STRUCTURE OF THE HOST-PARASITE INTERFACE OF BOSCHNIAKIA HOOKERI WALPERS (OROBANCHACEAE)

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SUMMARY

The host-parasite interface of *Boschniakia hookeri* Walpers (Orobanchaceae) parasitic on *Gaultheria shallon* Pursh is radially grooved, and shows several significant contrasts to that known for *Orobanche*. Unlike the latter, *Boschniakia* has a large, perennial interface, and the host surface is made up almost entirely of differentiated xylem. The xylem-xylem contact involves both fiber-tracheids and vessel elements on the host side, and vessel elements on that of the parasite; open xylem connections across the interface are relatively common. The phloic continuity and transfer-like cells known from *Orobanche* have no counterpart in *Boschniakia*. No meristematic zone is present along the interface, the initiation of the latter being brought about by an early inversion of the host cambium. The term "tuber", even though not completely appropriate, is used for the swollen *Boschniakia* organ directly above the interface, and the term "soma" rejected.

1. INTRODUCTION

The family of the Broomrapes (Orobanchaceae) consists of holoparasitic plants which are relatively common and accessible in many parts of the world. It is, therefore, surprising to find that the haustorial organs in the family are very inadequately known. In *Orobanche* itself we have the recent studies by DOERR & KOLLMANN (1974, 1975, 1976) and ATTAWI & WEBER (1980). The former studies provide a detailed account of some extremely interesting ultrastructural features discovered especially in connection with the phloem-like cells present in the haustorium itself. There are a number of older studies on haustorial anatomy of *Orobanche*, but those by DOERR & KOLLMANN in some respects supersede nearly all other information. The subject of their work, however, as was that of ATTAWI & WEBER was the secondary haustorium of an annual genus attacking a herbaceous root. Our present study of the host-parasite interface of *Boschniakia* deals with the primary haustorium (no secondary ones being formed) of a perennial genus parasitizing a woody root. A very brief account of the anatomy of the *Boschniakia* haustorium was published earlier by OLSEN & OLSEN (1981).

The haustorial organ is unusually large in *Boschniakia*. Thus, it is necessary to limit the present study, and we have chosen to focus on the nature of the mature interface which demarcates the two partners and the tissues immediately adjoining this contact surface. The swollen organ which is attached to the host root, and from which the inflorescences eventually spring, is here referred to

as the *tuber*. This term is not fully justifiable morphologically but will neverthe-less be used in the absence of one which is more acceptable (see Discussion). The tuber as a whole is an organ of great structural complexity, but enters our account only peripherally.

The early developmental history of the broomrape genus itself (*Orobanche*) is known to involve the chemical stimulation of germination by certain com-pounds liberated by a young host root as it grows in the immediate vicinity of the dormant seed (BROWN et al. 1952; KUIJT 1969). Although this feature has not been demonstrated for *Boschniakia*, it is likely to be present there, also. However, an interesting additional germination feature has recently been sug-gested for this genus by OLSEN & OLSEN (1979,1981). These authors propose that the very large, alveolate outer cells of the testa, which radiate out from a common center near the radicular pole of the embryo, physically guide growing young host roots toward the latter, after which germination takes place. In other words, germination in *Boschniakia* may be partly a matter of entrapment of the host root; it almost certainly also involves the subsequent activity of a germi-nation stimulant exuded by the host root while growing through the *Boschniakia* testa. Whether any chemical interaction between host and parasite exists prior to the former entering the cells of the testa is a different matter. The fact that the early primary haustorium does not grow beyond the testa would seem to confirm the OLSEN & OLSEN hypothesis.

In any case, penetration of the host root occurs immediately behind the latter's apex (OLSEN & OLSEN 1981). This effectively slows and eventually stops the root's longitudinal growth, and it quickly dies distal to the parasite. The massive expansion of the host-parasite interface which takes place subsequently com-pletely obliterates any evidence that a root apex was ever present, and the grow-ing haustorium thus almost invariably occupies a seemingly terminal position (see, for example, fig. 22 in OLSEN & OLSEN 1981, and fig. 4–19d in KUIJT 1969).

2. MATERIALS AND METHODS

The materials for this study were gathered from one locality at Wickaninnish Bay, Vancouver Island, British Columbia, during early May, 1981, and late Oc-tober, 1982. At both times all different stages were present, and there thus seems no need to differentiate between the two collections. The site is among dense stands of the main host, *Gaultheria shallon* Pursh, interspersed by individuals of *Maianthemum dilatatum* (Wood) Nels. & Macbr. At ground level much *Hyla-comium splendens* (Hedw.) B.S.G. is present, and old Sitka spruce, *Picea sitchen-sis* (Bong.) Carr. shelters the otherwise exposed site, which is just behind the open ocean beach. A thick layer of raw humus covers the ground and is sharply delimited from the sand below.

