contain very little, if at all, of the reserve starch (Fig. 21).

These modified tissues of the host extend just so far as the duramen of the haustorium extends. In one instance, I have seen that not only in the part of the host just beneath the haustorium, but even in the part far removed from it, the older rings undergo the same modification into a kind of duramen. It seems therefore probable that the formation of the duramen in the old host-root necessarily induces the same change or process of disorganization in the older tissues of the haustorium, that are connected with the duramen of the host.

This formation of the duramen in the haustorium was found exclusively in old specimens, which were, judging from the number of the annual rings of the host-root, from fifteen to twenty years old, or thereabout. These old haustoria were discovered by me only on *Abies*, and the occurence of such a modification in the haustoria found on other hosts still remains undetermined.

6. The Attaching-Fold, Sucker and Striated Band.

As has been stated above, the haustorium acquires a few pairs of the folds already during its primary growth; but afterwards we can observe no increase in their number, and generally, in the old haustorium, they disappear entirely. The question then arises, how do they disappear? To clear up this question, haustoria of various ages were examined and compared with one another. In the young haustorium the folds adhere, as

was before stated, firmly to the cortex of the host, compressing and deforming the tissue of the latter between the sucker and themselves (Fig. 7).

The cortical tissue of the host, however, continues, during the secondary growth, to die away gradually from the outside and becomes replaced by its new layers formed from the cambium; and when the outermost decayed tissue of the cortex comes to be cast away, the folds, which were formerly in contact with it, detach naturally from the surface of the host, imitating a roof projecting laterally on the lateral side of the haustorium, as will be seen in the advanced stage of Fig. 10 (*at*). While the fold is thus gradually removed from the host, another change occurs which causes the disappearance of the fold.

Generally towards the end of the primary growth, the formation of the corky layer is observed under the superficial parenchyma of the fold, and those cells lying outside this corky layer will ultimately detach from the fold and be cast off. As the age advances, therefore, the folds are no longer sharply edged as before and form only rounded elevations.

At last after the successive formation of the corky layer, the folds disappear entirely, so that the surface of the haustorium becomes homogeneous throughout (Fig. 21).

While the modification of the structure is thus going on in the frontal portion of the cortex, the shape of the central part at the apex of the haustorium will gradually deviate from that which it had at first. Now the frontal part of the haustorium, when young, is distinctly divided into the peripheral and the central portion, which are respectively the attaching-folds and the sucker; the latter however being simply imbedded in the tissue, especially in the cortex, of the host shows no difference

whatever in its structure from other parts behind it, as I have already pointed out (*cf.* Sec. IV). During the secondary growth, the cambium of the sucker, after having joined with that of the host, produces new elements in the same direction and nearly with the same activity as the cambium of the host produces its own elements, and so the sucker is able to expand more and more laterally. Hence, after the obliteration of the primarily formed cortical tissue of the host-root, which at first had enveloped the lateral sides of the sucker, the parallel growth in thickness of both haustorium and host no longer allows the cortex of the host to grow over the sucker, or the cortex of the haustorium to overlap the host, as it was the case in the primary growth (Figs. 4, 9, 10).

In this way the contact surface, which is at first wavy and irregular, especially when the folds are numerous, becomes simple, the greater part of the surface being now occupied by the front of the sucker (Figs. 9, 10). At the same time the sucker, which we have conveniently distinguished as such in the primary growth by its being imbedded in the host, can no longer be distinctly separated from the other part in such an old haustorium.

Together with all these changes we see that on the whole surface of the haustorium, excepting however a small portion of its apex, the corky layer is formed successively under the superficial layer of the cortical parenchyma, which is torn off sooner or later from the haustorium, while new cortical parenchyma is constantly produced by the cambium. During this process the striated band, which is originally situated along the median portion of the cortex, changes its position gradually towards the periphery, until finally it is cast off together with the corky layer and the cortical parenchyma.

