Comparative Morphological Studies On The Hop (Humulus Lupulus L.) And The Japanese Hop (H. Japonicus Sieb. ET ZUCC.). I

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COMPARATIVE MORPHOLOGICAL STUDIES ON THE HOP (*HUMULUS LUPULUS* L.) AND THE JAPANESE HOP (*H. JAPONICUS* SIEB. ET ZUCC.). I

KAORU EHARA

I. INTRODUCTION

The cultivation of the hop, a species of *Humulus* L., is recent in Japan. The governmental Sapporo Hop Garden was established in April 1877 and the test growing of the hop was started with German and American hop strains. In Japan, the cured hop for brewing had been imported from Germany in the old days and from America in rather recent days, therefore Japanese hop culture was very inactive. However, due to the China Incident and the Second World War, the import of the hop was stopped. Consequently, the Japanese brewers had to depend on the hop cultivated in Japan, and the hop cultivation was increased in Hokkaido, Nagano, Fukushima and Yamagata Prefectures.

As large scale hop culivation was new in Japan, there was hardly any research work on it and necessary informations were not available. Thus, the hop culture had to face a big obstacle, and in 1938, the Ministry of Agriculture established a hop research laboratory designated by the Ministry in Nagano Prefectural Agricultural Experiment Station. The author was appointed the first chief agronomist of the Laboratory, and started research on breeding, culture and curing of the hop. However, due to insufficiency of basic information on the plant, the author has experienced great difficulty. Thus, the author has studied the morphology of the hop for the purpose of establishing the basis

for hop research and published the morphological illustration of the hop in 1943.

Research on the hop is scarce not only in Japan, but also in other countries. However, there are some noteworthy investigation in Germany, America, England and U.S.S.R.

There was no report on the morphological study of the hop in the past, and only short morphological descriptions of the hop are found in books on hop culture by Fruwirth (4), Gross (5) and Myrick (14).

The author has always been interested in the morphology of hop, and has studied the comparative morphology of the hop and the Japanese hop, both of which belong to *Humulus*, so as to complete the foundation of "The Morphological Illustration of the Hop." The author has almost accomplished the work and wish to report the results. Comparative morphology of a crop within its genus is very important, but there has not been any studies of the kind on the *Humulus*.

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II. On The Genus *Humulus*

The genus *Humulus* has two species, namely *Humulus lupulus* L. (the hop, the common hop) and *H. japonicus* Sieb. et Zucc. (the Japanese hop, Japanese name: Kanamugura or Rittsuso). The hop is cultivated mainly for use in brewing beer and the Japanese hop morphologically resembles it. The Japanese hop is indigenous to forest and bushes in Japan, China and in the adjacent area, and is occasionally grown as an ornamental plant, but appart from this, it has no economic value.

The wild hop grows in the rather cold temperate zone in

Europe and Asia and it is perhaps identical with the cultivated. The Japanese name for the wild hop is Karahanaso. The scientific name of the wild hop is *Humulus lupulus* L. var. *cordifolius* Maxim., and it is universally regarded as the ancestral stock for the cultivated variety. This plant generally has heart-shaped leaves and has less lupulin, which is the most important component of the hop, and feebler aroma, but excepting these points the wild type is morphologically identical with the cultivated one.

Salmon (18) regarded the American hop as a different species from *Humulus lupulus* because of its botanical characteristics, such as leaves and aroma, and named the American hop *Humulus americanus* but his opinion is not universally supported.

In this study the author has divided *Humulus* into two species: *H. lupulus* L. and *H. japonicus* Sieb. et Zucc., and all varieties in *Humulus* are included in these two.

III. Material and Methods

1. *Material*

The hop is a perennial and in Japan, according to the author's experiments, the plant under normal conditions, attains the nearly constant bearing power in three or four years after planting. Thus, farms with one to four years old plants were selected for sampling. Hops used in this study were grown on the Nagano Hop Research Laboratory designated by the Ministry of Agriculture, and the variety used was mostly "Shinshuwase" which was the commonest variety in Japan.

This study was mainly carried on at the Nagano Hop Research Laboratory, and since the author was transferred to the Kyushu University the work was continued at the University. In the latter case, hop cuttings were sent from the Nagano Hop Research Laboratory of Dainippon Brewing Co. Ltd.

The author has made utmost efforts to collect various varieties of the hop. Locating hop researchers throughout the world by means of various publications, the author tried to get as many varieties of hop as possible from them through the mail. However, due to the international situation at the time it was very difficult to obtain foreign varieties for the most part. It was impossible to get any European varieties directly, because the

Table 1. The list of the hop varieties that were used in this study.

Variety or strain	Growing district	Variety or strain	Growing district
Shinshuwase	Nagano Prefecture, Japan	Nagano No. 16, ♂	Saitama Prefecture, Japan
Sapporo No. 5	Hokkaido, Japan	Nagano No. 56, ♂	Osaka Prefecture, Japan
do	Korea	Cat's tails	U. S. A.
Sapporo No. 6	Hokkaido, Japan	Canadian	Hokkaido, Japan
do	Korea	Auscher Rote	U. S. A.
Saaz	do	Riverside seedling	do
do	Hokkaido, Japan	Kaitakushi	Hokkaido, Japan
do	Manchuria	Humphrey	U. S. A.
Hallertau	do	Spalt	Hokkaido, Japan
do	Korea	do	U. S. A.
do	Hokkaido, Japan	Spalter (Simon)	do
New Hallertau	Yamanashi Prefecture, Japan	Spalter	U. S. A. (from Germany)
America No. 2	Korea	Samling	U. S. A. (from France)
America	Nagano Prefecture, Japan	Nagano No. 80	U. S. A.
Nagona No. 17	Saitama Prefecture, Japan	Nagano No. 81	do
Nagano No. 18	do	Late Cluster	do
Fuggles	U. S. A.	California Cluster	do
Early Zug	Hokkaido, Japan	Burgunder (Simon)	do
Sonoma	do	Early Green Dauba (Zecoslovakia)	do
English Cluster	do	Nagano No. 99, ♂	Nagano Prefecture, Japan
do	U. S. A.	Nagano No. 100, ♂ (Saaz)	Hokkaido, Japan
Nagano No. 79	do	Nagano No. 103, ♂ (B. C. Golding)	U. S. A.
Nagano No. 82	do	Nagano No. 104, ♂ (Fuggles)	do
Red Vine	do	Nagano No. 105, ♂ (B. C. Kent Golding)	do
Golding	do	Nagano No. 106, ♂	do
Nagano No. 76, ♂ (Early Cluster)	do		
Nagano No. 84, ♂ (Fuggles)	Miyagi Prefecture, Japan		

export of the hop cutting was prohibited by law in these countries, especially in Germany.

Mr. E. R. Fore of Oregon Agricultural Experiment Station, U. S. A. sent me not only American varieties but all European varieties that he had on his farm. The Brewing Companies in Korea and Manchuria also gave the author many varieties of the hop.

The varieties of the hop that the author has collected are listed in Table 1.

The variety name of the hop is as a rule given to female plant. The variety name in parenthese of the male plant in table 1 is considered the name of the main female variety among which the male plants are found, because unlike Japan and Germany, a few male plants are generally grown among many female plants in American and British hop gardens. However, it seems improper to give female variety name to male plants.

The seedlings of the Japanese hop were collected by Mr. Hideo Kuriyama, former assistant of Kyushu University, on Mar. 25, 1947 in Ishisaka Cho, Onga Gun, Fukuoka Prefecture, Japan, and were transplanted into the pots at the Faculty of Agriculture, Kyushu University. Indigenous Japanese hop plants found at the university campus also were used for this study.