Haustoria of various sizes were exposed and removed along with at least sever-al cm of host root and quickly submerged and trimmed. Fixative and procedures were as in TOTH & KUIJT (1976). Selected blocks were trimmed and sectioned with glass knives, the sections stained with toluidine blue. The surface contours
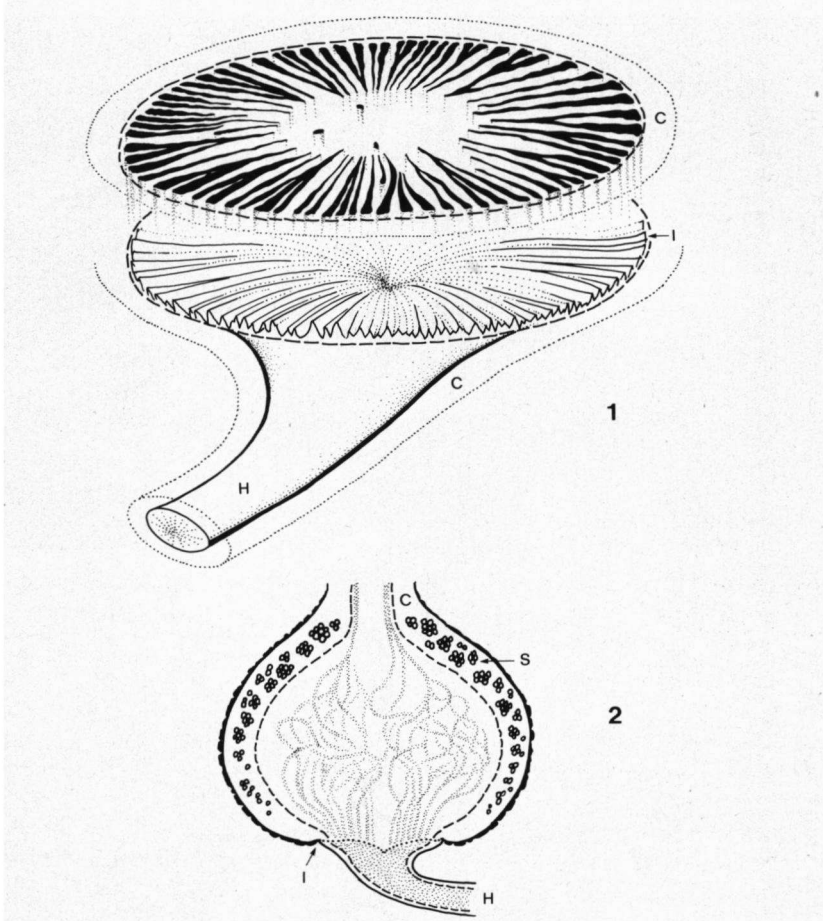
Plate I. Figs. 1–2. Diagrammatic views, based on free-hand sections, of the *Boschniakia-Gaultheria* interface. C, cortex; H, host; I, interface; S, sclereids. The broken line represents the position of the vascular cambium (host) or the separation of cortex from central, vasculated core (parasite).

Fig. 1. Representation of the xylem connection between a young *Boschniakia* tuber (above) and the supporting root of *Gaultheria* (below). The radial system of the parasite's bundles represents an optical cross-section which, for the sake of clarity, has been lifted away somewhat from the host placenta below.

Fig. 2. Longitudinal, median section of young, flowering tuber showing the convoluted system of tuber bundles connecting the interface with the stem of the parasite, above.

