The Hyperparasitism by *Taxillus tsaii* S. T. Chiu (Loranthaceae)

Shau-Ting Chiu

Department of Botany, National Museum of Natural Science, Taichung, Taiwan 404, R.O.C.

(Received November 10, 2005; Accepted December 16, 2005)

Abstract. There are no records of the hyperparasitism by *Taxillus tsaii* S. T. Chiu in Loranthaceae to date. Two cases those were found at Lien-Hua-Chih in the Nantou County, the hosts of *T. tsaii* were *Viscum angulatum* Heyne and *Loranthus delavayi* Van Tieghem. Specimens were deposited in the Botanical Herbarium of the National Museum of Natural Science at Taichung, Taiwan (TNM). The anatomy of the endophytic system in this case showed that the haustorium had progressively grown into the cambial cylinder and had penetrated the secondary xylem of the host branches. The xylary strands derived from the haustorium periclinally extended and centrifugally expanded in the host xylem. The penetration had induced thinning the host's cell walls of the invaded tissue, enhancing cytoplasm density, forming conspicuous plasmodesmata and pits, and triggering cell division. This differs from the development of the endophytic system in *Phoradendron* and *Arceuthobium*, whose sinkers derived from the cortical strands penetrate inwardly. The xylary strand and centrifugal outgrowth consisted of parenchyma with ergastic granules and a small amount of vascular tissue. It is possible to increase the water absorption and/or water storage with a high solute concentration in parasite tissues. This study also indicates that the occurrence of hyperparasitism in *T. tsaii* may be related to the diet and defecation of flowerpeckers and the phenology and seed germination of mistletoes. The majority of *T. tsaii* shows the primary parasitism but the hyperparasitism by this species also possibly occurs.

Key words: Hyperparasitism, Loranthaceae, mistletoes, *Taxillus*, woody parasites.

INTRODUCTION

Mistletoe of Taiwan has mostly been studied for taxonomic purposes (Chao, 1973, 1976; Chen, 1987; Liu *et al*., 1988; Chiu, 1996a, b; Yang *et al*., 1997) and pharmacognosy (Chen and Chiu, 1982; Lin and Kuoh, 1983). After taxonomic studies of the Loranthaceae in Taiwan in the 1990s, *Taxillus* was revised to contain 11 species and *T. tsaii* S. T. Chiu is distinguished from *T. rhododendricolus* (Hayata) S. T. Chiu and *T. lonicerifolius* (Hayata) S. T. Chiu. The use of the names *T. rhododendricolus* and *T. lonicerifolius* in different publications and the accuracy of identification by different persons might refer to the old taxonomic system which grouped the three species under the same name which is referred to as *T. lonicerifolius* (*sensu lato*) in this paper. Despite this confusion, classification of the studied mistletoes clearly follows the revision of the Loranthaceae by Chiu (1996a, b).

Past investigations on host species of woody parasites in Taiwan did not report hyperparasitism of either *T. rododendricolus* or *T. lonicerifolius* (Chen and Lo, 1992a). Only *Loranthus kaoi* (Chao) Kiu was definitely categorized as being a hyperparasite (Chao, 1973, 1976; Liu et al., 1988; Chen, 1987; Chen and Lo, 1992a). In addition, *Viscum angulatum* Heyne and *Viscum articulatum* Burm. are known to sometimes parasitize other mistletoes (Chen, 1987; Chen and Lo, 1992a). However, a field botanist noted two cases in which *T. lonicerifolius* (*sensu lato*) parasitized *Taxillus matsudai* (Hayata) Danser and *Viscum alniformosanae* Hayata in Taiwan. Cases of the hyperparasitism by *T. lonicerifolius* or *T. rhododendricolus* have never been documented.

Prior to this study, *T. tsaii* had never been found to be infecting on *Viscum angulatum* or *Loranthus delavayi* Van Tieghem. This investigation includes the anatomy of the hyperparasitic infection and possible reasons for this hyperparasitism.

---

*Corresponding author. E-mail: stchiu@mail.nmns.edu.tw

MATERIALS AND METHODS

Plant materials. The specimens of *Taxillus tsaii* S. T. Chiu, *Viscum angulatum* Heyne and *Cinnamomum camphora* (L.) Nees & Eberm. were collected in a broadleaf forest at Lien-Hua-Chih, Nantou Co., Taiwan in May of 1994 and deposited in the Botanical Herbarium of National Museum of Natural Science (TNM), Taichung, Taiwan.

The investigation of host species of the Loranthaceae was based on field notes and herbarial specimens from TAI, TNM, TCF, TAIF, TNU, NCKU, HAST, and NTUF herbaria.

Anatomical studies. The infected stem segments were sampled, fixed in FPA with 15% glycerol, dehydrated in TBA, embedded in paraffin and sectioned on the AO rotary microtome (Johanson, 1940). Paraffin sections of 10μm were hydrated, stained with 0.5% Safranin O and 0.1% Fast Green, and dehydrated in the ethanol series (Johanson, 1940). Observations and micrographs were taken using a Nikon SMZ-U dissecting microscope and a Zeiss Axioplan optical microscope.

RESULTS

The hyperparasitism of *T. tsaii* occurred on at least two occasions that involved two host species of mistletoes; *i.e. V. angulatum* and *L. delavayi*. The first case, which showed *T. tsaii* parasitizing on *V. angulatum* which parasitizing on *C. camphora*, was found at 120°52'31"E and 23°55'14" beside the Lien-Hua-Chih Research Center of Taiwan Forest Research Institute on May 13, 1994 (Figs. 1, 2). The elevation was about 710 m above the sea level. Specimens with the collection numbers, S.-T. Chiu 2232 and S.-T. Chiu 2233, were deposited in TNM. The second case with the host *Camellia oleifera* Abel., the primary parasite *L. delavayi*, and the hyperparasite *T. rhododendricolus* was found in an oil camellia cultivation area at Lien-Hua-Chih. There were two other cases that were observed by Mr. Ching-Chen Shen at Chia-Yang and Li-Shan, Taichung Co., but he did not distinguish *T. tsaii* from *T. rhododendricolus* and *T. lonicerifolius*. It is possible that the hyperparasitism of *T. lonicerifolius*, observed on the *T. matsudai* and *V. alniformosanae*, could be the cases of *T. rhododendricolus* due to misidentification between *T. rhododendricolus* and *T. lonicerifolius* and thus this species may have a wide distribution in the area. Therefore, these two cases of hyperparasitism would be grouped as *T. lonicerifolius* (*sensu lato*). Based on the recent discoveries, herbarium specimens and publications, records of hyperparasitism in the Loranthaceae in Taiwan are synthesized in Table 1.