7. The Connection of the Haustorium with the Mother-Root.

The final point in the structure of the haustorium, to which I wish to refer, concerns the connection of the haustorium with the mother-root. This was omitted in the description of the young haustorium, as I deemed it better to study the point on the haustorium which had already undergone the secondary growth. To begin with the wood of the mother-root, it is composed of pitted vessels, wood-parenchyma and thin-walled wood-fibres, traversed by medullary rays with lignified walls. At the place where the haustorium occurs, vessels are exceedingly numerous and some of them are directed towards the haustorium as a massive strand of reticulated vessels, which, after passing a certain distance, comes in contact with the bottom of the vascular strand of the haustorium (Fig. 7 *ne*). This part which thus connects the haustorium with the mother-root, is called the *neck* of the haustorium. In the median portion of the neck the vessels are exceedingly small in number, mostly forming isolated chains of vessels among the parenchyma. The longitudinal and cross sections reveal very clearly the course of the vessels in this region (Fig. 12).

In a section taken near the mother-root the vessels are arranged compactly in radial rows (Fig. 19 *a*); and again near the bottom of the vascular strand they unite and fuse together into those of the strand.[1)]

1). A similar structure was ascertained in *Lathræa* by HEINRICHER. He says (Cohn's Beitr. loc. cit. p. 334): "Die Tracheen verlaufen in derselben in bogigen Curven, welche mehr minder senkrecht an die Tracheen des Wurzelstranges ansetzen, da und dort finden sich zwischen den Tracheen noch parenchymatische Elemente eingeschaltet." (Compare his illustration, Taf. VII, Fig. 2). In the young haustorium of *Buckleya*, in which the develop-

In Fig. 12. *b* the course of the vessels of the neck is shown in longitudinal section. The vessels in this part are more or less stretched, so that they are longer than those of the axial part. They have transverse walls at both ends (Fig. 13).

Generally, as the vascular strand of the old haustorium surpasses in growth the woody part of the mother-root, the vessels in the neck diverge towards the bottom of the haustorium.

As to the cortical part of the neck, it will not be worth while to say more than that it has the same structure as that of the main part of the haustorium, consisting entirely of parenchymatous cells of equal size and arrangement, but with no striated bands among them (Fig. 12. *a*).

The study of the secondary growth of haustorium makes it very easy for us to understand its outer form, which is mainly determined by the form and arrangement of the constituent tissues. In the young stage the axial part is comparatively smaller than the cortical part, so that it is the latter that chiefly determines the form at that stage; for instance, the development of the attaching-fold determines the form, according to the degree of its thickness and size.

The length of the neck is also a factor in determining the form of the young haustorium: the shape of the latter is that of a long cone if the neck be moderately long. In one case I have found a conical-shaped haustorium 3 years old, and 7 mm. in height, of which 3,5 mm. formed the length of the neck—the

ment of vessels is not yet completed, the part of the so-called neck is only with difficulty distinguishable. In *Osyris* judging from the figure given by SOLMS-LAUBACH (loc. cit. Taf. XXXII, Fig. 7), one pair of arch-shaped strands of vessels composing the axial part of the haustorium seems to start directly from the sides of the wood of the mother-roots.

longest neck I have ever seen. During the secondary growth, however, the axial part is the most important factor in determining the outer form of the haustorium, for, as it was before explained, this part is the most changeable in form, so that the form of the haustorium mainly accords with that of the axial part. When the axial part becomes rounded in cross-section, the outline of the haustorium is also rounded; and when in the old haustorium the axial part becomes again elliptical, the surface view of the haustorium is also elliptical. The chief modification of the cortical part is then that the attaching-fold obliterates, leaving in a certain stage concentric furrows along the front of the haustoria, which however disappear in very old specimens. That the old haustorium does not increase at all in its height and thus becomes flat, has already been briefly stated.