of the host interface were studied using a small number of "placentae" (that portion of the interface belonging to the host) found at the collecting site in which virtually all parasitic tissues had decayed away. These were washed with a gentle jet of water and camels hair brush. Selected portions of the placentae
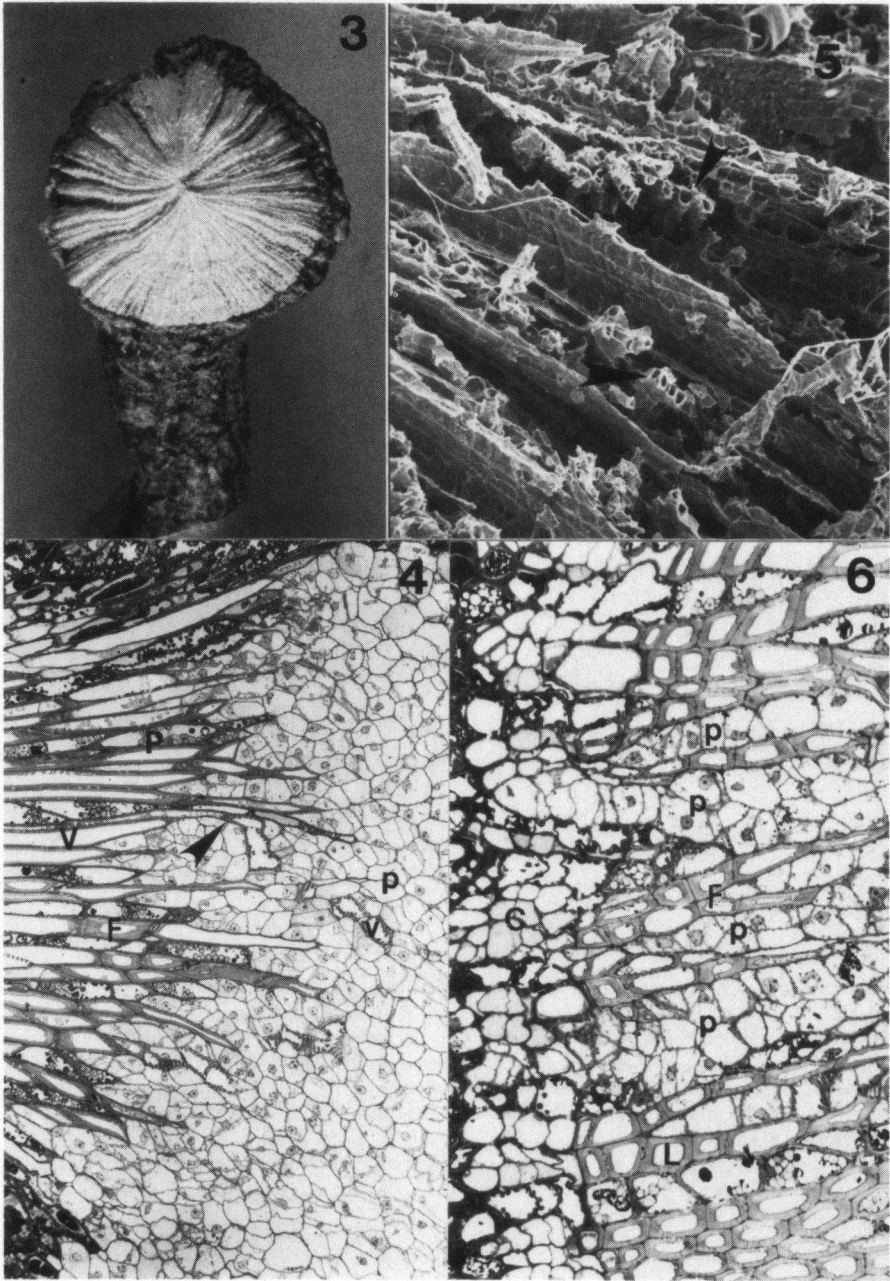
were air-dried from ethanol, mounted on aluminum stubs with colloidal silver paste, sputter coated with gold (15 nm or 150 Å thick), examined and photographed on a Hitachi S500 scanning electron microscope.

3. RESULTS

The youngest tubercles that may be found are very light brown and small enough to be still enclosed by the testa. Subsequently, the tuber grows in size and becomes progressively darker, the corky surface layer becoming fissured to delimit irregular polygons. Radial growth of the supporting root also takes place, the interface becoming an expanded, radially fluted surface the overall shape of which is more or less flat *(fig. 1, 3)*. The host tissues which adjoin the interface, being nutritive with respect to the haustorium, will together be referred to as the *placenta*. In the strict sense of the word it is thus difficult to speak of an endophyte in this mature condition, as no part of the haustorium is truly enclosed by host tissues except the earliest stage of the invading organ and the radial processes mentioned below. When the tuber reaches a certain size an inflorenscence is formed at its upper pole, perhaps endogenously as in other Orobanchaceae (KUIJT 1969). The primary haustorium thus remains the only absorptive organ.