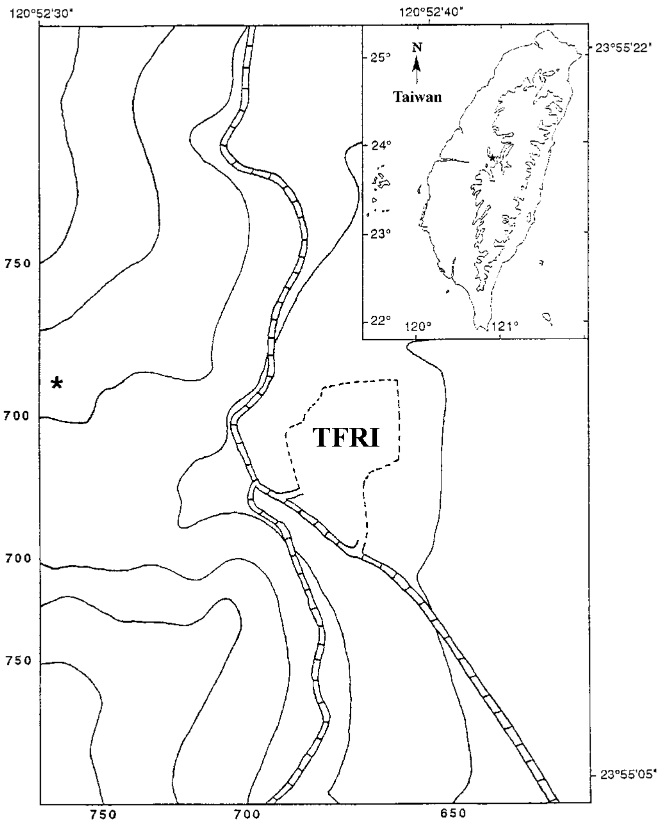

Fig. 1. Maps showing the location where the specimens were collected. The black asterisk on the map of Taiwan, with the contour line at an elevation of 1000 m, indicates the location of the Lien-Hua-Chih Research Center of Taiwan Forest Research Institute (TFRI). The black asterisk on the map of Lien-Hua-Chih indicates where the hyperparasitic *Taxillus tsaii* S. T. Chiu was found.

In the hyperparasitism of *T. tsaii* on *V. angulatum*, the major haustorium of hyperparasite settled on the branch of the primary parasite (Fig. 2). The growth of runners from the hyperparasite produced several disc haustoria that attached onto the branches of *V. angulatum* (Fig. 2A-C). As the first axis of the hyperparasite grew, the major haustorium developed by deeply penetrating the branch xylem of *V. angulatum* (Fig. 2D). At this stage, swelling of the *V. angulatum* branch was not obvious, but the *T. tsaii* portion at the junction seemed to be expanded and to include development of the cortical fusion between the hyperparasite and its host (Fig. 2D). It looked as if the major haustorium of the hyperparasite was

Fig. 2. Hyperparasitism of *Taxillus tsaii* on *Viscum angulatum* Heyne. A. Junction between *T. tsaii* and *V. angulatum*. B. Back view of the junction. C. Front view of the junction. D. Section view through the junction. The upper green part belongs to *V. angulatum* and the lower whitish part belongs to *T. tsaii*. Hx, host xylem. S, xylary strand. Bars = 10mm (A-C), 1mm (D).

Table 1. Records of hyperparasites and primary parasites which host hyperparasites in Taiwan[1]

	Primary parasites (as hosts of hyperparasites)						
Hyperparasites	*L. delavayi* Van Tieghem	*T. lonicerifolius* (Hayata) Chiu (*s.l.*)	*T. liquidambaricolus* (Hayata) Hosokawa	*T. matsudai* (Hayata) Danser	*V. alniformosanae* Hayata	*V. angulatum* Heyne	*V. articulatum* Burm. f.
Loranthus kaoi (Chao) Kiu	–	+	+	–	–	–	–
Taxillus lonicerifolius (Hayata) Chiu (*s.l.*)	–	–	–	±[2]	±[2]	–	–
Taxillus parasiticus (L.) Chiu	–	–	–	–	–	–	+
Taxillus tsaii Chiu	+	–	–	±[2]	±[2]	+	–
Viscum angulatum Heyne	+	–	–	–	–	–	–
Viscum articulatum Burm. f.	–	+	–	–	–	–	–

[1] Data were combined from this study and other publications (Chen and Lo, 1992b; Liu *et al.*, 1988)

[2] Field observations by Mr. Ching Chen Shen who did not separate *T. rhododendricolus* from *T. lonicerifolius*.

embedded in the cortical substrate of the primary parasite and the xylary strands developed from the haustorium were periclinally penetrating the xylem below the cortical substrate (Figs. 2D, 3). The penetration formed several periclinal xylary strands that expanded the endophytic system into the xylem of *V. angulatum* (Figs. 2D, 3).

The infected branch of *V. angulatum* had a thick cuticle covering the remained thick-walled epidermal cells (Fig. 3). The periderm initiated at the cortex underneath the epidermis within limited portions. Many druses had formed in the cortical tissue that was mingled with the parenchyma and several groups of sclereids. The cambial zone of the branch of *V. angulatum* had produced a large amount of secondary xylem that did not show clear growth rings (Fig. 3). The mean ratio of produced secondary xylem to secondary phloem was 19.33 ± 3.19 (s. e.). The pith was filled with loosely arranged parenchyma and groups of sclereids at the boundary of the primary xylem.

The endophytic system of *T. tsaii* had formed several periclinally arched xylary strands penetrating the secondary xylem of *V. angulatum* (Fig. 3). The increasing outgrowth of a single xylary strand anticlinally and centrifugally penetrated the outer part of the xylem where the xylary strand was located. The outgrowth of the outermost xylary strand possibly reached the cambial cylinder, the secondary phloem, or the cortical region (Fig. 3).

The interface between the host tissues and the xylary strands contained dense necrotic cytoplasm of the host (Figs. 3, 4). The expansion of the parasitic endophytic system mostly occurred at the tip of the xylary strands and the formation of the centrifugal outgrowth. The tip of the xylary strands caused secretion and necrosis of the host cells (Fig. 4A-D). Dense cytoplasmic materials filled the intercellular spaces and the interface surrounding the xylary strands. Many cell divisions of the host tissue aligned around the tips of the xylary strands (Figs. 3, 4B-D). Most of the host cells under the influence of the tip of the xylary strand restored their totipotency including the sclerenchyma and tracheary elements. The phenomena included thinning of the cell walls, enhancement of the density of the cytoplasm, formation of conspicuous plasmodesmata and pits, and triggering of cell divisions. (Figs 4C-D, 5A).