VI. GENERAL REMARKS AND SUMMARY.

It would be of much interest to inquire how far the above described structure of the haustorium of *Buckleya* resembles that of the same organ in the allied species, and to what extent my interpretations concerning the nature of its tissue can be applied to others; but, as to the latter point, I can refer only to a few species, since in many parasitic Santalaceæ the structure of the haustorium has not yet been studied. In *Thesium*, *Santalum*, *Osyris* and *Buckleya* the structure of the haustoria is the same in general respects; thus we find in all of them the cortical and axial part,[1] including the sucker, attaching-fold and striated

1). The part called by me the axial part does not correspond to the "Kern" defined by other authors in other species, for they included in "Kern" the cambium as well as parenchyma, which latter must be properly included in the cortical part according to my designation above given.

band. Judging from the haustoria of *Buckleya*, I think I may venture to say that some points in the interpretations of the tissues and the comparative studies on the structures of haustoria of different species, made till now by various authors, are more or less imperfect. Our knowledge of the anatomy of *Thesium*-haustoria we owe especially to CHATIN, PITRA and SOLMS-LAUBACH. The last author has also studied the haustoria of *Osyris* and mentions the following characters as distinguishing that genus from *Thesium* :—

a). A very small and narrow axial part (Kern).

b). A sucker which does not differ markedly from the axial part histologically.

c). The more extensive growth of the border of the sucker.

It appears to me that in comparing the structure of the haustoria of various species, the age and the secondary growth in thickness must be considered. In all haustoria it may be conjectured that the "Kern" or the axial part should be very small in the earlier stages of development. Since, in *Buckleya*, the thickness and general form of the vascular strand in the youngest haustoria are nearly similar to those of the adult haustorium of *Thesium*, it would not be improper to conclude that in *Osyris* the comparatively thin vascular strand, as was mentioned by SOLMS, should be found only in a young haustorium.

As regards the sucker, its existence was ascertained in Rhinanthaceæ, *Lathræa*, Santalaceæ, etc., each having its characteristic structure. In all these cases, the name sucker was given to that portion of the haustorium, which is imbedded in the host. In Santalaceæ it seems that its tissue was distinguished by SOLMS-LAUBACH[1] from that of the "Kern" by its more elongated cells;

1). loc. cit. p. 556.

so, he remarks that the sucker of *Osyris* is somewhat different from that of *Thesium* in that its tissue is composed of unelongated cells, "unmittelbare Fortsetzung derer des Haustorialkernes."[1] When we take into consideration the structure of the haustorium of *Buckleya*, it seems to me to be needless to distinguish the so-called sucker from the "Kern," since the "Kern" itself must be regarded as an absorbing organ, and since, further, it is impossible to find any anatomical difference whatever between the sucker and the "Kern." This view will seem quite natural when we examine the haustorium which is advanced in age and possesses a discoidal shape (Figs. 9, 10).

SOLMS-LAUBACH has pointed out in *Osyris* that the sucker, after having reached the wood of the host-root, expands along it, thus lifting up the bast, and that in some cases the lateral sides of the sucker are divided into finger-shaped processes, which terminate in the bast with the wood of the host interposed between them.[2] He thought that this is due to marginal growth, but did not say whether this growth is primary or secondary; nor did he say anything about the growth of the entire haustorium, in spite of the existence of a meristematic zone bordering the vascular strand. In *Buckleya* I have only rarely found that the sucker is divided as in *Osyris*. In such a case, as the end of each division is applied to the bast of the host and its cells elongate themselves towards the bast, each division must increase its length correspondingly with the growth of the host-root. This instance confirms the existence of the marginal growth of the sucker in *Buckleya* also, but it must be considered as an abnormal case. I have also ascertained that the sucker, as soon as it meets

1.) loc. cit. p. 556.

2). Compare the figure of SOLMS-LAUBACH (loc. cit. Taf. XXXII, Fig. 8).

the wood of the host, grows laterally and tangentially along the cambium ring of the latter, imitating the marginal growth. We must, however, consider that this growth is confined only to the period of development, and no secondary growth of the margin is observed. Applying these features found in *Buckleya* to *Osyris*, which in every respect resembles the former, it is highly probable that the marginal growth of the sucker in *Osyris* occurs during its primary growth only, and that, on the other hand, the secondary growth concerns its thickness only.