2. *Growing of materials*

The synopsis of growing methods of the materials used in this study is as follows:

a. The hop (wire trellis system)

Distance between rows.....1.8 m.
Distance between stocks in the rows.....1.8 m.
Time of planting.....Early April
Time of cutting .....Middle of April
Manures and fertilizers used were as follows: compost, potassium chloride, superphosphate, ammonium sulphate and limestome.
Cultivation and hand hoeing.....Middle and latter part of May and middle of June.

Tying up of the vines.....Two vines per plant were tied up in middle of May.

Controls of diseases and pests.....Bordeaux mixture and a mixture of lime and sulpher were sprayed for the control of the hop downy mildew, red spider etc.

The hop cuttings sent from U. S. A. were much weakened by long trip and as they arrived in winter the cuttings were wintered at the greenhouse of Konosu Division, Agricultural Experint Station, Ministry of Agriculture, and were transplanted to the Nagano Hop Research Laboratory in the following spring.

b. The Japanese hop

On March 25th, the seedlings of the Japanese hop were transplanted into unglazed pots (diameter 22 cm., height 21 cm.) of the Faculty of Agriculture, Kyushu University. The Japanese hop plant was grown in the greenhouse till the plant reached a height of 1.5–2.0 meters, then the pot was moved into the net house, and were left to climb the net. The indigenous Japanese hop found on the campus were left to grow in the natural state.

3. *Methods*

The external morphology of all the organs such as leaf, stem and female inflorescence were investigated with the green materials, and as occasion demanded the anatomic and histological studies, observations and sketches of the organs were carried out. When cutting sections were needed for cytological, anatomical and histological observations of organs and cells, free hand or microtome were used.

a. Free hand cutting sections: Green materials were soaked in elder pith before sectioning and were cut with a sharp razor blade. Then the object was mounted in a drop of water or reagent under a coverglass and was observed through a microscope. Cells containing special substance such as tannin were treated with corresponding chemicals and examined. Detailed examinations on these special treatments will be given as they come up.

b. Paraffin method: The materials were cut with a sharp razor blade and immediately immersed in Carnoy's fluid for 15 minutes to 2 hours and fixed. The formula for this is:

Absolute alcohol.....6 parts,

Chloroform .....3 parts,
Glacial acetic acid .....1 part.

After the above process the usual paraffin method was used in most cases. Chloroform was used as the infiltration medium. Sections were cut from 8 to 12 microns thick with a microtome and stained with Haidenhain's iron-alum haematoxylin. The fixed materials requiring a long period preservation were kept in 75 per cent alcohol. The results of the microscopic and naked eye observations were described and illustrated.

IV. Results and Discussion

The results obtained in this study were put together according to the organs and described with illustrations. The priority in description was given to the comparative morphology and anatomy of the hop and Japanese hop. In the past there was somewhat detailed description of the hop strobile. However, there has hardly been any research made on the vegetative organ. Thus, the author tried to fill up this gap in this study.

1. *The seedling*

Originally, the hop does not depend on seeds for propagation. However, to obtain better varieties, crossing must be undertaken. In case of the Japanese hop, it solely depends on seeds for propagation. Therefore, the comparison of the two will be started from this standpoint.

Except a brief description on the primary root of hop seedling by Percival (17) there has not been any study on the hop seedling. The author does not know of any comparative morphological study made between hop and Japanese hop. In this investigation, special attention was paid to the observations of the cotyledon and hypocotyl of the two plant seedlings.

As shown in Plate 1-1, the cotyledons of the hop seedling are long and slender, and the hypocotyls are long and are often light purple. The seedlings of the Japanese hop are as a whole much larger than those of the hop as illustrated in Plate 1-2A and 2B. This probably is because of the difference in fruit size of the two plants as will be mentioned later. Proportionally the cotyledon of the Japanese hop is much longer as compared to the hop. There-

fore, the appearence of the Japanese hop cotyledons is much leaner than that of the hop. According to the author's measurements, the cotyledons of the hop are from 1.5 to 2.0 cm. long and from 0.3 to 0.4 cm. wide, while those of the Japanese hop are respectively from 4.0 to 5.0 cm. and from 0.4 to 0.5 cm. The cotyledons of the Japanese hop are thicker and longer those of the hop.

The hypocotyles of the Japanese hop are long and dark purple, and give a more delicate impression than those of the hop. The hypocotyles of the hop grow from 2.0 to 4.0 cm. long, and those of the Japanese hop from 4.0 to 5.0 cm. and they both stop growing while the cotyledons continue to grow. The veins of the cotyledon with the exception of the mid-rib are indistinct. A pair of the first foliage leaves emerge while the cotyledon is elongating (Plate 1–2B). At this time the first foliage blades begin to split in about 3 lobes as shown in Plate 1–3B. The primary root of the Japanese hop develops more rapidly and bigger than the hop.

2. *The rootstock*

Fruwirth (4), Gross (5) and Myrick (4) illustrated the rootstocks of the hop, but the illustrations are simple and not detailed, so the author observed comparatively the rootstocks of the hop and the Japanese hop plants. In the hop plant, it is difficult to distinguish by outward appearance the border of the stem and the root. Beside, the so-called rootstock, the general term for the stem base and the root, is important for agricultural practices, so observations were made on that part. Under the Japanese climatical conditions, one of the essential differences between the hop and Japanese hop is the life period of the plants. The former is a perennial herbaceous plant while the latter is an annual herbaceous plant. In late autumn, as soon as vegetation is arrested, the aerial portions of the hop plant die down; and in the ensuing spring new shoots are thrown out from the buds on the underground stems that have stood the winter, or else adventitious shoots appear. The hop is particularly long lived, if it has once gained a footing in the soil, it is practically not necessary to replant with new cuttings in the course of about 20 years.

According to the author's survey in Nagano Prefecture, the hop plant kept its full productivity for 22 years after planting under the most favorable conditions. In Europe, the time, the

plant is used economically, is considered to be about 12 years (24), but in Japan in the absence of reliable data nothing definite can be stated as to the time. The author believes that if the hop farm is well managed and is free from the hop canker, *Bacterium tumefaciens* Smith et Towns., the hop plant perhaps remains in full bearing for about 20 years. According to the author's experiences, the high ground-water level in soil shortens the longevity of a hop stock as a rule.

In late autumn, the aerial portions of the hop plant die down, while the underground portions survive and somewhat thicken every year. The tap root of the hop plant penetrates downwards as much as 2 to 4 m. and attains a diameter of 4 to 8 cm. These numerals approximately agree with those of Kraft and Fruwirth (11) and Zade (24). The thick roots are covered with reddish brown bark. Because of the deep roots, the hop plant is able to resist the serious drought in summer such as makes cracks in the upper layer of soil. In spite of the deep penetration of the tap root into the soil the other roots and the under ground runners extend near and parallel to the surface.

As shown in Plate 1–4, the underground portions of the hop plant consist of the base of stem, the underground runner and the root. Plate 1–4 shows the development of the underground runner. The base of stem and the underground runner have many buds, and if the rootstock is not managed well, the underground runners will become too abundant in the soil for tillage if left alone. The rootstock must be cut every year for the above mentioned reason. The cutting of the hop stock is to remove the superfluous stems, underground runners or eyes, and to restrict the number of sprouts per stock in spring.

The cutting is one of the most important works in the hop cultivation and the task demands great skill as pruning fruit cultivation.

The old thick basal stem covered with the reddish brown bark has many buds as shown in Plate 1–4, and this has an important meaning in the hop cultivation.