The tissue of the xylary strands consisted of a large amount of parenchyma with many starch grains (Fig. 5A-D). At the core of each xylary strand, the parenchymatous tissue was differentiated into the vascular system, however, it was not differentiated as well as that of most terrestrial vascular plants. The vascular system of the xylary strands still consisted of tracheary elements but the development of phloem was not obvious in the vascular strands (Figs. 5B-D). The parenchyma adjacent to the vascular tissue was smaller and more longitudinal than the other surrounding parenchyma (Fig. 5B, D).

In the second case, the hyperparasite *T. tsaii* was found on the primary parasite *L. delavayi* on the host *C. oleifera*, *T. tsaii* was at juvenile stage. Usually, *T. tsaii* is a primary parasite and very frequently parasitizes cultivated oil camellia instead of *L. delavayi* in the same area. The host, *C. oleifera*, is a tall shrub with diffuse porous wood and growth rings (Fig. 6A). The stem of *T. tsaii* consists of a thick cuticle covering the epidermis, cortical and phloic parenchyma with high phenolic contents, xylary cylinder with grouped vessels and wide rays, and parenchymatous pith with phenolic cells (Fig. 6B). No obvious growth rings were observed in *T. tsaii* (Fig. 6B). As a primary parasite, the xylary strands of *T. tsaii* haustoria had also penetrated the xylem of the host (Fig. 6C). When the host grew, the accompanying expansion of xylary strands and haustoria caused torsion of the xylem and swelling of the junction (Fig. 6C). Cells at the boundary between the host and parasite had dense cytoplasm and firm walls. Inside the layer of cells, there was thin walled parenchyma with many ergastic granules. The parenchyma had formed an easily collapsed matrix surrounding the vascular core of the xylary strand (Fig. 6C). The increasing outgrowth of the xylary strand was anticlinal. Therefore, the inner boundary of the xylary strand was usually rigid (Fig. 6C).

The haustorium types in both cases of *T. tsaii* were recognized as being aerial parasites with the epicotical roots bearing secondary haustoria (Fig. 2) and the primary haustorium developing from the radicular pole of the holdfast of the embryo (Figs. 3, 7A). The shafts of the endophytic system grew anticlinally and centrifugally outwardly to penetrate the cambial zone. The inward interface between *T. tsaii* and the host was shaped around the shaft and disc (Fig. 7A). No obvious bark strands had developed in *T. tsaii*. Some other loranthacean primary haustoria had formed haustorial sinkers that penetrated the vascular stele and sprouts of budding from the endophytic

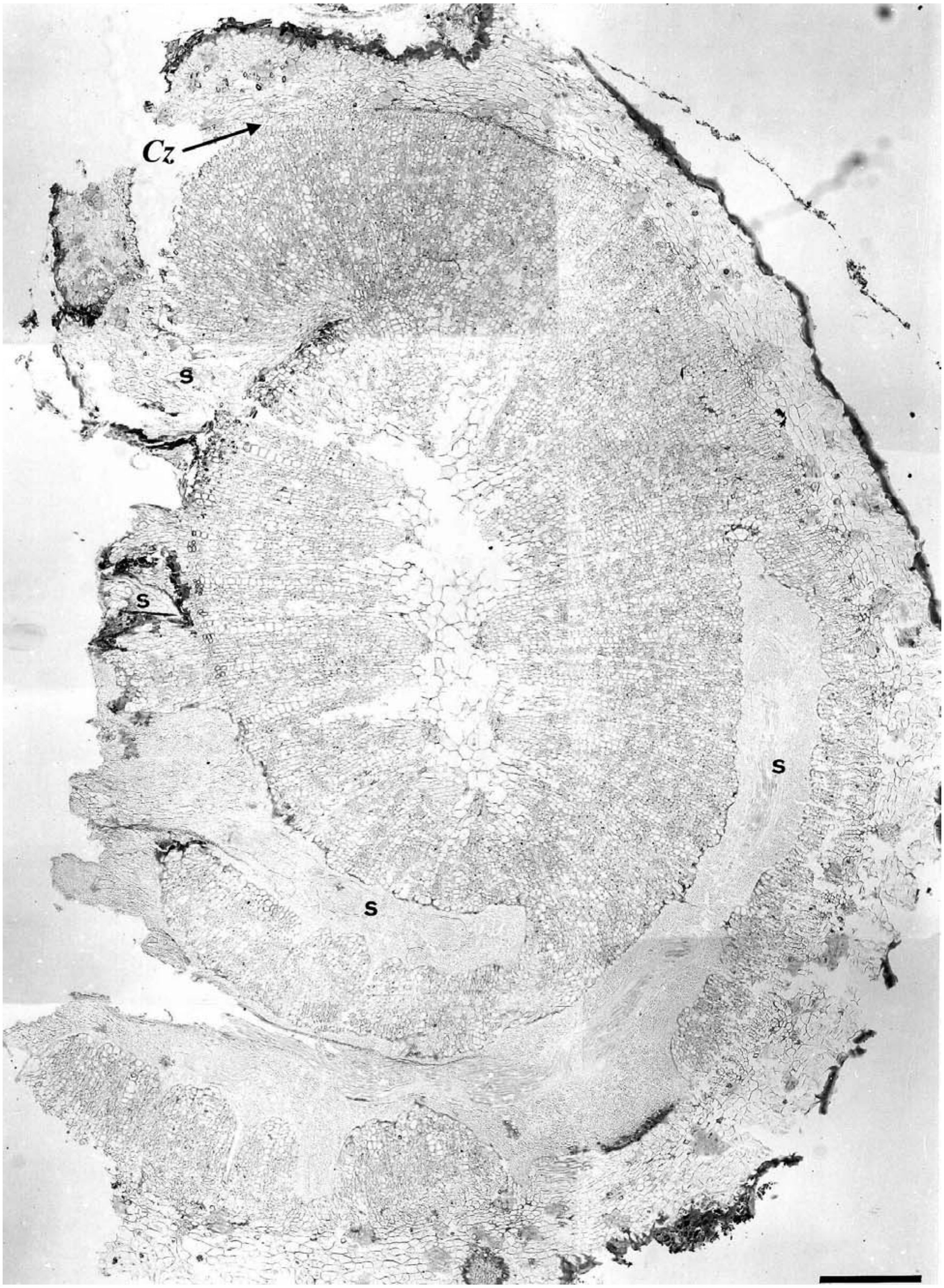

Fig. 3. Transection micrograph through the *Viscum angulatum* stem of the junction. Cz, cambial zone. S, xylary strand of *T. tsaii*. Bar = 0.5mm.