The gross structure of the host placenta is remarkably similar to that of mistletoes of the genus *Psittacanthus* (KUIJT 1964, 1970), although usually less than one cm in diameter *(fig. 3)*. The center of the interface, corresponding to the initial point of entry, is often somewhat depressed, but at other times is nearly flat or even somewhat raised. From this center a large number of very thin and sharp ridges of host xylem of different heights radiate outward. The ridges appear to increase in height slightly toward the periphery and are lowest at the center. While in most cases the placenta is radially symmetrical or approximately so, narrow sectors are occasionally much raised above, or depressed below its general surface. In SEM views of the interface this may show as a deep trench, in sections as a massive parenchyma wedge. Alternating with the host's sharp

Plate II. Figs. 3–6.
Fig. 3. A host placenta, seen from above, from which the parasite's decayed tissues have fallen away completely; the host bark is still present. × 5.
Fig. 4. A somewhat oblique section of the interface, the host tissues to the left composed of fiber-tracheids (F) and starch-bearing parenchyma (P) and long vessel members (V). The parasite's tissues to the right are composed of parenchyma without starch (p) and a few short vessel members (v). Note the short parasite vessel composed of three members attached almost perpendicularly to the host vascular tissue (arrow head). See also *fig. 5* for similar structures. × 140.
Fig. 5. SEM detail of a placenta similar to that shown in *fig. 3*, showing radiating narrow plates of the host's fiber-tracheids to which irregular clusters of the parasite's vessels remain attached (arrow heads) similar to that observed in *fig. 4*. × 140.
Fig. 6. Section of the interface's periphery, the narrow flanges of the host's fiber-tracheids seen in cross section, the section thus approximately perpendicular to the interface. Parasite parenchyma (p) can be seen to alternate with the host ridges mostly composed of fiber-tracheids (F). Host cambium (C). × 210.

ridges are radiating flanges of the parasite's parenchyma which is actively dividing in a serial fashion *(figs. 6, 9, 10)*. Such radial expansion appears to result in occasional engulfment of nearby host tissues *(fig. 10,* arrow).

The host xylem is made up of three types of cells, i.e., vessel elements, fiber-tracheids, and short, starch-containing parenchyma cells with heavy secondary walls. Vessel elements which are part of the placenta are fairly long and narrow, their oblique end walls bearing scalariform perforation plates. Vessel elements are found on the interface only occasionally, however. The fiber-tracheids have very thick secondary walls with bordered pits, and constitute the greatest part of the host interface. They are tapered *(fig. 4)* but their sides, when corresponding to the ridge crests, may be irregularly lobed *(fig. 5)*. Cell alignment is in a more or less parallel fashion with respect to the placental ridges, which in most cases are extremely thin.

Although SEM photographs of the interface only rarely show this clearly, sectioned material frequently demonstrates specialized xylem-xylem contacts of two types across the interface. The most common of these are pits. In *fig. 7,* for example, we find a single host vessel element with several such connections to different vessel elements of the parasite. In two of the areas involved, portions of only the host cell walls are present, and they are very thin. The complementary interruption of the secondary wall of the parasite, instead, seems to have more of the character of a perforation. We assume that a primary wall, however thin, still extends across this contact at least on the host side, as granular material in nearly all cases seems to be "banked up" on either side of the interface. Secondly, there are also genuinely open places of contact *(figs. 8, 9)*, even though they are more rare. In *fig. 8* the host cell is a vessel member and in *fig. 9,* a fiber-tracheid. In both cases, the perforation has developed on the lateral wall. In the case of the host vessel, parasite contact might have occurred at a perforation area but in the case of the fiber-tracheid, perforations do not normally form. Contact is relatively common also between the heavy-walled, starch-bearing parenchyma of the host and the parenchyma of the parasite *(fig. 10)*. One would anticipate a visible depletion of starch in such host cells, but we have observed no evidence of this.