The Japanese hop is an annual herbaceous plant and does not have a rootstock, but as shown in Plate 1–5 the root development is remarkable and the tap root penetrates deeply into the ground. The tap root of the Japanese hop is from 150 to 200 cm. long and

the diameter ranges from 7.0 to 15.0 mm. at the thickest point. The tap root sends forth several branch roots and numerous fibrous roots on all sides. The Japanese hop does not have any eye in the part of the stem that remains in the ground, therefore, unlike the hop, it does not have any underground runner.

3. *The cutting*

Gross (5) and Myrick (14) made simple descriptions of the morphology of the hop cutting. The author compared the morphology of the cutting from the basal part of stem with that from the underground runner, and named the former the stem cutting and the latter the runner cutting.

These cuttings are obtained when hop stocks are cut. In general the cuttings with 2 or 3 nodes are recommended for planting and the eyes are found on the opposite sides of the joint, and a joint can throw out from three to a dozen buds. According to the author's measurement the internodes of the so-called stem cuttings are shorter and thicker than those of the so-called runner cutting. In Japan the good stem cuttings should be 5.5 to 10.0 cm. in length and 1.5 to 2.5 cm. thick, while the corresponding figures of the runner cuttings are to be respectively 6.5 to 12.0 cm. and 1.0 to 2.0 cm. But these figures differ very widely according to the hop varieties. On the other hand, the Japanese hop plant is grown from seeds and the plant is not obtained from cuttings.

4. *The sprout*

In the past the morphological study of the hop sprout has not been made and the comparable organ of the Japanese hop, namely the young shooting has not been studied morphologically. The author made a comparative morphological study of the above mentioned organ of both plants.

In spring the buds of the hop rootstock throw out many sprouts which appear above the surface of the ground as shown Plate 1-7, therefore in practice 2 or 3 sprouts should be selected among them. In the sprout stage, anthocyan is found abundantly specially on the stem. But the appearence of sprout in the ground closely resembles that of the etiolated asparagus (Plate 1-8), and in foreign countries the etiolated sprout of the hop is used as a

substitute for the asparagus. In this case the leaves of the hop do not elongated (Plate 1-8), but pairs of stipules grow on opposite sides of the nodes, and the tips of some stipules split into two pieces and the others do not. The stipules in the ground are pale yellowish brown.

The terminal bud of the hop sprout are closely enveloped with the stipules. When the elongation of the internodes begin the leaves come out from the place between two stipules. This growing point of the sprout is repeatedly protected mainly by the stipules as shown in Plate 6-1. The stipules develop at the early stage of the differentiation and envelop the primordium of the leaf. The axillary bud is seen in the leafaxil, but its development is much slower than the terminal bud.

The Japanese hop is grown from seeds, therefore does not have so-called sprout, but in this paper, the young shoot which morphologically closely resembles the sprout will be described. The internodes of the hop young shoot is more or less longer than that of the Japanese hop and the leaves of the former is less developed than those of the latter (Plate 1-7, Plate 2-1, 2). The stipules and leaves of the Japanese hop are opposit like those of the hop, but the axillary buds develope in the leafaxil as early as the sprout stage and this is a point in which Japanese hop differs from the hop.

In addition, with the progress of the growth, the internodes of the Japanese hop begin to elongate, and the appearance of the plant in this stage resembles the hop. However, in this case, the leaf development of the Japanese hop is more rapid than that of the hop.

The young shoot of the Japanese hop contains little anthocyan, but with the progress of growth the stems become dark reddish-purple and the leaves become pale purple. At this growth stage, the first to second internode attains a diameter of about 3.0 to 5.0 mm. in the hop plant, while that in the Japanese hop is 2.3 to 2.8 mm.

5. *The stem, vine, bine*

In the past a morphological description of the stem was made by Fruwirth and Gross, but the description was imperfect and especially the morphological figures were next to none. The

Japanese hop stem has never been studied and a comparative morphological study on both plant stems has not been carried out. The author was interested in this investigation and has obtained the following results.

As is well known, the hop and the Japanese hop are climbing plants and without any support they are incapable of supporting their own weight, therefore the stems of these plants are called vines or bines. The Japanese hop and the wild hop cling to trees and the other natural supports in natural condition (Plate 2-4). The poles and high vertical-string frame are used for the training of the cutivated hop. As a rule, the poles are 5 to 8 meters long, and the frames are about 6 m. high in Japan. The hop stem always winds clockwise. The hop bine has two motions: the first motion is a twist of the stem from right to left, the second is a spiral or revolving motion, which winds the vine around its support. This climbing is aided by rough-hooked hair on stems, petioles and leaves. The author has observed varietal difference in the climbing of the hop and some varieties cling very loosely so that the stem sometimes fall from the support string to the ground. The Japanese hop also winds clockwise. According to the author's observation the stems of the full grown Japanese hop plant has generally darker shade of reddish-purple than the hop.

The number of nodes of the main stem of the hop varies according to the varieties, and the main stem of the two year old plants of the variety "Shinshuwase" have 30 to 40 nodes, while those of the other varieties have 30 to 45 nodes. The main bine of Japanese hop has 30 to 40 nodes, which is quite numerous for an annual plant.

The distance between the two nodes of the hop main stem varies according to the location of the nodes. In the 2 year old plant of "Shinshuwase" an average length between the nodes at the tenth to fifteenth nodes from the bottom is 19.0 to 22.1 cm., while it is 12.5 to 28.0 cm. in the other varieties. The distance between the nodes among some of the 4 year old Shinshuwase, was as long as 28.0 to 40.0 cm. According to the author's observation, the distance between the nodes depends on the environment, especially on climate. For instance, the distance between the nodes of the Shinshuwase was 27.0 to 32.3 cm. long at Nagano Prefectural Experiment Station (about 380 meters above sea-level)

but it was 39.0 to 44.3 cm. at Togakushi Experiment Station (about 1,000 meters above sea-level). The distance between the nodes of the hop stem in the high and cold places is much longer than that in the low and mild places.

In the Japanese hop main stem, an average distance between the nodes at tenth to fifteenth nodes is about 20.0 to 30.0 cm.

As already stated, every spring new shoots come forth the buds on the underground stems and the aerial portions of the plant dies down in fall. The underground stems that will live through winter are thickend and have the reserves of another year's growth.

According to the author's measurement, the main stem of one year old plant reaches a height of 4.0 to 7.0 meters. The hop plant over three years old attains a height of 8.0 to 12.0 m., and these figures agree with Kraft and Fruwirth's and Percival's results. As already mentioned, it was found that the growth is more rapid and that the plant grows taller on a high and cold place than on low and mild place. In the Japanese hop, the creeping stem on the ground in a wild condition attains a length of 2.5 to 5.0 m., while the creeping stem in a cultivated condition with a support, it becomes 5.0 to 6.0 meters long and the growth is very rapid for an annual plant.

In cross section, the stem of both plants are hexagonal (Plate 2–3, 6 and 7), and externally, the bines carry six spirally arranged sets of climbing hairs as shown in Plate 2–3. As already mentioned, the stems of the plants wind to the supports with the progress of growth and at the same time twist themseves, but this motion is more marked in the hop than in the Japanese hop. The young bines of the hop and the Japanese hop are solid, but as they grow the stems become hollow except at the nodes (Plate 2–3). Hitherto, the histological studies on the stem of the hop and the Japanese hop were not undertaken, and the author has histologically investigated the transverse sections on the stems of both plants. Especially the author was interested in the development of pericyclic-fibre from a standpoint of crop science.