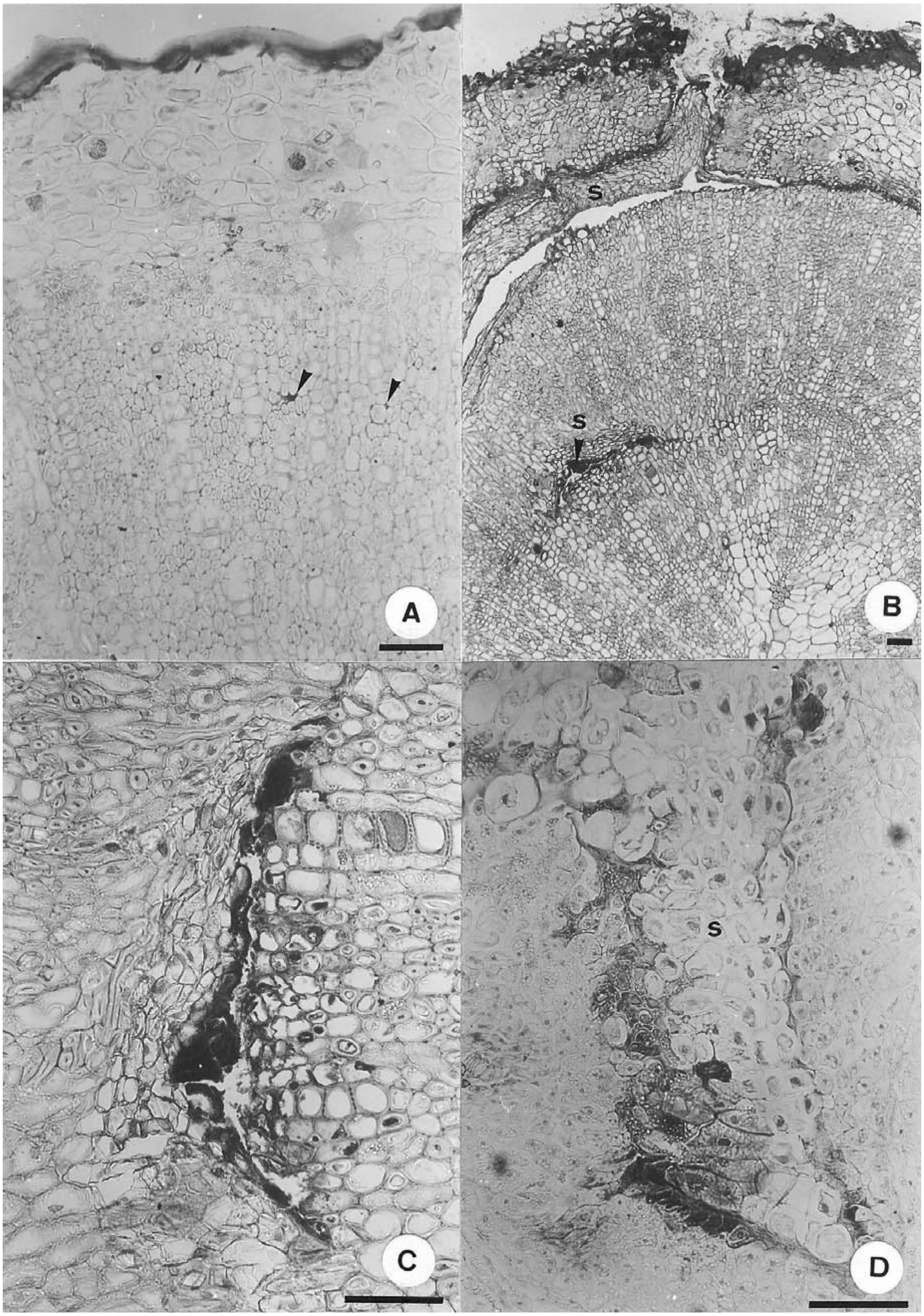

Fig. 4. Micrographs of the penetration of the xylary strands from *Taxillus tsaii* into the xylem of *Viscum angulatum*. A. Transection of the host stem showing the frontier (arrowhead) of the xylary strand. B. Periclinal xylary strands (S) deeply penetrating the inner part of the host xylem. C. Penetration induced dense cytoplasm, wall thinning, cell division, and finally tyloses as well as necrosis. D. Interface between the periclinal xylary strands and the host tissue. Bars = 0.1mm.