The surface of the interfacial ridges of the host shows a complex but faint

Plate III, figs. 7–10.
Fig. 7. Detail of interface, showing a host vessel member (V) cut approximately longitudinally, with pit-like connections to several vessel members of the parasite (v). Starch-bearing host parenchyma (P), parasite parenchyma (p). Note the large pits of the host corresponding to a perforation in the parasite's vessel member (arrow head). × 540.
Fig 8. Detail of interface showing an open connection between a host vessel member (V) and a parasite vessel member (v). × 390.
Fig. 9. Detail of interface showing an open connection between a host fiber-tracheid (F) and a parasite vessel member (v). × 350.
Fig. 10. Radial section of placental interface, showing radial arrangement of interface parenchyma of both partners and an engulfed cluster of starch-bearing parenchyma cells of the host (arrow). × 85.
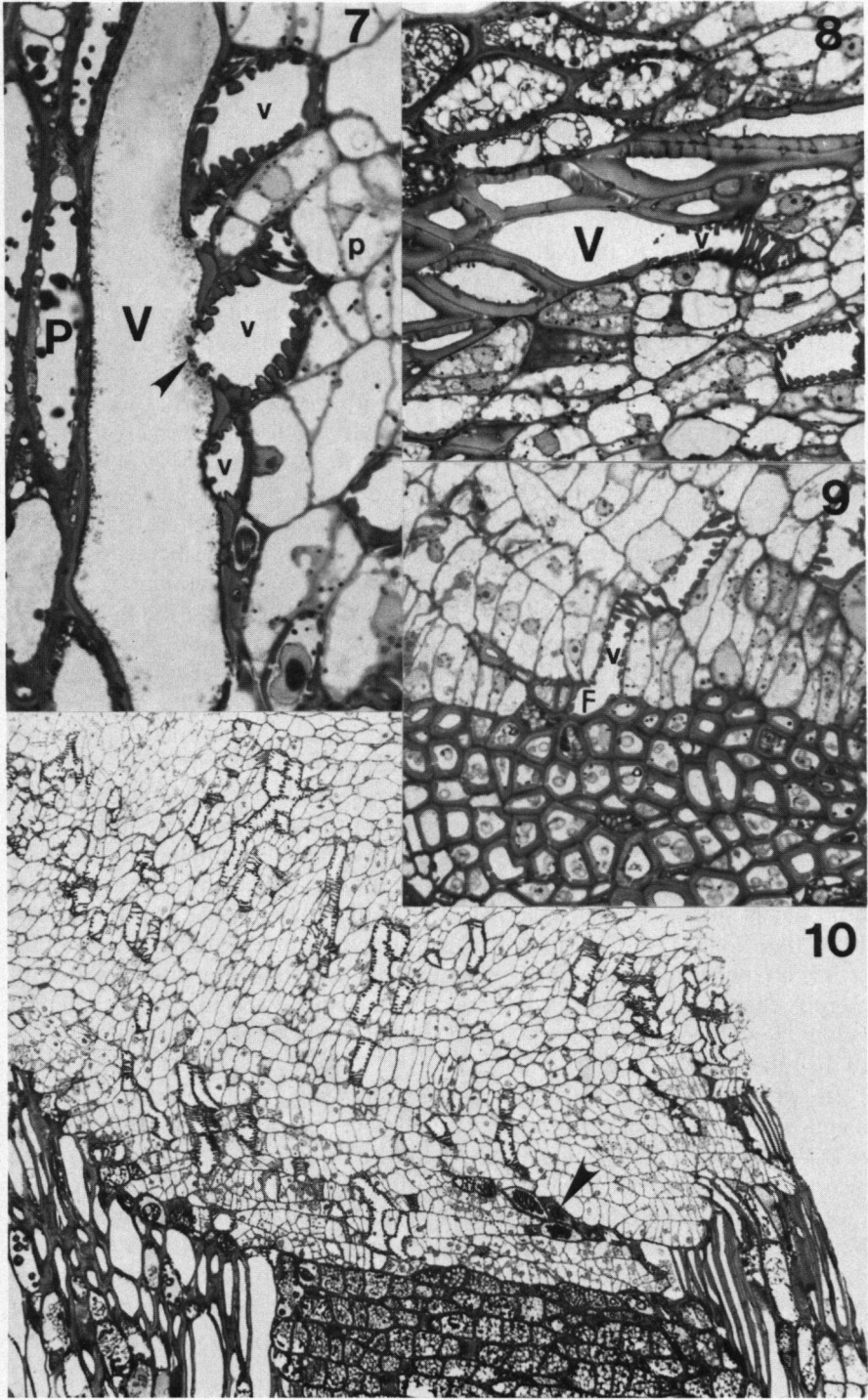
system of outlines *(fig. 5)*. Some of these appear to indicate the position of the fiber-tracheids within. Others probably constitute imprints left by the parasite's parenchyma cells which have fallen away, corresponding to the interfacial tissues seen in *fig. 10*.

In the parasite's interfacial cells we find two cell types, parenchyma and vessel members. While the individual cells of the former lack an obvious alignment, the parasite's vessel members are placed perpendicularly to the interface as a whole *(figs. 4, 5)*, forming vessels which can be traced upwards, the numerous vessels joining to form the plate-like vascular bundles described above and visible in *figs. 1* and *2*.

Since in two closely related situations the claim has been made that the haustorial xylem of the parasite consists of tracheids (DOERR & KOLLMANN 1976, OZENDA & CAPDEPON 1978), a brief description of vessel members seems required, as based on macerations. Vessel members are somewhat longer than wide, their length being 50–70 µm. The secondary walls are extremely thick and deposited in irregular helical fashion *(figs. 7–10)*, the successive parts of the coil leaving only narrow pits. All perforations seen are simple and more or less circular in outline, the perforation plate being transversely oriented *(figs. 9, 10)*. The differentiated tracheary elements of the *Boschniakia* interface do not seem to contain granules as in numerous other parasites (see the summaries in FINERAN & INGERFELD 1982 and FINERAN 1983; WEBER & NIETFELD 1984); however, the possibility of xylary granules occurring in tuber xylem cannot be excluded.