As shown in Plate 2–6 and 7, the transverse sections of the stem of the Japanese hop and the hop are morphologically similar. In transverse section, the mature stem shows the following structures:

There is one cell layer beneath the epidermis, sometimes these cells contain anthocyan. The chlorenchyma, which consists of one to three layers of cells containing chlorophyll, develops inside the layer of cells which contain anthocyan. The development of collenchyma on the angles of the hexagon is distinguishing and one to three layers of parenchymatous cells are observed in parts other than these angles.

Inside the above mentioned structures, there is the endodermis and inside it the pericyclic fibre which consists of two to four layers of cells are seen. The development of the pericyclic cells is very remarkable in both the hop and the Japanese hop. According to the author's measurement, the length of each fibre cell is from 5.10 to 7.00 millimeters and its diameter from 6 to 9μ in the hop, while these of the Japanese hop are 6.55 to 11.30 mm. and from 6 to 9μ. Thus, the fibre of the Japanese hop is somewhat longer than that of the hop. The above fact may suggest the possibility of utilizing the fibers of both plants for textile industry.

Inside the pericyclic fibre, the phloem, the cambium, then lignified xylem are found. Phloroglucin in a 5 per cent aqueous or alcoholic solution applied with hydrochloric acid give lignified walls a reddishviolet color. Plate 2-6 shows only the primary xylem of the young hop bine, but in the older stem of the Japanese hop the secondary xylem are seen outside the primary xylem as shown in Plate 2-7.

The laterals sprout out from the axils of the leaves, and from the nodes of these laterals come out brachlets carrying flowers. It is important to increase and elongate the laterals for hop growers. The length of the hop lateral varies according to varieties. The laterals of the three year old hop plants (Shinshuwase) are from 3.0 to 5.0 meters, but those of Fuggles and Early-Zug are only about 1.0 m.

The laterals of the Japanese hop sprout out from nodes which are much lower than those of the hop, but in natural conditions the lower laterals of the Japanese hop die. The laterals of the Japanese hop are from 1.0 to 3.0 meters. The lowest nodes from which laterals sprout in the hop varies with age. In one year old plant, the lowest node is from 8th to 15th node and in 3 year old plant it is 5th to 12th node.

6. *The leaf*

Morphological description of the hop leaf was made by Fruwirth, Gross and Myrick, but they were far from complete as in case of the stem. The author made a histological study of the hop and the Japanese hop leaves and their structures were compared:

The leaves of both plants are opposite, and start from the nodes. The stipules are broad, and in opposite leaves, the adjacent stipules unite to form a single broadly-triangular lobe. The leaves have long petioles as shown in Plate 3-1, 2, 3 and 4 the petioles are approximately one-third to one-half of the blade length in the hop plant, while those of the Japanese hop are from half to three-second of the blade. The petiole of the latter is somewhat longer than that of the former. The size of the blade and the petiole vary according to the location of the node from which the petioles grow. We found that the length at the longest point of the blade is from 8.0 to 20.0 cm. in the three year old plants of the Shinshu-wase, while that of the Japanese hop is from 6.2 to 12.5 cm. Although there is no uniformity in the shape of hop leaves, but foundamentally it is palmate. Among the leaves that grow on top part of the stem, especially on the laterals, and on the young seedlings the cordate shape ones also are found (Plate 3-1B). According to the author's observation, the wild hop and the variety "Saaz" mostly have heart shaped leaves. On the other hand the variety "Shinshuwase" mostly three- to five-lobed leaves as shown in Plate 3-1A, 2A and 2B, and seven-lobed leaves in exceptional case. It was observed that the leaves of the American hop varieties particularly had more lobes.

The first foliage leaves of the Japanese hop (rarely up to the third leaves) are three-lobed though occasionally four lobed. From the second to fourth leaf on, they are five lobed and the ones on the extreme top are mostly seven-lobed (Plate 3-3 and 4). As shown in the Plate 2-9, the edge of the leaf is coasely serrated. Close observation reveals that the edge has needle like projections, and this projection is generally sharper in the Japanese hop than in the hop.

As a rule, the leaves of the Japanese hop are somewhat purple in young growth stage, but this color is not seen in the hop leaves.

Ut to the present time no anatomical study on the cross section of the leaves has been reported, so the author found it necessary to study the structures of the leaves and report the result (Plate 4–3 and 4). The leaf structure of the hop is similar to that of the Japanese hop. The cells of the upper epidermis are slightly larger than those of the lower epidermis and are much more heavily cutinized. Epidermal hair and glands are found on both surfaces of the leaves to which the author will pay more particular attention later. The mesophyll cells except the cells adjacent to the veins, consists of a single layer of slender, elongated palisade cells which occupy slightly more than half the thickness of the leaf. The spongy parenchyma is very loosely organized, and large intercellular spaces leading to the substomatal cavities are found there. The histological descriptions on the transverse sections of the veins and the petioles will be made in the succeeding sections.

7. *The vein*

The results of the anatomical investigations on the leaf veins of the hop and the Japanese hop are as follows;

The morphology of the vein of hop leaf resembles that of the Japanese hop: in each leaflet, the midvein extends throughout its entire length, and lateral veins branch off. These rebranch to form a net-veined system in which the ultimate veinlets end in the mesophyll (Plate 3–1, 2, 3, and 4). As shown in Plate 4–3 and 4, the transverse sections of the veins of the hop and the Japanese hop are heart-shaped. The midvein of the leaflet is reinforced by the strongly developed collenchyma which is located below the upper epidermis. There is also a zone of mechanical tissues two to five cells in width immediately inside the lower epidermis. Next to the collenchyma are the several layers of large parenchymatous cells, and the phloem and the somewhat lignified xylem were surrounded by the parenchyma. Various hairs and glands, to which I will refer to later, also are occasionally found on the vein.

8. *The petiole*

The petioles of the hop and the Japanese hop are mostly pale reddish-purple. The transverse section of the petiole is sub-

triangular having a groove extending along its adaxial surface, as shown in Plate 4-5 and 6. Except at the adaxial epidermis, a layer of about one cell which sometimes contains anthocyan is located below the epidermis. The one- to two-layered chlorenchyma is arranged within the anthocyan containing cell layer. The chlorenchyma is almost completely surrounded by the two- to three-layered collenchyma, the development of which is heavier in the adaxial portion than in the other portions. Inside the collenchyma is filled with the pith which consists of large parenchymatous cells. Pith is dotted with the vascular bundles which develop the phloem to the outside and the xylem to the inside. The degree of lignification of the xylem is not pronounced in either the Japanese hop or the hop. Various hairs and glands are produced on the surface of the petiole. These will be described in the succeeding section.

9. *The hairs and the glands on the stem and the leaf*

a. Climbing hair

As already mentioned, the stem carries six spirally arranged sets of double- and single-hooked hairs externally, and they prevent the bine from slipping off the support, thus helping the bine to climb the support. The length of the two armed grappling-hair found on fully developed stem of the hop are from 0.240 to 0.510 mm. (Plate 3-5A). The double-hooked climbing hair of the young bine is shorter than that of the older stem and the hooks of the hair incline lengthwise, and the one pointing upward almost touches the surface of the stem, and the one pointing downward bends upward as shown in Plate 3-5B. The average length of the hook is from 0.222 to 0.450 mm. and this shorter type of the double-hooked hair changes into the longer type later, but some remains in that state.

