THE FEMALE REPRODUCTIVE ORGANS OF *CHAMAECYPARIS*

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Abstract: The female strobili and mature cones of *Chamaecyparis formosensis* Mats. and *Ch. obtusa* Sieb. et Zucc. var. *formosana* Rehd. were collected and dissected to observe the number and arrangement of their scales, ovules, and seeds. The flower branches with female strobili were collected and cultured in water in the laboratory to observe the development of the ovules and the secretion of the pollination fluid. The morphology of the female organs in this genus is redescribed and the development of the ovules and seeds are discussed.

PREVIOUS RESEARCHES

Although recently adopted systems of plant taxonomy are constructed on the basis of comparative morphology, reproductive mechanism, phytochemistry, and even cytogenetics (cytotaxonomy), the classification and identification of conifers are mainly based upon the characteristics of mature cones. Drs. Harlow and Harrar, the American dendrologists, wrote "the fruits of many conifers are obtainable at any time of the year, either attached to the branches or scattered on the ground under the tree. Therefore, in western forests the use of cones in distinguishing closely related species is not infrequently the only reliable means of separation in the field" (Harlow & Harrar, 1937).

A mature cone of a conifer is the consequence of a long term development of a female strobilus affected by many variable factors such as: the position of the strobilus on the tree, pollination, fertilization, nutrition, and especially the climate. In the early nineteen thirties Hagerup pointed out that "the uncertainty of the correct interpretation of the female cones of the conifers was at least partly due to the fact that previous investigators had in too high a degree contented themselves with studying the adult stages, and had thus neglected the developmental point of view" (Hagerup, 1933). The following two tables are brief reviews of the previous descriptions of the cones and seeds of the genus *Chamaecyparis* and the two species of this genus growing in Taiwan. (Table 1 and Table 2)

Some of the above records were found in the description of the genus or species but most of them were used in the keys for the identification of the plants.

According to my investigations of the morphology of the young strobili, mature cones, and seeds, the matter is not so simple as above the record would suggest. The results of my study are as follows.

MATERIALS AND OBSERVATIONS

1. Materials

The mature cones and young strobili of *Chamaecyparis formosensis* Mats. and *Ch. obtusa* Sieb. et Zucc. var. *formosana* Rehd. were collected from about fifty year

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Table 1. Descriptions of the cones of *Chamaecyparis*

Author	Year of publication	Number of scales/cones	Number of seeds/scale
Sargent	1896	—	1-4
Rehder	1914	—	2-5
Dallimore & Jackson	1923	—	1-5
Harlow & Harrar	1937	4- 8	—
Li	1950	—	2-5
Li	1953	6-12	3
Li & Keng	1954	—	1-5
Li	1963	8-12	2-5*
Liu	1964	—	1-5
Liu & Liao	1967	—	2-4

* Ovules on the scale of strobilus.

Table 2. The principal differences between the two native species of *Chamaecyparis* in Taiwan

Author	Year	*Ch. formosensis*		*Ch. obtusa formosana*	
		No. of scales per cone	No. of seeds per scale	No. of scales per cone	No. of seeds per scale
Shirasawa	1900	—	—	7- 9*	4*
Matsumura	1901	10-11	2	—	—
Rehder	1914	10-11	—	8-10	2-5
Dallimore & Jackson	1923	10-11	2	7-10	2-5
Kanehira	1936	10-13	—	8-10	—
Li	19 0	10-13	—	8-10	—
Li & Keng	1954	10-13	1-2	8-10	2-5
Li	1963	10-13	—	8-10	—
Liu	1960	10-13	1-3	8-10	2-3
Liu	1964	10-13	1-2	8-10	—

* *Chamaecyparis obtusa* of Japan.

old trees in natural stands on Alishan (alt. 2000 m) in three consecutive years between 1968–1970. All the cones and strobili were freshly dissected to observe the number and arrangement of the scales and ovules or seeds on the scales. Water cultured branches of the female strobili were used to study the number and arrangement of the ovules on each scale, and the order of secretion of the pollination fluid. The seeds on each scale of the mature cone were separately removed and a germination test was run to examine their viability.

2. Number and arrangement of scales on the female strobilus

Although the number of scales on a strobilus in these two related species is different the arrangement on them is the same. They are arranged in opposite pairs one rudimentary growing point at the apex (a terminal piece). The uppermost pair of scales are always sterile and connate with a terminal piece at the flowering stage. The actual number of the scales and the presence or absence of ovules are shown in Table 3.