At least in larger tubers, the vessel members group themselves in distinctive radial plates or bundles when followed upward *(figs. 1, 2)*. These bundles become thicker and frequently dichotomize centrifugally, occasionally additional ones being interpolated as radial growth proceeds. In the core of the tuber at this level we find a pith-like area, and a cortex-like layer surrounds the entire bundle system. If we follow the bundles upward into the tuber we find that they quickly dissociate themselves into a very complex and apparently chaotic reticular system of branching bundles of various sizes which undulate in all directions but eventually feed into the stele ot the inflorenscence (see OLSEN & OLSEN 1981, figs. 15, 16). In the tuber itself a distinctive cortex is maintained, but a pith is no longer recognizable. The cortex even just above the interface has numerous clusters of thick-walled sclereids; these clusters become very large just below the inflorescence, but are found neither in the stem itself nor in the core of the tuber.

In two other genera of Orobanchaceae, *Orobanche* and *Epifagus*, sieve elements have been conclusively demonstrated (DOERR & KOLLMANN 1975; WALSH & POPOVICH 1977), and phloem may therefore be expected in at least the stem also of *Boschniakia*. In the tissues adjoining the interface, however, we have failed to find any phloem-like cells. The structure of the interface suggests that phloem, if present, should occupy a position outside the *Boschniakia* xylem and just above the interface. We have paid special attention to this area without positive results. As in most other parasites, therefore, continuity of vascular tissues between *Boschniakia* and its host involves the xylem only. We are also

able to report that the parasite's interfacial parenchyma cells exhibit no unusual ultrastructural features.

4. DISCUSSION

There has, in the past, been little agreement on the terminology used to refer to haustorial organs (KUIJT 1969, 1977, 1979). This is not wholly surprising, as haustoria are exceedingly variable in structure, and may originate from the apical root meristem, laterally from small roots, from the stem, or even from leaves in different groups of plants including at least one species of *Orobanche* (KUIJT 1969; KUIJT et al. 1978; WEBER 1979, 1980). They have been referred to as modified roots, or stems, or *organs sui generis*, or even hypocotyls (KUIJT 1969).

In those Orobanchaceae which have been studied in this regard it is clear that the haustorial organ is produced by the radicular pole of the undifferentiated embryo. In most species of the genus *Orobanche* itself, a small tubercle develops above the primary haustorium from which secondary roots grow out on which, eventually, secondary haustoria may appear (KUIJT 1969). *Boschniakia* produces a prominent tubercle almost immediately upon penetration (OLSEN & OLSEN 1981), but secondary roots never appear, and the tubercle expands directly into the mature tuber which eventually begins to produce inflorescences. As mentioned above, we can scarcely speak of an endophyte in the older haustorium, as its active surface is a complex, radially pleated interface the general orientation of which is more or less flat.

The term *tuber* is often restricted to swollen stem-like organs. In that sense our use of the term is technically incorrect, for the *Boschniakia* organ in question is at best only transitional to the stem above it. There is no unanimity in restricting the term to stems, however, as can be seen in the definitions found in JEPSON (1951) and LAWRENCE (1951). Largely because of the organ's dissimilarity to stems, OLSEN & OLSEN (1981) have recently suggested an alternative term for it, viz. the *soma*, which is defined as "the entirety of this plant exclusive of its reproductive organs." Whatever the value of this concept, this definition is not acceptable: presumably the stem and leaf scales are not regarded as part of the soma. But, even if OLSEN & OLSEN had in mind to equate the tuber (as here used) with the soma, we submit that this term is not appropriate especially because of its specific zoological connotations, which can never apply to vascular plants. Another problem with the soma is that it includes, as per OLSEN & OLSEN's definition, the haustorium or haustorial surface itself. Are we to equate the soma (or a part of it) in *Boschniakia* with what has traditionally been called the haustorium in other Orobanchaceae, in the closely related parasitic Scrophulariaceae, or even in other parasitic angiosperms? Since no swollen tuberous organ is present in many of the latter, this would lead to a near-equivalence of "soma" and "haustorium" and lead to much further confusion.