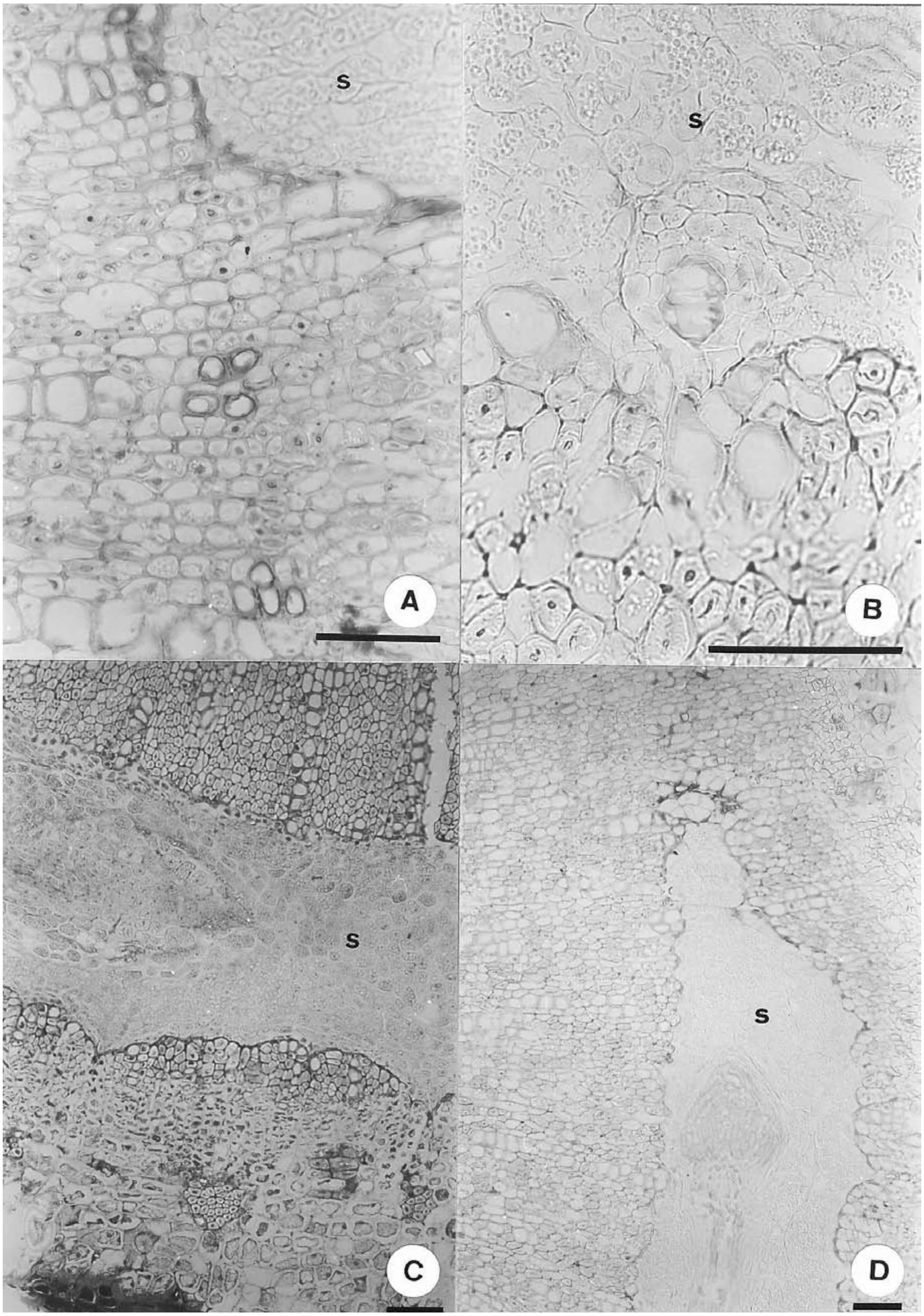

Fig. 5. Micrographs of the interface between the xylary strands (S) and host tissue. A. Loose wall of host cells formed by the influence of the penetration of the xylary stands. B. Xylary strand with a small strand of tracheary elements, surrounded by starch-rich parenchyma, which radially penetrates the host xylem. C, D. Xylary strands mostly with tracheary elements and starch-rich parenchyma. There is a dense interface between most xylary strands and host tissues. Bars = 0.1mm.

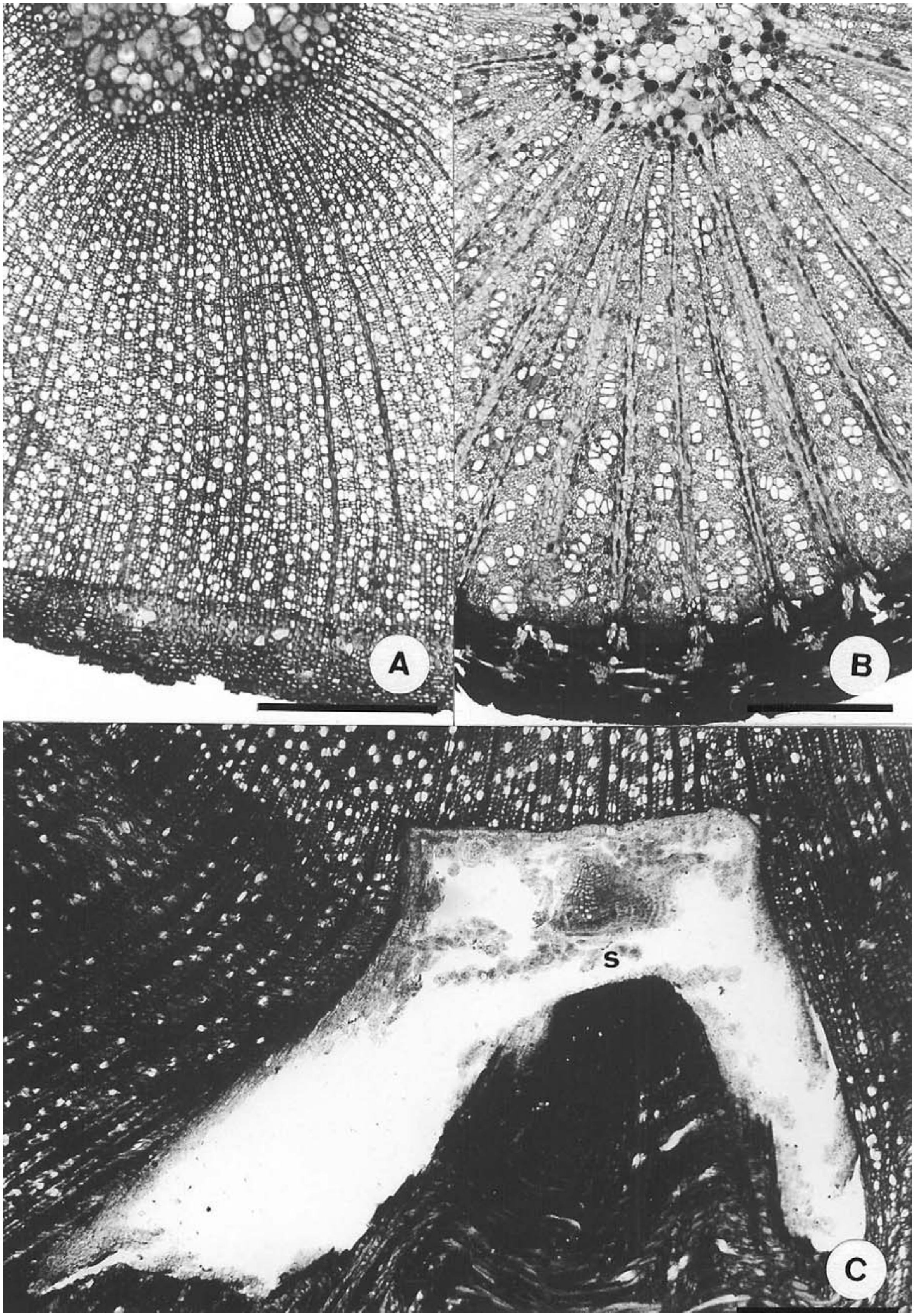

Fig. 6. Micrographs of transections. A. Host stem of *Camellia oleifera* Abel.; B. parasite stem of *Taxillus tsaii*; and C. junction showing the xylary strands (S) which have penetrated the host xylem (C. o.). Bars = 0.5mm.

system (Fig. 7B). Both endophytes in above-described haustorium types deeply penetrated the vascular stele. The third endophytic system was prostrate in the cortex zone with the xylary strands invading the host xylem with perpendicularly inward strands (Fig. 7C). Certain endophytic systems in other parasitic plants combining the xylary strands and phloem tissue also occurred which formed a network in the host branch (Fig. 7D).

DISCUSSION

This is the first time to bring the attention on the hyperparasitism of *Taxillus* in Taiwan. Hyperparasitism of vascular angiosperms had been noticed in the curious examples of *Phacellaria* in the Santalaceae (Danser, 1939), and *Viscum capitellatum* (Weeraratna, 1960), *V. angulatum*, *V. articulatum* (Chen and Lo, 1992a; Chen, 1988), *Dendrophthora epiviscum* (Kuijt, 1961), *Ixocactus* (Kuijt, 1967), *Phoradendron bolleanum* subsp. *bolleanum* (Wiens, 1964; Hawksworth and Wiens, 1966), and *Loranthus kaoi* (Chao, 1973 and 1976; Liu *et al.*, 1988) in the Loranthaceae. A spectacular case of hyperparasitism was the three-storied parasitism of *Loranthus ferrugineus* on *Viscum articulatum*, the latter of which was on *Elytranthe barnesii* that parasitized the durian, *Durio zebethinus* (Sands, 1924). It might be countered that *T. tsaii* and other habitual hyperparasites are in occasional cases.