Table 3. The number of scales on the strobilus

Sample no.	*Ch. formosensis*				*Ch. obtusa formosana*			
	Number	1st pair	Last pair	Apex	Number	1st pair	Last pair	Apex
1	8 pairs	sterile	fertile	+	5 pairs	fertile	fertile	+
2	8 pairs	sterile	fertile	+	5 pairs	fertile	sterile	+
3	8 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
4	8 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
5	8 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
6	8 pairs	fertile	sterile	+	4 pairs	fertile	sterile	+
7	8 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
8	8 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
9	7 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+
10	7 pairs	fertile	sterile	+	5 pairs	fertile	sterile	+

Note: Fertile means with ovules; sterile means without ovules.
+ Means the terminal piece is present.

3. Number of ovules and their arrangement on the ovule scales

The size of the ovule scales corresponds with the natural curve of the growth period. The first pair of scales at the base of the strobilus is smaller, the middle pairs of scales are larger, and the uppermost pairs of scales are the smallest. The number of ovules on each scale is proportional to the size of the scale. Table 4 is a record of the observations.

From table 4 some general conclusions may be drawn. (1) The number of ovules on each scale is quite variable, with a range of from two to eight. This range not only makes a representative average impossible but the good seeds on a cone are almost always developed from the middle scales which have more ovules. Therefore the average number of ovules cannot be used as an important character of identification. (2) The number of ovules on each scale are usually proportional to the scale size and to its position on the strobilus. The third and fourth pairs of scales in *Ch. formosensis* and the second and third pairs in *Ch. obtusa* var. *formosana* bear the highest numbers of ovules. The first and the last pairs of scales do not bear ovules or only a few ovules. (3) On most of the scales the number of ovules are usually an even number. From Plate I–A. and B., it is seen that the ovules on a scale are divided into two rows with a central gap between them. If there is an odd number scale it may be an acquired character.

4. The order of maturation of ovules on a scale

It has long been known that in many conifers when an ovule reaches maturity and is ready to accept pollen that a drop of pollination fluid is secreted from the micropyle (Baird, 1953; Coulter & Chamberlain, 1910; Doyle & Kane, 1943; Doyle & O'Leary, 1935a, 1935b; Haupt, 1941; Konar & Oberoi, 1969; Lawson, 1904; Saxton, 1910, 1930; Snow, Dorman & Shopmeyer, 1943). But the order of secretion from

Table 4. Number of ovules on each ovule scale

Order of scales	Number of strobili observed																											
	Ch. formosensis												*Ch. obtusa formosana*															
	1		2		3		4		5		6		1		2		3		4		5		6		7		8	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
8th pair	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7th pair	2	2	2	2	2	2	2	2	2	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6th pair	4	4	4	4	2	2	2	2	4	4	4	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5th pair	4	4	4	4	4	4	4	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
4th pair	8	8	6	6	4	4	4	4	6	6	6	6	4	4	2	2	2	2	2	2	2	2	4	3	4	3	4	4
3rd pair	8	8	6	6	6	6	4	4	6	6	6	6	7	6	6	7	6	6	4	4	4	4	4	4	4	4	4	4
2nd pair	4	4	4	4	2	2	2	2	2	2	4	4	6	6	4	4	5	5	6	7	4	6	4	5	6	6	7	8
1st pair	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	4	4	4	4	4	4	2	2	0	0	2	2
Total	60		52		40		36		48		52		33		33		34		33		28		28		27		35	
Average*	4		3		3		2		3		3		3		3		3		3		3		3		3		4	

* Approximate number of ovules per scale; L and R represent a pair of scales, where L stands for the left and R the right scale.

the ovules on the same scale has never been observed. In *Chamaecyparis* the pollination fluid is first seen on the innermost ovules of each row of the same scale (Plate I–C.) and then on the outer ovules of the row. Usually one ovule in each row is matured per day (two on each scale). The pollination fluid of an ovule can last for 2–3 days at room conditions of 85–95% R. H. But it dries out in 30 minutes after pollen grains are accepted (Plate II–A. & B.). This record is very similar for the development of ovules in *Callitris* in which the pollination fluid dried up in 10–20 minutes after the ovule was pollinated (Baird, 1953).

The separate maturation of the ovules in the two rows affirms the above mentioned hypothesis that even numbered ovules are produced on each scale.