We feel there is a limit to the strictness with which we can apply, to parasitic angiosperms, morphological terminology which is historically based on more

"normal", autotrophic plants. Thus we prefer the simple term *tuber*, even though the organ combines characteristics of the stem (in having at least at both ends a siphonostelic skeleton) with those of a root (absence of leaves). It is interesting to note, in parentheses, that the top of a similarly swollen base in some large species of *Orobanche* (for example, *O. crenata* Forsk.) does bear leafy organs; in fact, the entire swollen base of *Cistanche* does (OZENDA & CAPDEPON 1977).

The primary haustorium of *Boschniakia* is extremely different from the secondary haustorium of its close relative *Orobanche*. Since work on the latter represents the only modern haustorial account in the family (DOERR & KOLLMANN 1974, 1975, 1976; ATTAWI & WEBER 1980) it is necessary to give a brief resumé (see also KUIJT 1977).

The *Orobanche* endophyte may be a simple, peg-like structure in some cases, and a much fragmented system in others. The endophyte is made up of parenchyma predominantly, but vascular tissues of two types are present. At least the parasite's contact xylem in *Orobanche* is said to be of a tracheid-like type, being imperforate; only pits connect the two systems, no open connections having been observed. In addition to this xylary continuity there is a degree of phloic continuity between the two partners (DOERR & KOLLMANN 1975) involving more or less regular sieve tube members flanked by companion cells, and unusual transitional sieve elements. Beyond the transitional sieve elements are one to several parenchyma cells which apply themselves to individual sieve tube members of the host.

It can be seen immediately that significant contrasts to several of these features are present in *Boschniakia*. There is, first of all, the very great difference in the size and morphological integrity of the haustorium as a whole. More importantly, in *Boschniakia* nearly the entire host interface is made up of differentiated xylem *(fig. 3)* only the peripheral contact zone being parenchymatous. Open connections between the xylary systems of both partners, while perhaps not common, do occur in *Boschniakia*. In contrast to *Orobanche*, no evidence has been seen of invasion of host tracheids by *Boschniakia* cells. It is clear both from sectioned material *(figs. 8, 9)* and from SEM *(fig. 5)* that the parasite's xylem system at least near the interface consists of vessel members only, in contrast to the tracheids of *Orobanche* (and possibly *Xylanche*; see below). We have seen nothing resembling transfer-like cell tips in *Boschniakia*. Finally, evidence of a specialized phloic conduit as described by DOERR & KOLLMANN for *Orobanche* has not been observed in our material.

A few comments are required with regard to the significance of interruptions of the secondary wall in regions of xylary contact. As stated above, both pits and perforations are characteristic of xylary connections. In the former case, a perforation of the parasite cell is frequently matched with pits of the host cell. The latter are not always characteristic of the host cell, however, especially where we are concerned with its lateral wall *(figs. 7, 8)*. It is possible that the host's interfacial xylem differentiates before the parasite's, as has been documented in *Orobanche* parasitism (DOERR & KOLLMANN 1976), where the topographic features of the parasite's secondary wall adapt themselves to the existing

ones of the host.

From the available information it is impossible to conclude whether the striking contrasts between *Orobanche* and *Boschniakia* are related to the nature of the haustorium (secondary vs. primary, respectively), or have a systematic basis, or both.

With regard to the older work by SCHUMACHER & HALBSGUTH (1938) on *Orobanche* it is unfortunate that no clear indication was given of whether the haustoria studied were primary or secondary; our impression is that the former was the case. These authors, as KOCH (1887) had done before them, pointed to the cloven appearance of the interface, the parasite's lobes and the cells within them often being extremely attenuate. To this extent we see a comparable situation in the extremely sharp-backed ridges of the *Boschniakia* interface and the sharp keels of the parasite's parenchyma masses *(fig. 4)*. However, the multinucleate tip cells of haustorial lobes described and illustrated by SCHUMACHER & HALBSGUTH for *Orobanche* spp. have no counterpart in our *Boschniakia* material or, apparently, in the *Orobanche* material used by DOERR & KOLLMANN. We suggest that the exceedingly thin cross-walls of haustorial lobes were overlooked by SCHUMACHER & HALBSGUTH, thus giving the impression of long, multinucleate cells.