It was imaginable that the Japanese hop also had the climbing hairs on the stem, and the following results were obtained from the author's investigation: In the Japanese hop, the double-hooked climbing hair is always the shorter type which is found on the young stem of the hop. The average length of the hook is longer than that of the hop and ranges from 0.390 to 0.600 mm.

consequently, together with the additional hairy covering it imparts a rougher feeling than the Japanese hop plant.

In the hop and the Japanese hop, the petiole and the base of the midvine carry numerous double-hooked climbing hair. In the petiole of the hop, the shorter type of the two-armed grappling-hairs are more numerous. The way the hook of the Japanese hop is inclined quite resembles that of the hop. As already well-known, the hop plant has short conic hairs and the Japanese hop plant also are found to have short conic hairs. According to the author the length of these hairs are from 0.06 to 0.120 mm., and the direction in which they point is irregular, but the conic hairs pointing downward assist the ascent of the bine. These hairs of the Japanese hop are larger and more numerous than those of the hop. In the hop, the somewhat longer conic hair ranging from 0.240 to 0.300 mm. are few, but they are more numerous in the Japanese hop (Plate 3-6C). Besides, since the Japanese hop has more short hairs than long ones, the Japanese hop seems more fit for climbing. As shown in Plate 3-6B, the Japanese hop carries fish-hooked hairs. The length of these hairs from their base to the bent portion are from 0.060 to 0.062 mm. As a rule, these hooks point downward, and assist the ascent of the bine, but some of them do not point downward. The fish-hooked hairs are more numerous on the petiole and the vine than on the stem.

b. Conic hair

The description on the conic climbing hair was made in the preceeding section, so in this section, the description on the other kind of conic hair will be made. Gross and Myrick made brief mention of the conic hair of the hop, but there has not been any report on the conic hair of the Japanese hop. Therefore, the author has made a comparative study of the conic hair of the hop and the Japanese hop.

There are various types in the conic hair, as shown in Plate 5-1. The longest hair of the hop is about 0.573 mm. and that of Japanese hop about 0.500 mm. Those hairs of both plants occur only on the leaf-vine and the base of the hairs is made of many cells. The leaf-vine carries other kinds of hair which differ in length. The longer ones are from 0.300 to 0.400 mm., and the shorter ones are from 0.120 to 0.180 mm., and the intermediate

ones also are numerous. These conic hairs mostly bend toward the leaf tip and points in all directions and mostly consist of one cell. The Japanese hop also carries many conic hairs which are similar in length and in the way they grow. As shown in Plate 3–7, the vines and the upper- and lower-surfaces of the leaves carry typical conic hairs with very thick base. Their length is from 0.060 to 0.180 mm.

c. Clubbed gland

As is already well known, the hop plant carries a large number of the clubbed glands (Plate 3–8). The glandular hairs have multicellular structure, and are formed by repeated subdivision of the mother cells. Each one of the mother cells is separated, at an early stage, into a crown cell and base cell by a partition wall. In the clubbed glands the crown cell subdivides in a direction parallel or tangential to the axis of the head, and developes a small tissue. The basal cell formed by the primary subdivision of the mother cell is, in many clubbed glands, converted by repeated longitudinal and transverse subdivisions into a longer or shorter multicellular stem.

According to the author's investigation, the Japanese hop also has many of these clubbed glands, and the length of them is about 0.036 mm., and the diameter at the head is somewhat shorter than the height in both plants. The clubbed glands occur on the young stem, the petiole and the leaf vine in both the Japanese hop and the hop. However, these glands are specially numerous on the petiole and the vine of the Japanese hop.

d. Disc gland

Some simple descriptions on the disc gland of the hop were made by Fruwirth, Gross and Myrick, but the author tried a more detailed study and completed Plate 5–2, 3 and 4. On the disc gland of the Japanese hop there has not been any report made.

As shown in Plate 5–2A, the pale yellowish small grains are scattered on the lower surface of the hop leaf. The microscopic examination of them reveals the multicellular structure of the disc glands. Some of the cells are disc-shaped (Plate 5–2B and 2C). According to the author's observation, the Japanese hop carries many disc glands, as shown in Plate 5–3 and 4. The disc glands

are multicellar structure, and are formed by repeated subdivision of the mother cells. Each one of the mother cells is separated at an early stage into a crown cell and base cell by a partition wall. The stems of the disc glands are short, and mostly consist of the original basal cell which is divided into two daughter cells. The crown cell undergoes repeated subdivision, and shapes a disc; and a secretion is deposited between the outer walls of the gland cells and the cuticle, thus raising the latter to some extent. The diameter of the glands of the hop is from 0.060 to 0.072 mm. in the young leaf, while that of the old leaf is from 0.108 to 0.120 mm. The disc glands of the Japanese hop are slightly shorter than that of the hop and the diameter is from 0.077 to 0.078 mm. As shown in the figures, the disc glands are mostly disc shaped, but the younger ones are pale yellowish and indented in the center. The somewhat older glands are yellowish and are slightly raised at the upper cuticle in the center.

In both plants, the disc glands are thick on the young leaf, and thin on the old leaf. As a whole, the disc glands of the Japanese hop are slightly paler yellow and the numbers of the cell are smaller than those of the hop. The disc glands are few on the stem and the petiole, but are abundant on the leaf vein in both plants. The upper surface of the leaf does not have any disc glands.

e. Cystolith

A brief mention of the cystolith of the hop was made by Gross, but there has not been any morphological report on the cystolith. The following results were obtained from the author's studies on the comparative morphology of the cystolith of the hop and the Japanese hop.

The hop and the Japanese hop develop on some of their cell-walls peculiar calcified thickenings which are termed cystolith. These bodies are restricted to the foliar epidermis, where the outer wall of certain epidermal cells—generally distinguished by their size—are provided with stalked spherical or ovoid processes covered with projections. These projections may be blunt or more or less pointed. The swollen part of the process may thus be compared to a mulberry suspended from the outer wall by its stalk. In the hop, this stalk is very short. The cystoliths are

strongly impregnated with calcium carbonate. The mineral substance is dissolved by hydrochloric acid and produces carbonic acid gas. The cystoliths of the hop range from 0.048 to 0.072 mm. in diameter (Plate 5–5A), and generally its projection is slightly bent. The cystoliths of the Japanese hop is slightly smaller than that of the hop and are from 0.036 to 0.046 mm. in diameter (Plate 5–5B and 5C). The morphology of the cystolith of the Japanese hop resembles that of the hop, while the projection of the former is sharper than that of the latter.

RÉSUMÉ

1. This paper gives the results of comparative morphological studies on the two species of *Humulus*, the common hop (*Humulus lupulus* L.) and the Japanese hop (*H. japonicus* Sieb. et Zucc.). There are only two species in the genus *Humulus*.

2. One of the essential differences between the hop and the Japanese hop is the life period of the plants; the former is a perennial, while the latter is an annual herbaceous plant.

3. The cotyledon of the Japanese hop are much longer than those of the hop, this fact is related to the fruit size of the two plants. The cotyledons of the hop are from 1.5 to 2.0 cm. long and from 0.3 to 0.4 cm. wide, while those of the Japanese hop are respectively of the 4.0 to 5.0 cm. and 0.4 to 0.5 cm. The hypocotyl of the Japanese hop is longer than that of the hop.

4. Many underground runners grow from the rootstock of the hop every year, but there is no underground stem in the Japanese hop.

5. In practise, the hop is raised solely from cuttings, but the propagation of the Japanese hop is performed from seeds exclusively. So-called "stem cuttings" obtained from basal stem of the hop are shorter and thicker than so-called "underground cuttings" and the internode of the former is shorter than that of the latter.