Prior to our investigation, the host-specificity of *T. tsaii* was known to have a wide range and was not particularly inexplicable.

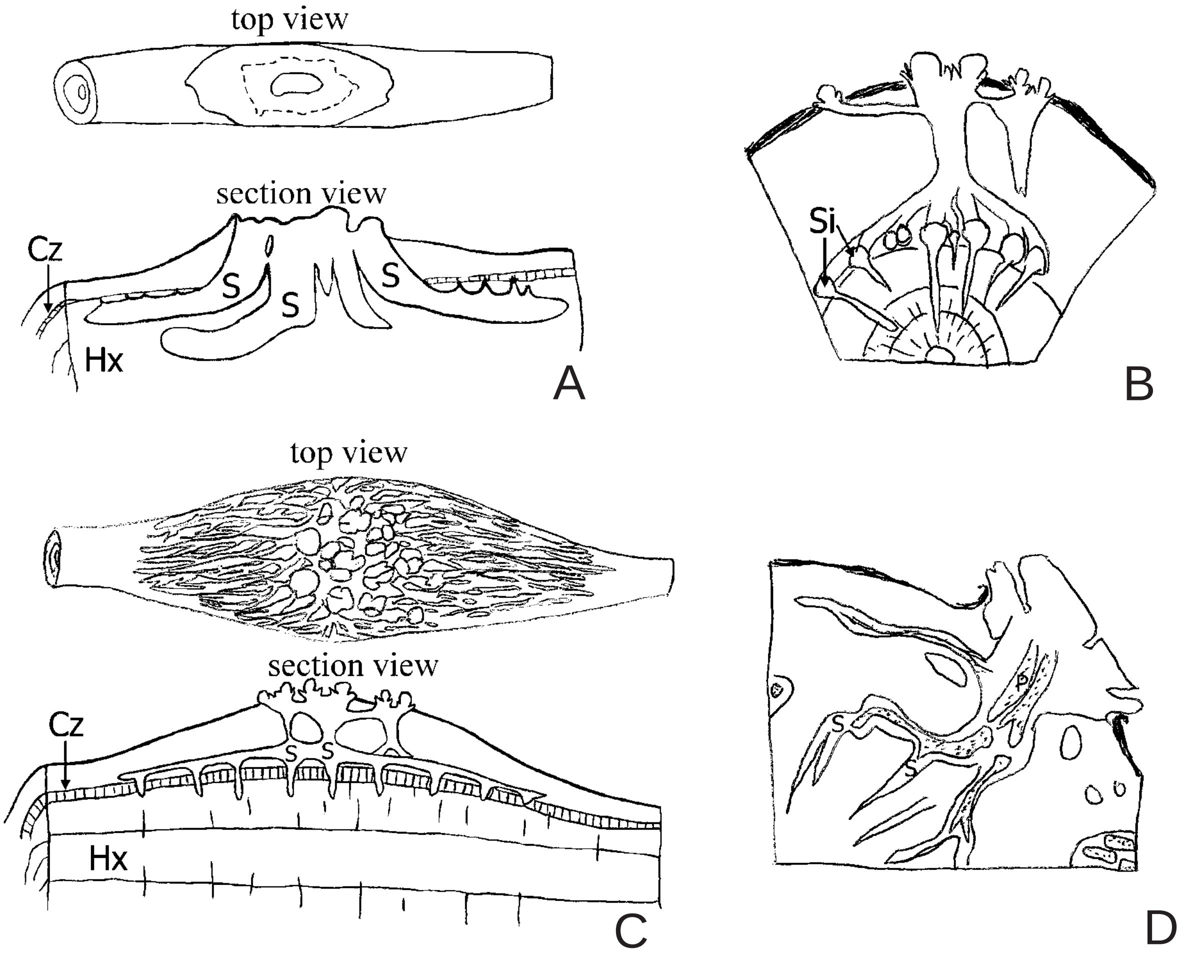

Fig. 7. Comparisons of endophytic types. A. Primary haustorium *Taxillus tsaii* developed from the radicular pole of the holdfast of the embryo. The endophytic system grew as shafts anticlinally and centrifugally outwardly and penetrated the cambial zone (Cz). B. Primary haustorium forming the haustorial sinkers (Si) which penetrated the vascular stele, and sprouts of budding from the endophytic system. C. Endophytic system prostrate in the cortical zone with the xylary strands (S) invading the host xylem (Hx). D. Endophytic system combined with the xylary strands and phloem tissue (P) to form a network in the host branch.

Host specificity can evolve only where there is an abundance of a single host species (Kuijt, 1969). However, the case of *T. tsaii* on *L. delavayi* and the latter on *C. oleifera* occurred in an area of cultivation with an abundance of *C. oleifera* existing for at least 30 years. Host specificity in *T. tsaii* might not have evolved yet. The specificity of tropical parasitic angiosperms, if exists, would seem to be a special situation brought about by dispersal agents (birds) which are selective in the plants they frequent (Kuijt, 1969). The investigated cases of hyperparasitism of *Taxillus* revealed mostly young hyperparasites. These newly established instances of hyperparasitism indicate that increasing diversity of the preferred hosts may be occurring. According to observations of the feeding habits and the defecating behavior of flowerpeckers (*Dicaeum* spp.)and other birds which feed on mistletoe nectar and fruit, there are abundant opportunities for birds to deposit seeds on branches where they perch (Reid, 1989). When the reproductive cycles of different mistletoe species overlap, there are increased chances for the transfer and deposition of seeds of one mistletoe species to another by avian vectors. The acceptability and rejection of the hosts mostly depend on the characteristics of the host epidermis. However, the most-important factor with the establishment of parasites is the timing of infection. The reported cases of hyperparasitism of *T. tsaii* might have been due to proper timing, a successful setting, and breakthrough of the host barriers.