A recent study by OZENDA & CAPDEPON (1978) has dealt with the haustorial organ of yet another member of Orobanchaceae, *Xylanche himalaica* (Hook.f. & Thomas) G. Beck. *Xylanche* is a small Asiatic genus which is very closely related to *Boschniakia* (in fact, at one time it was united with it). It forms a tuber which at least externally is very similar to that of *Boschniakia*, lacks secondary roots, and is likely perennial also. The description of the host-parasite interface by OZENDA & CAPDEPON, however, is at variance with our *Boschniakia* account: the tuber itself is said to be made up of interlocking tissues of both partners. The host surface radiates into expanded xylary portions which dichotomize and are blunt at the tips; these structures are referred to as "petaloid processes". They are said to ramify far into the tuber, their ultimate ends often being continuous with the irregular plexus of small bundles which the parasite possesses in the uppermost portion of the tuber. Vascular continuity is strictly xylary, and consists of tracheids only, but is rather infrequent. Thus, the *Xylanche* tuber would be comparable to that of *Balanophora* (Balanophoraceae) in being a dual organ, combining the complexly interlocking tissues of both partners. The authors suggest most materials obtained by *Xylanche* are transferred via a parenchyma interface.

We see a number of problems with OZENDA & CAPDEPON's interpretation. First of all, the excessive contrast with the *Boschniakia* tuber leads us to suspect that those authors have failed to recognize the actual interface between the host and the parasite. Such a misinterpretation might easily occur where the interface contours are complex and marginally dissected, and when the haustorium is sectioned somewhat obliquely. Several other reasons exist for doubts about OZENDA & CAPDEPON's description. The total absence of any visible demarcation between the two systems is very surprising and, indeed, commented upon

by those authors. Their illustration of an instance of xylary continuity by means of tracheids (fig. 30) is not convincing and compares closely to a small strand of vessel elements in the tuber of *Boschniakia*. Their suggestion would require the intrusive growth into *Xylanche* tissues of slender parasitic strands of the host with distinctive apical meristems; this growth would undoubtedly leave necrotic zones or zones of demarcation, and no signs of such activity are available. We believe, therefore, that all or most of the larger bundles illustrated by OZENDA & CAPDEPON are comparable to the radial plates or bundles described by us for *Boschniakia*; and that all of the small bundles and strands of the tuber belong to *Xylanche* and compare to the complex reticular system in the *Boschniakia* tuber. We make these suggestions realizing that only a detailed study of the *Xylanche* tuber can clarify the situation. The most important feature of such a study would be the exact demarcation of the interface. It is clear from OZENDA & CAPDEPON's account, meanwhile, that this interface is more complex than that of *Boschniakia*. In each case the host belongs to Ericaceae, that of *Xylanche himalaica* being an endemic species, *Rhododendron campylocarpum* Hook. f.

In *Boschniakia* the basic orientation of cells on both sides of the interface is perpendicular to each other *(figs 5, 7)*. Cell connections across the interface tend to involve the tip of the parasite's terminal vessel element and the flanks of the host element. This also seems to be the basic alignment of the phloic conduit in *Orobanche* (DOERR & KOLLMANN 1975).

A striking resemblance exists between the contours of the *Boschniakia* interface and that of certain mistletoes such as *Psittacanthus* (Loranthaceae: KUIJT 1969, 1970). Although Mexican "rosas de palo" of these mistletoes have been long known, their exact structure has never been detailed. An early paper on *P. schiedeanus* provides little information (HOFMANN 1932). In a more recent paper (KUIJT 1964) the development of wood roses is almost certainly misinterpreted through the suggestion that a meristematic layer of both partners lines the interface. A different interpretation, agreeing more closely to the *Boschniakia* situation, was outlined in KUIJT (1970). There it is proposed that an inversion of the host cambium takes place following establishment of the parasite, so that the wood rose is added to only at its outside flanks (KUIJT 1970, fig. 7). Since the parasite above the interface similarly expands by means of a vascular cambium, the cambia of both partners are likely to be continuous (cf. KUIJT 1983).

The growth dynamics of the host-parasite interface of *Boschniakia* are difficult to visualize. Its structural details are undoubtedly stable after the adjacent host cells are fully differentiated. This, in turn, implies that the placental contours are established and perpetuated at the periphery, where the parenchyma tissues of the two plants meet. The radial haustorial wedges which occupy the placental grooves possibly continue to impose these contours by growing out into the host tissues external to the cambium. This mechanism implies a degree of intrusive growth. In fact, there is sometimes considerable evidence for this type of growth in the area mentioned. Occasionally, clusters of host cells can be seen completely surrounded by haustorial tissue *(fig. 10,* arrow). This would seem to be strong

evidence that some intrusive growth takes place at the periphery of the hausto-rium. This view also corrects an impression that, in contrasts to other parasitic angiosperms with sinker-like processes, the radial sinker-like wedges of *Bosch-niakia* mentioned above have grown towards the host cambium *from the xylem side (fig. 6)*. In reality, the structural connection between host and parasite seems to be defined by a dynamic interaction between their meristematic paren-chyma.

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