6. Both the hop and the Japanese hop are right-hand twiners, namely the free apex of the stem twin persistently clockwise.

7. The stem, the petiole and the basal portion of the vein of leaf in both plants have double and single hooked climbing hairs, and they prevent the stem from slipping off the support. The young stem and the petiole of the hop have many short double

hooked climbing hairs, but there are many tall ones on the old stem. The double hooked climbing hairs in the Japanese hop are numerous and short, but the hooks are longer than those of the hop, and impart a rough feeling to it.

8. The hop stem is very tall. The stem of the 3 year old hop plant attains a diameter of 0.8 to 1.3 cm., a height of 8.0 to 12.0 m., and 30 to 40 nodes, though there are big differences in these points according to the varieties. The Japanese hop is annual, but the stem attains a diameter of 0.3 to 0.5 cm., a height of 4.2 to 6.0 m. having 30 to 40 nodes.

9. Transections of the bines of the hop and the Japanese hop are hexagonal, and hollow, especially in somewhat older part of stem. The development of collenchyma on the edges of the hexagonal is distinguishing, and the climbing hairs grow from these edges. The pericyclic fibers develop very remarkably in both plants. Fibers of the Japanese hop are from 6.55 to 11.3 mm. long and are longer than the hop-fibers, which are 5.10 to 7.00 mm.

10. The leaves of both plants occur opposite at nodes. The shape of the leaf is generally palmate,—there are gradations, from cordate to seven lobed. The margin of leaf is serrated; according to the detailed observation, there are needle-like projections and they are sharper in the hop than in the Japanese hop. The transections of vein and petiole of both plants are morphologically identical and the development of collenchyma is remakable.

11. Besides the climbing hairs, the leaves and the stems of both plants have conic hairs, disc glands, cystoliths and clubbed glands. There are many types of conic hairs in both plants; from the unicellular short types to the multi-cellular long types. The disc glands are scattered sparsely on the old leaves but are found thickly on the young leaves. The disc glands of the Japanese hop are a little smaller and paler and have less cells than those of the hop.

Explanation of Plates

Plate 1

1. Seedling of the hop.
2A and 2B. Seedling of the Japanese hop.
3A. Cotyledon of the Japanese hop.
3B. First foliage leaf of the Japanese hop.
4. Rootstock of the hop.
5. Rootstock of the Japanese hop.
6A. Runner cutting of the hop.
6B. Stem cutting of the hop.
7. Sprout of the hop.
8. Sprout of the hop under the ground.

AR .....adventitious root
BT .....branch root
BU .....bud
CO .....cotyledon
HY .....hypocotyl
LA .....lateral
LE .....leaf
MT.....main tap root
PR .....primary root
SP .....stipule
ST .....stem
UR .....underground runner

Plate 2

1. Young plant of the Japanese hop.
2. Shoot apex of the young plant of the Japanese hop.
3. A portion of the hop stem.
4. Climbing of the Japanese hop stem.
5. Climbing of the hop stem.
6. Transection of the stem of hop.
7. Transection of the stem of Japanese hop.
8. Pericyclic-fibre of the stem of Japanese hop.
9A. Margin of the leaf of hop.
9B. Margin of the leaf of Japanese hop.

CA .....cambium
CH .....chlorenchyma
CL .....collenchyma
CM .....climbing hair
CO .....cotyledon
EN .....endodermis
EP .....epidermis
LA .....lateral
LE .....leaf
PF .....pericyclic-fibre
PH .....phloem
PI .....pith
SP .....stipule
ST .....stem
XY .....xylem
XY_1.....primary xylem
XY_2.....secondary xylem

Plate 3

1A, 1B, 2A and 2B. Leaf of the hop.
3A, 3B, 4A and 4B. Leaf of the Japanese hop.
5A and 5B. Climbing hair of the hop.

6A. Double-hooked climbing hair of the Japanese hop.
6B. Fish-hooked climbing hair of the Japanese hop.
6C. Single-hooked climbing hair of the Japanese hop.
7A, 7B and 7C. Conic hair on the vein of Japanese hop leaf.
8A, 8B, 8C and 8D. Clubbed gland on the lower surface of the leaf of Japanese hop.

PT .....petiole VE .....vein

Plate 4

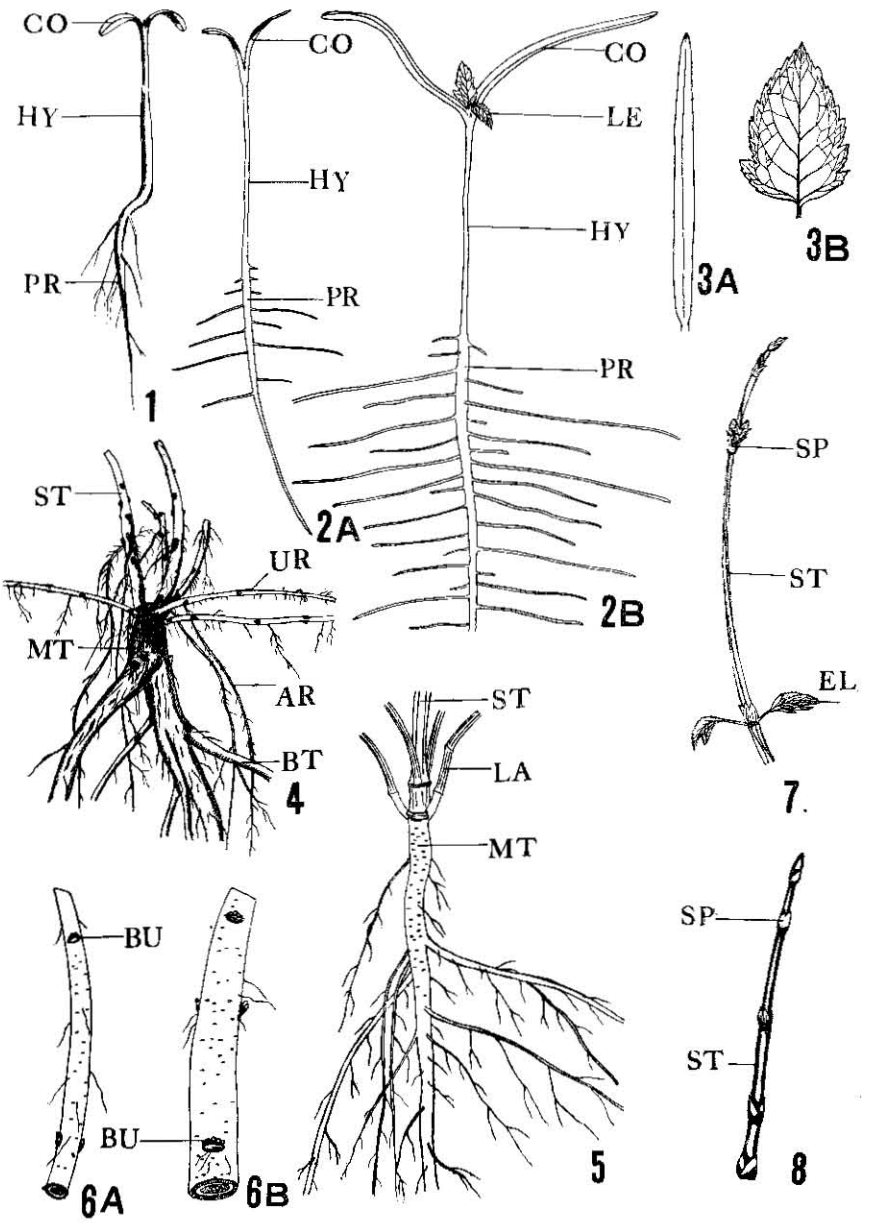
1. Growing point of the hop sprout.
2A. Longisection of the pistillate inflorescence bud of hop.
2B. Bud of the pistillate inflorescence of hop.
3. Transection of the vein of hop leaf.
4. Transection of the vein of Japanese hop leaf.
5. Transection of the petiole of hop.
6. Transection of the petiole of Japanese hop.