This stimulated interesting thinking about how important mechanical barriers and biochemical incompatibility that help a host to prevent infection are. When seeds of *Phoradendron macrophyllum* were placed on cuttings, a corky layer or wound periderm, formed locally beneath the mistletoe seeds regardless of whether a susceptible or unsusceptible host was used (Lichter and Berry, 1991). In the case of *T. tsaii* on *V. angulatum*, seeds of both species were found on the branches of *V. angulatum*. There is no direct evidence but a survey of hosts (Liu *et al.*, 1988; Chen and Lo, 1992a) suggested that *V. angulatum* had no self-parasitism. The presented anatomical studies indicate that both species have thick cuticles covering the epidermis of their branches, but the area beneath the epidermis of *T. tsaii* filled with phenolic cells. Whether the bark of *V. angulatum* allows easy penetration by the haustoria needs to be studied further. In addition, the germination of Taxillus seeds begins with the sprouting of primary leaves, followed by the formation of the haustorium. The haustoria of *T. tsaii* usually penetrate into the xylem of hosts. This indicates that as the settlement of haustoria occurs, the capability for deep penetration by *T. tsaii* has evolved. Therefore, if the infection timing is proper, the establishment of hyperparasitism by *T. tsaii* is possible.

The factors which ensure that the holdfast formation and haustorium penetration are successful may depend on host compatibility. In the establishment of *P. macrophyllum*, aerial shoot formation is influenced by the availability of local moisture availability, but other stages such as seed germination, holdfast formation, renewed greening of mistletoe tissue, and swelling of the underlying host branch are independent of water or nutrient sprays (Lichter and Berry, 1991). The expansion of the haustoria and xylary strands of *T. tsaii* in the host branches reveals a great induction of changes in the host tissue. This mechanism shows little similarity to the formation of the endophytic system of *Phoradendron* (Calvin, 1967a, b; Calvin *et al.* 1991) and *Arceuthobium* (Cohen, 1954; Calvin *et al.* 1984). It is possible that *T. tsaii* has a strong capability of penetration, which makes infection easy when its haustoria have successfully settled into the host.

In this kind of loranthaceous mistletoes, the haustorium penetrates the host bark and phloem, embedding itself in the xylem; this is similar to the development of the primary haustorium in *P. macrophyllum* (Lichter and Berry, 1991). This suggests that the inquiry of water supply may be important for the early establishment in order to induce the further development of shoots. However, the further development of the endophytic system of *T. tsaii* differs from that of most mistletoes in *Phoradendron* (Calvin, 1967a, b; Dawson *et al.*, 1990; Calvin *et al.*, 1991; Lichter and Berry, 1991) and *Arceuthobium* (Cohen, 1954; Calvin *et al.* 1984). Instead of the radiate cortical strands in *Phoradendron* and *Arceuthobium*, the xylary strands of *Taxillus*, which arise from the haustorium as it penetrates the host cortex and phloem, grow through the xylem of the host branch. The extensive penetration of the xylary strands includes the periclinal expansion in the xylem and centrifugal outgrowth to the phloem or cortex. Most periclinal xylary strands of *Taxillus* were embedded in the host xylem. The centrifugal xylary strands derived from the periclinal strands penetrated outwardly. This is in contrast to the secondary penetrating direction in *Phoradendron* and *Arceuthobium* which is inwardly. In other words, the "sinkers" derived from cortical strands of *Phoradendron* and *Arceuthobium* which grow centripetally (Cohen, 1954; Calvin, 1967b; Dawson *et al*., 1990; Calvin *et al*., 1991; Lichter and Berry, 1991).

When the infection is successfully established, the endophytic system of mistletoes is well developed. The major tissue of the haustoria and xylary strands of *Taxillus* were thin-walled parenchyma with ergastic granules. The possible role of the parenchyma surrounding the tracheary elements could be to increase the water absorption and/or water storage due to the high solute concentration.

The interface between the host tissues and xylary strands is composed of necrotic cytoplasm. Whether the parenchymatous xylary strands are integrated into the tissues of the host or parasite depends on the definitions. The composite bundles occurring in *Balanophora*, *Langsdorffia*, and *Thonningia* consists mainly of host vascular tissues inside which parasite transfer cells are located (Hsiao *et al*., 1994, 1995). However, most mistletoes form a disklike haustorium and their hosts contact each other across a discrete interface (Fineran and Hocking, 1983). The boundary of the two individuals is clearly defined (Calvin *et al*., 1991; Dawson *et al*., 1990). In the studied cases, the haustoria and xylary strands consisted of a small amount of vascular tissue but mostly parenchyma. The vascular ratios of the haustoria and xylary strands of *T. tsaii* are similar even with the different hosts, *Viscum* and *Camellia*. Compared to *Phoradendron* (Calvin, 1966; Dawson *et al*., 1990; Calvin *et al*., 1991), the small ratio of vascular tissue in the haustoria and xylary strands of *T. tsaii* indicates different mechanisms or efficiencies of absorption.

Haustorium types can be classified as an aerial parasite with or without a primary haustorium, with the epicotical roots bearing or not bearing secondary haustoria, and bark strands that spread within the host bark (Polhill and Wiens, 1998). Both cases of *T. tsaii* in the present report were recognized as being aerial parasites with epicotical roots bearing secondary haustoria and the primary haustorium having developed from the radicular pole of the holdfast of the embryo. The endophytic system was composed of shafts which grew anticlinally and centrifugally outwardly to penetrate the cambial zone. This is very different from most other aerial parasites. Comparisons of the endophytic types indicated that *T. tsaii* has evolved a high level of vascular association between the parasite and host; and this was also the case with the hyperparasitism (Fig. 7).

ACKNOWLEDGMENTS

I wish to express my sincere gratitude to Mr. Jien-Nan Chen for his enthusiastic help with collection and sectionings and also to the Lien-Hua-Chih Research Center of the Taiwan Forest Research Institute for providing lodging and hospitality during the field work.

REFERENCES

Calvin, C.L. 1966. Anatomy of mistletoe (*Phoradendron flavescens*) seedlings grown in culture. Bot. Gaz. 127(4): 171-183.

Calvin, C.L. 1967a. The vascular tissues and development of sclerenchyma in the stem of the mistletoe, *Phoradendron flavescens*. Bot. Gaz. 128(1): 35-59.

Calvin, C.L. 1967b. Anatomy of the endophytic system of the mistletoe, *Phoradendron flavescens*. Bot. Gaz. 128(2): 117-137.

Calvin, C.L., F. G. Hawksworth and D. M. Knutson. 1984. Phloem in *Arceuthobium globoscum* (Viscaceae). Bot. Gaz. 145(4): 461-464.

Calvin, C.L., C.A. Wilson and G. Varughese. 1991. Growth of longitudinal strands of *Phoradendron juniperinum* (Viscaceae) in shoots of *Juniperus occienctalis*. Ann. Bot. 67: 153-161.

Chao, J.M. 1973. Genus *Hyphear* of Taiwan. Taiwania 18(2): 169-171.

Chao, J.M. 1976. Loranthaceae. Flora of Taiwan 2:237-253.

Chen, C.-C. and N.-Y. Chiu. 1982. Pharmacognostical researches of the Chinese crude drug produced in Taiwan (II) Pharmacognostical research on the Loranthaceae in Taiwan. China Med. Coll. Annu. Bull. 13: 153-210.