SOLMS-LAUBACH has described in the haustorium of *Santalum album* that the sucker extends like a fish-tail: "Der colossale Saugfortsatz hat durch seine beiden sich zwischenschiebenden Lappen die Rinde zu $^3/_4$ vom Holz heruntergeschält, sie zwischen deren Oberseite und die Ansatzfläche einpressend."[1]

This way of extention of the sucker I could confirm in *Buckleya*, and in my case the degree of extention seems to depend upon the character of the host and, even in the same species of the host, upon the conditions of its growth. It is doubtful whether this extention in *Santalum* will continue during its further growth; for, from the description of SOLMS-LAUBACH, it may be inferred that the haustorium investigated by him was only one year old, *i. e.*, he could observe its structure only in its primary stage. If I am not mistaken, the sucker would not keep such a form for a long time,[2] but it will grow in thickness in the same manner as *Buckleya* and take a similar form (Compare Figs. 9, 10).

Though our knowledge of the structure of the haustorium of *Osyris* and *Santalum* is in some respects still insufficient, the

1). Foot-note by SOLMS-LAUBACH in SCOTT's loc. cit. p. 149.

2). From analogy it may be considered that the haustorium of *Santalum* may maintain a perennial growth.

similarity of the structure of the four species till now studied strengthens, in every respect, our view that the haustorium of the above two plants will follow the same fate as that of *Buckleya*, for instance, as to the mode of the secondary growth as well as to the modification of the structure then occuring, provided they will sustain their activity during many years.

Lastly I may here say something about the attaching-folds. Their number as well as form are different in different species of hosts; thus the haustorium of *Thesium* has numerous attaching-folds on Monocotyledons, but only a pair on Dicotyledons, while in *Osyris* and *Santalum* a single pair is always developed.[1] In *Buckleya* I found that numerous folds are developed on various dicotyledonous and coniferous roots. But the haustorium of *Buckleya* on monocotyledonous roots has not yet been found, nor has the number of the folds yet been decided. That the development of the folds differs with different kinds of hosts—that they are not formed during the secondary growth of the haustorium —that they disappear in old specimens—all these facts lead us to regard them as organs subordinate in their functions and to consider their function of attachment to be but of minor importance.[2]

The results of the studies on the structure of the haustorium of *Buckleya* are briefly as follows:—

1. The haustorium is provided with a cambium ring between its cortical and axial parts, whereby a continued growth

1). Whether the dovelopment of the single pair of the folds in *Osyris* and *Santalum* is found on monocotyledonous or dicotyledonous root is unknown to us.

2). HEINRICHER (loc. cit. p. 323) has already published the same view on the haustorium of Lathræa: "Wir haben also vor allem gezeigt, dass die „replis préhenseurs," die Zangenfortsätze, eine ganz nebensächliche Erscheinung an den Haustorien sind."

in thickness is accomplished. The cambium of the haustorium joins that of both the host and the mother-root, and together forms a complete thickning ring. Any noticeable secondary growth in length does not take place.

2. The form and structure of the haustorium are changeable according to age.

3. In earlier stages the axial part of the haustorium has an elliptical form in cross-section, which has its major axis coincident with the longer axis of the host-root, but after a certain stage, owing to the more vigorous growth in lateral direction it becomes circular and then again takes an oval shape, with its major axis in the place of the minor axis of the former ellipse.

4. The haustorium possesses medullary rays.

5. The existence of sieve-tubes cannot be definitely ascertained.

6. The striated band in the cortex disappears in the older haustorium.

7. The attaching-folds undergo the same fate. At first, they detach from the host-root, project at the margin of the apex of the haustorium and sometimes produce striations or furrows.

8. The sucker, easily distinguishable in the younger stage, loses its demarkation from the part behind it after a certain degree of growth.

9. So long as the host-root is alive, the haustorium may be active and can maintain its life during many years.

10. Demarkations between the zones produced in each period of growth are visible, though faintly, in the vascular strand of the haustorium.

11. In the older haustorium the older part of its axis goes into the formation of the duramen.

In conclusion I wish to express my heartiest thanks to Professor Dr. M. MIYOSHI and Professor Dr. S. IKENO for much valuable advice and criticism throughout the work. I am also greatly indebted to Professor Dr. M. SHIRAI for useful information, which he has given me during his stay in Berlin.