AB .....axillary bud
BR .....bracteole
CH .....chlorenchyma
CL .....collenchyma
EP .....epidermis
HA .....hair
LE .....leaf
OV .....ovary
PH .....phloem
PI .....pith
PP .....palisade palenchyma
PR .....parenchyma
SB .....stipular bract
SO .....stoma
SP .....stipule
SR .....strig, spindle
SY .....spongy parenchyma
TB .....terminal bud
XY .....xylem

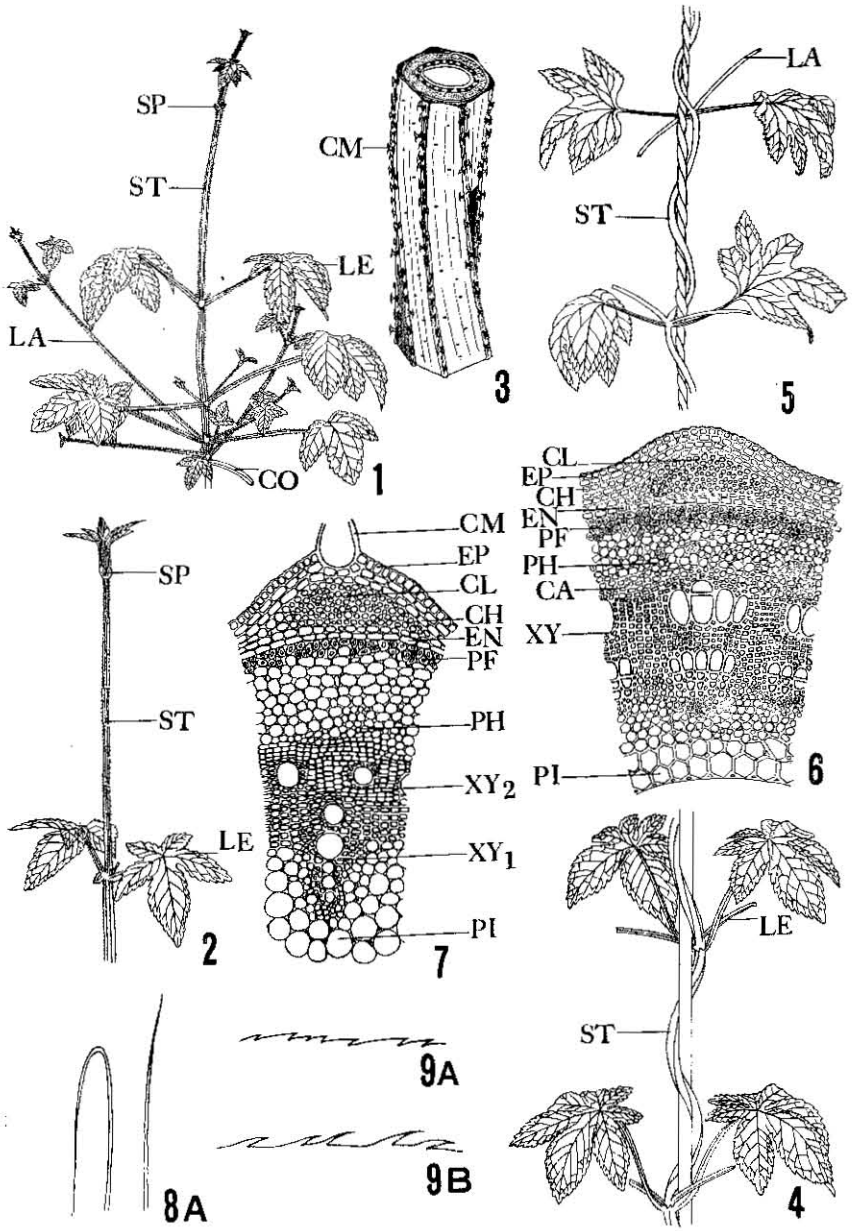
Plate 5

1A, 1B and 1C. Conic hair on the vein and the lower surface of Japanese hop leaf.
2A. Disc gland on the lower surface of hop leaf.
2B. Face view of the disc gland of hop.
2C. Side view of disc gland of hop.
3A. Disc gland on the lower surface of old leaf of Japanese hop.
3B. Disc gland on the lower surface of young leaf of Japanese hop.
4A and 4B. Disc gland of the Japanese hop.
5A. Cystolith of the hop leaf.
5B and 5B. Cystolith of the Japanese hop leaf.