Chen, C.-C. and H.-C. Lo. 1992a. Investigations on host-species of woody parasites in Taiwan. Q. J. Exp. For. Natl. Taiwan Univ. 6(2): 109-128.

Chen, C.-C. and H.-C. Lo. 1992b. Distribution of woody parasites of Loranthaceae in Taiwan. Q. J. Exp. For. Natl. Taiwan Univ. 6(4):109-130.

Chen, K.-L. 1987. Taxonomic studies of Loranthaceae in Taiwan. M.S. thesis. National Chung-Hsing Univ., Taichung, Taiwan.

Chiu, S.-T. 1996a. Notes on the genus *Taxillus* Van Tieghem (Loranthaceae) in Taiwan. Taiwania 41(2): 154-167.

Chiu, S.-T. 1996b. Loranthaceae. *In* Editorial Committee (ed.), Flora of Taiwan, Volume II, second edition, Department of Botany, National Taiwan Univ., Taipei, Taiwan. p. 269-286, 792-793.

Cohen, L.I. 1954. The anatomy of the endophytic system of the dwarf mistletoe, *Arceuthobium campylopodum*. Amer. J. Bot. 41: 840-846.

Danser, B.H. 1939. A revision of the genus *Phacellaria* (Santalaceae). Blumea 3:212-235.

Dawson, T.E., E.J. King and J.R. Ehleringer. 1990. Age structure of *Phoradendron juniperinum* (Viscaceae), a xylem-tapping mistletoe inferences from a non-destructive morphological index of age. Amer. J. Bot. 77: 573-583.

Fineran, B.A., and P. J. Hocking. 1983. Features of parasitism, morphology and haustorial anatomy in Loranthaceous root parasites. *In* M. Calder and P. Bernhardt (eds.). The biology of mistletoes. Academic Press, North Ryde, Australia. pp. 205-227.

Hawksworth, F.G. and D. Wiens. 1966. Observations on witches'-broom formation, autoparasitism, and new hosts in *Phoradendron*. Madroño 18: 218-224.

Hsiao, S.-C., J.D. Mauseth and L.D. Gómez. 1994. Growth and anatomy of the vegetative body of the parasitic angiosperm *Helosis cayennensis* (Balanophoraceae). Bull. Torr. Bot. Club 121: 24-39.

Hsiao, S.-C., J.D. Mauseth and C.-I. Peng. 1995. Composite bundles, the host/parasite interface in the Holoparasitic angiosperms *Langsdorffia* and *Balanophora* (Balanophoraceae). Amer. J. Bot. 82: 81-91.

Johansen, D.A. 1940. Plant microtechnique. McGraw-Hill, New York.

Kuijt, J. 1961. A revision of *Dendrophthora* (Loranthaceae). Wentia 6: 1-145.

Kuijt, J. 1967. The genus *Ixocactus* (Loranthaceae, *s.s.*): description of its first species. Brittonia 19: 61-66.

Kuijt, J. 1969. The biology of parasitic flowering plants. Univ. of California Press, Berkeley, California. 246pp.

Lichter, J.M. and A.M. Berry. 1991. Establishment of the mistletoe *Phoradendron macrophyllum* : phenology of early stages and host compatibility studies. Bot. Gaz. 152(4): 468-475.

Lin, J.-K. and C.-S. Kuoh. 1983. Anatomy of the mistletoe (*Scurrula ritozanensis*). Chia-Nan Annu. Bull. 9: 27-34.

Liu, Y.-C., F.-Y. Lu, C.-H. Ou and K.-L. Chen. 1988. Taxonomic studies of Loranthaceae in Taiwan. Q. Jour. Chinese For. 21(2): 3-24.

Polhill, R. and D. Wiens. 1998. Mistletoes of Africa. The Royal Botanic Gardens, Kew, UK. pp. 370.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology 70(1): 137-145.

Sands, W.N. 1924. Mistletoes attacking cultivated trees in Malaya. Malay. Agr. Jour. 12: 64-76.

Weeraratna, W.G. 1960. The ecology and biology of parasitism of the Loranthaceae of Ceylon. *In* J.L. Harper (ed.). The biology of weeds, Brit. Ecol. Soc. Symp. 1: 189-202.

Wiens, D. 1964. Revision of the acataphyllous species of *Phoradendron*. Brittonia 16:11-54.

Yang, Y.-P., S.-Y. Lu and S.-Z. Yang. 1997. Notes on some species of vascular plants of Taiwan. Taiwania 42(2): 86-90

蓮華池寄生的重寄生現象

邱少婷

國立自然科學博物館植物學組

桑寄生科（Loranthaceae）的蓮華池寄生（*Taxillus tsaii* S. T. Chiu）至今並無重寄生（hyperparasitism）記錄，臺灣學者僅有兩次目擊發現杜鵑寄生（*Taxillus rhododendricolus* (Hayata) Dancer）寄生於松寄生（*Taxillus matsudai* (Hayata) Danser） 和臺灣槲寄生（*Viscum alniformosanae* Hayata）。本研究主要於南投縣魚池鄉蓮華池研究中心發現蓮華池寄生寄生於柿寄生（*Viscum angulatum* Heyne.）和大葉榿寄生（*Loranthus delavayi* Van Tieghem）的重寄生現象，標本存於國立自然科學博物館植物標本館（TNM)，館號：S14101，採集號：邱2233。在此重寄生現象中，蓮華池寄生的寄生系統深入柿寄生的皮層、韌皮部、形成層及木質部，主要以木質部爲侵入範圍。吸器侵入寄主枝條的木質部中，其衍生的木質束（xylary strands）平周延伸，其分支則向外擴伸；與其他桑寄生類（如*Phoradendron*、*Arceuthobium*）不同，其他寄生的主要侵入在皮層和韌皮部，衍生之下沈器（sinkers）再深入形成層和木質部。組織交接部的寄主細胞先增生現象、細胞壁薄、細胞質濃，後瓦解或產生填充細胞。此在寄主內的內生系統（endophytic system）主要是木質部系統外環圍著含大量澱粉粒的薄壁細胞組成，侵入的木質束分支亦有小單位的木質部和薄壁細胞構成，推測此系統以增強水分之掠奪爲主。根據啄花鳥類的食性、排便行爲及桑寄生類的物候性（phenology）、種子萌發率，推測此重寄生現象只是偶發事件，蓮華池寄生主要仍爲初級寄生植物，但蓮華池寄生吸器若能侵入寄主，其延伸能力很強，故其重寄生現象發生仍然是可能性極高的。

關鍵詞：木本寄生植物，重寄生，桑寄生，桑寄生科，鈍果寄生屬。