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folds; *st*, striated band; *va*, vascular trand; *ne*, vessel in the neck; *mo*, wood of the mother-root; *ck*, corky layer; *pi*, pith; *w*, wood of the host; *ba*, bast of the host. ×25.

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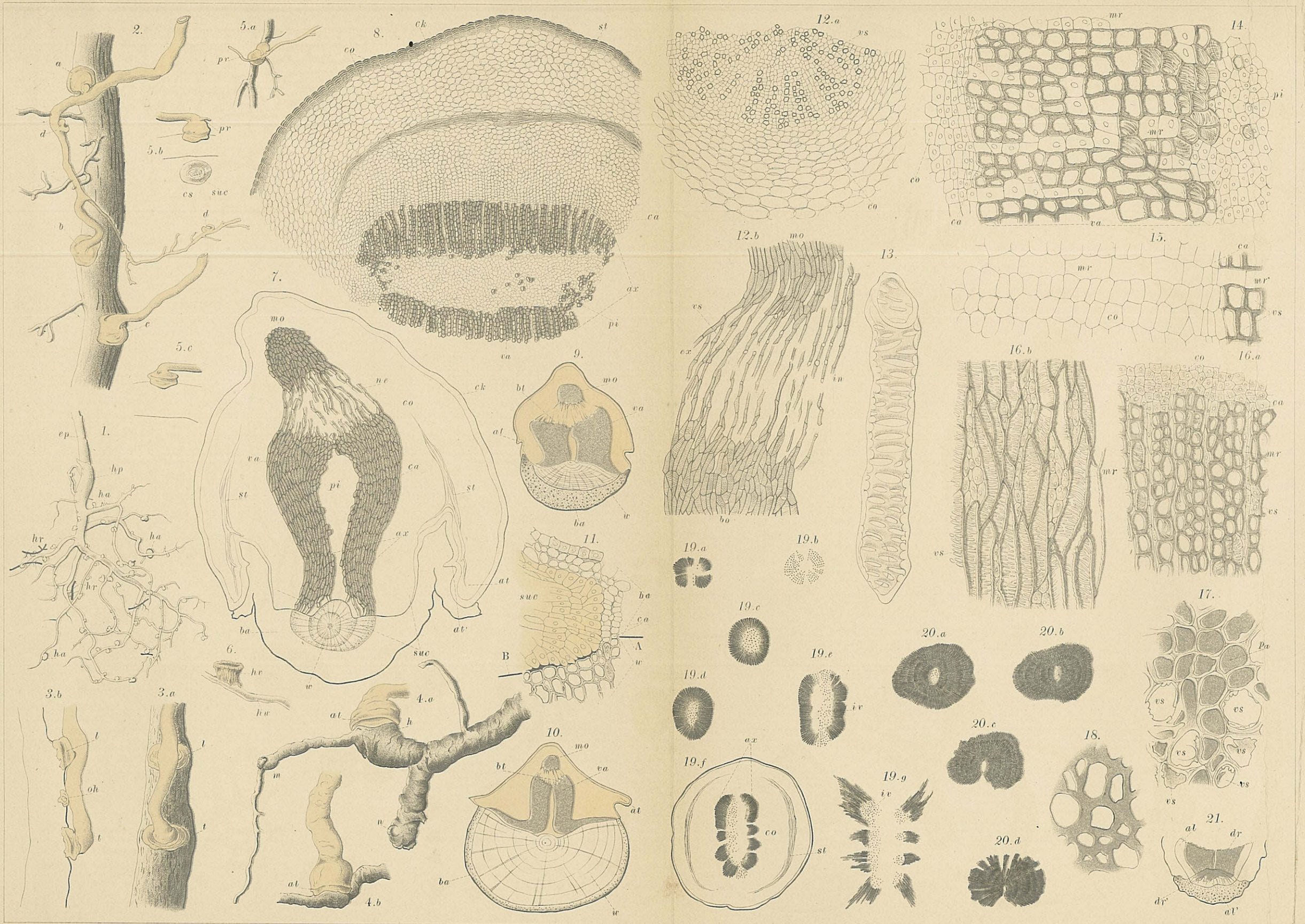

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