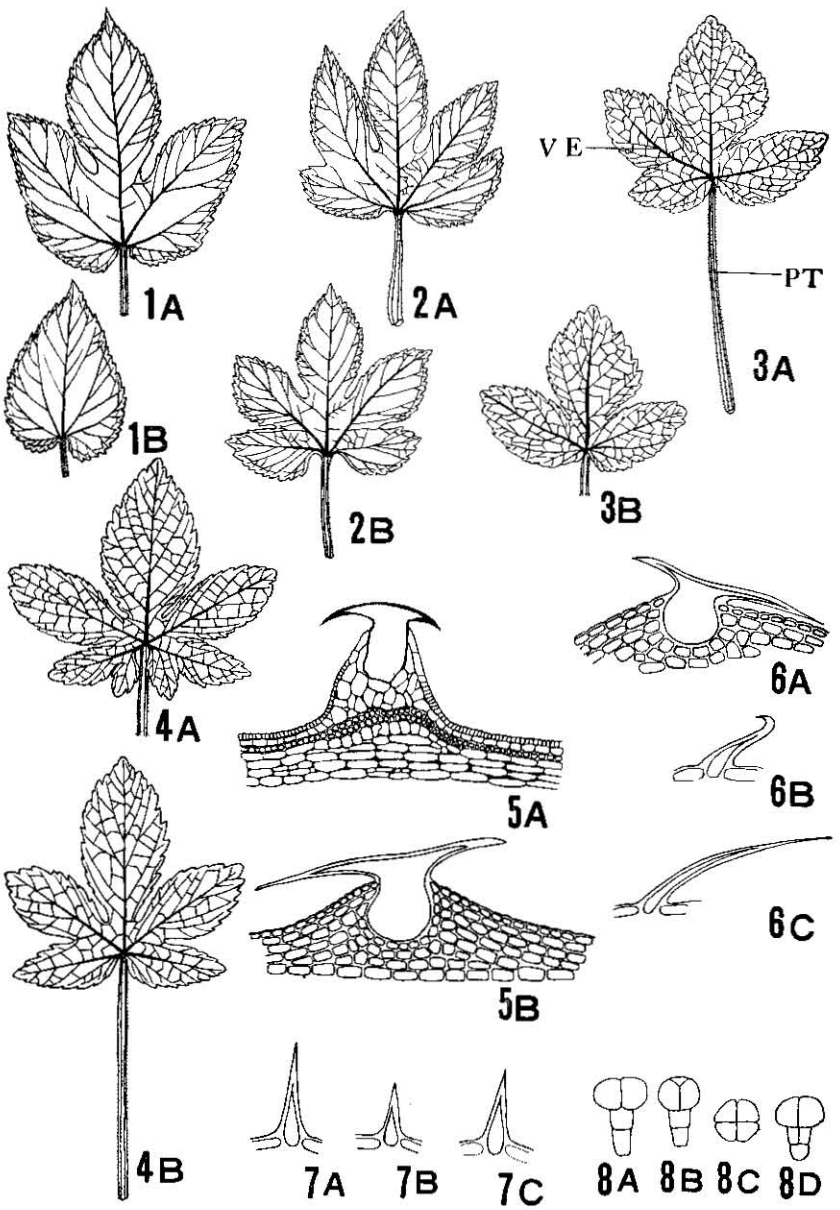
DG .....disc gland VE .....vein



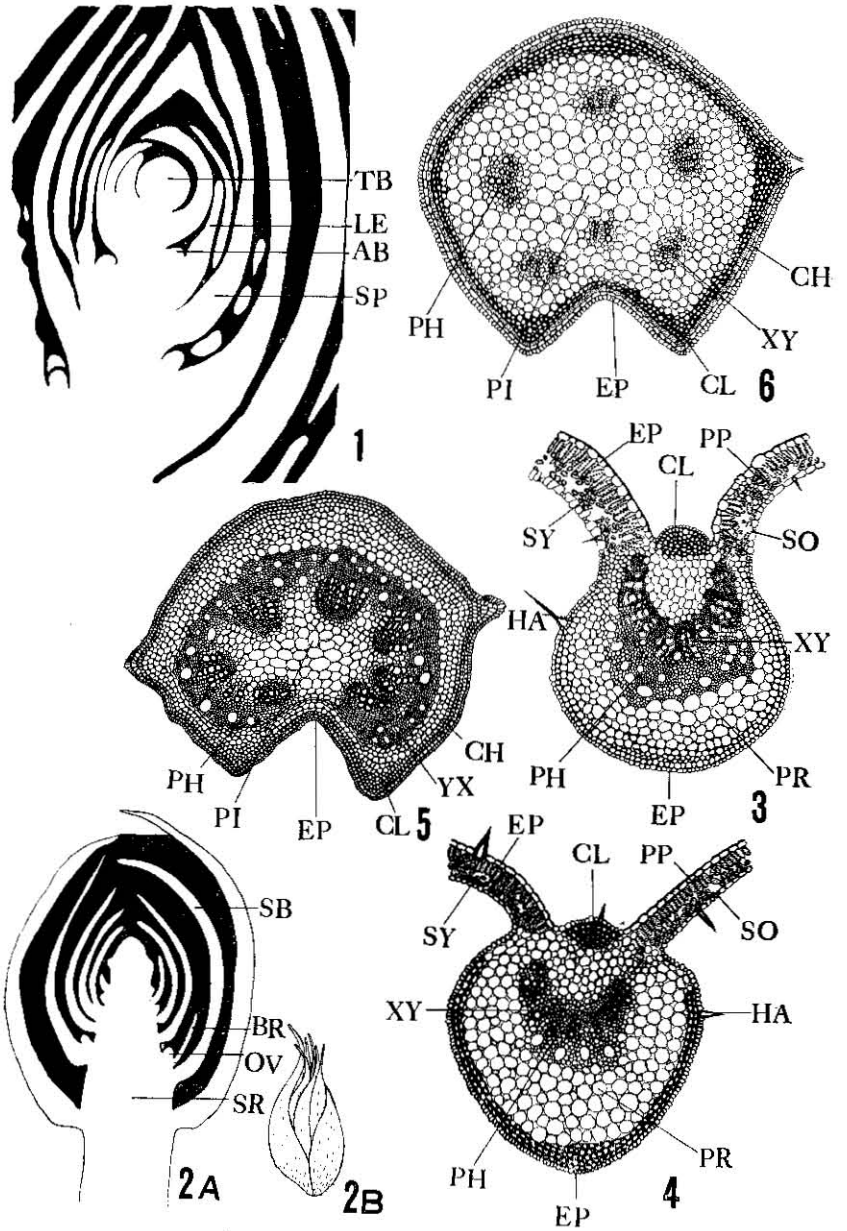
Studies on the hop and the Japanese hop



Studies on the hop and the Japanese hop



Studies on the hop and the Japanese hop



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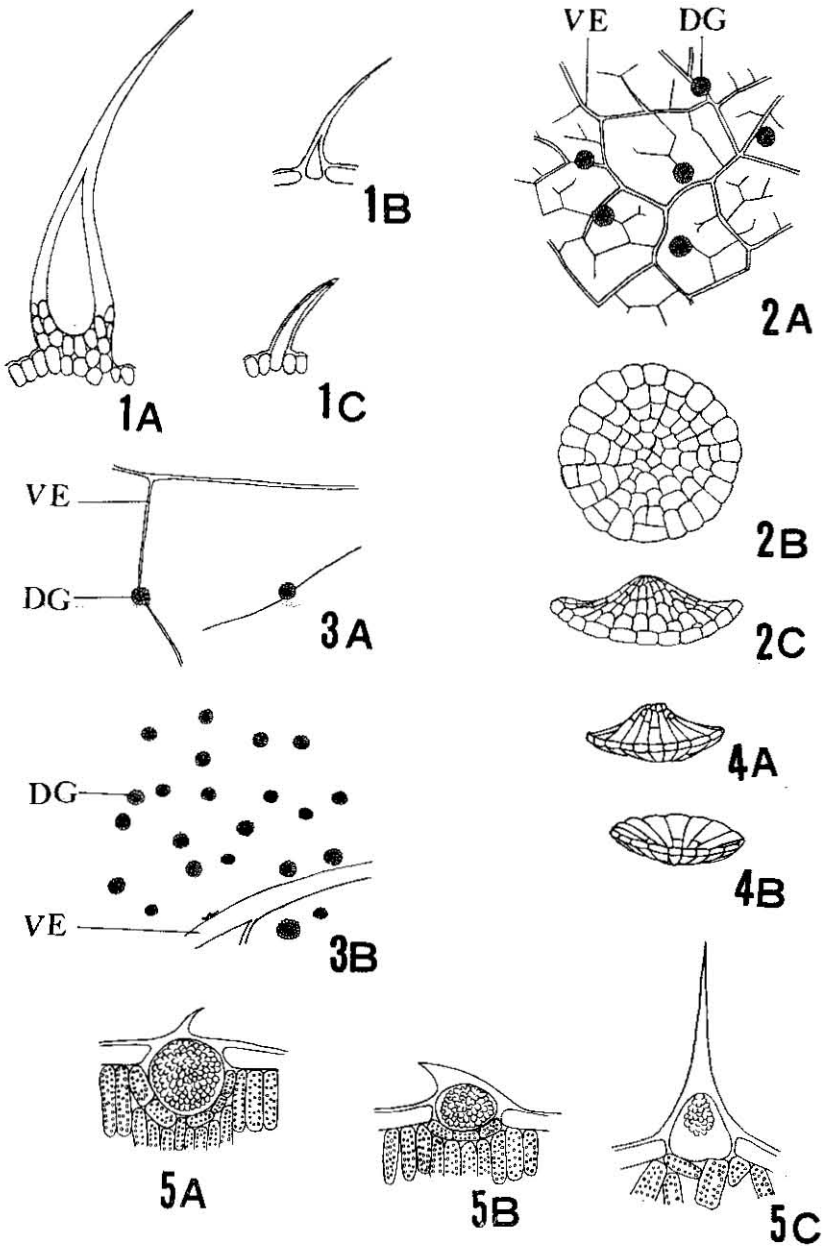

Studies on the hop and the Japanese hop