Another fact is that in a whole strobilus the ovules on the lower scales mature first and gradually mature upwards towards the apex. The uppermost pair of scales are always sterile and without ovules and are closely adherent to the rudimentary growing point. Each ovule on each scale matures at a different time. The period between the maturing of the first ovule to the last ovule may be as long as or longer than a week. This gives it an advantage of a much greater chance for pollination under variable climates.

5. The arrangement of cone scales on matured cones

After pollination in the spring the cones usually mature in November of the same year. The arrangement of the cone scales has been reported as valvate (Liu & Liao, 1967), but recent observations show that the imbricate covering of the scales in the strobilus has not been changed. The thickened scales are compressed alternately, with the upper and lower pair of scales forming a hexagonal connection (Plate I–E. & II–C.). In *Ch. formosensis* all the seeds are compressed into this suture and become flat with their side margins becoming wings. But in *Ch. obtusa formosana* the outermost seed in each scale is pressed into the corner of the region between three scales to form a triangular seed with three wings (Plate I-E. & II-D.). Based on careful counting, it has been found that about 22% of the seeds in *Ch. obutsa formosana* are triangular and that no seeds of this type are formed in *Ch. formosensis.* This distinct character, caused by the compression of the cone scales, provides an easy method for distinguishing these two species by their seeds. In other words, the cone scales of *Chamaecyparis* are imbricate in arrangement.

6. Number of seeds per scale

According to my observations the number of seeds on each cone scale of these two species of *Chamaecyparis* is not as recorded in Table 2 (i. e. 1–3 in *Ch. formosensis* and 2–5 in *Ch. obtusa formosensis*) nor is it as figured by Dr. Li (1953). On most scales the number of seeds is similar to the number of ovules in the strobilus. Only a few ovules do not develop into mature seeds. These undeveloped ovules can be easily seen in Plate II-J. The following table shows the results of my observations.

Table 5. Number of seeds on each cone scale

Order of cone scale	Cones of *Ch. formosensis* observed																					
	1		2		3		4		5		6		7		8		9		10		Average*	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
8th pair	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7th pair	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
6th pair	3	3	3	3	4	4	4	4	3	3	4	4	4	3	4	3	4	3	2	2	4	3
5th pair	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4	4	4	4
4th pair	4	5	4	4	6	6	5	6	5	4	6	7	5	4	4	5	4	4	4	4	5	5
3rd pair	8	7	7	7	6	6	8	8	8	7	8	8	8	6	7	6	3	4	6	6	7	7
2nd pair	5	5	6	4	4	4	4	5	7	6	4	4	4	8	7	7	6	3	4	5	5	5
1st pair	0	0	0	0	0	0	3	1	4	4	0	0	0	0	4	5	0	1	0	0	1	1
Total	52		50		52		62		61		57		54		62		4	4	4	5	55**	

Order of cone scale	Cones of *Ch. obtusa formosana* observed																					
	1		2		3		4		5		6		7		8		9		10		Average*	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
5th pair	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4th pair	4	4	3	2	4	4	4	4	2	2	4	4	4	4	4	4	4	4	4	3	4	4
3rd pair	6	4	5	4	5	5	4	5	4	4	4	4	6	4	4	5	6	4	5	5	5	4
2nd pair	6	6	7	7	4	4	6	6	5	6	5	5	4	6	5	4	6	5	6	4	6	5
1st pair	2	2	2	2	2	2	2	2	4	4	4	4	0	2	0	2	0	0	2	2	2	2
Total	34		32		30		33		31		26		30		28		29		31		30**	

* Approximate number of seeds per scale.

** Average seeds per cone.

L. & R. represent a pair of scales.

From the above table the number of seeds per cone scale is clearly seen. In these two species the number of seeds on each fertile scale is 1–8. Although sometimes an odd number is shown, this is due to averaging specimens counted and cannot be used to represent the number of seeds on the cone scale. Most scales used in preparing this table bore seeds in even numbers, and the terminal pairs are always sterile.

7. The viability of seeds on different cone scales

It is known that the germination percentages of the seeds of these two species are very poor (Liu, 1970). Usually among the seeds removed from mature cones there are many rudimentary ovules and even more empty seeds without embryos or endosperm. The cause for these empty seeds is very complex. Possible explanations are: unsuccessful pollination, imperfect fertilization, and defeciency of nutrients.

In this experiment the seeds from different scales were removed separately for germination tests. The results are shown in Table 6.

Table 6. The germination rates and reproductive potential of the seeds of different cone scales of *Ch. formosensis* (sum of five cones)

Order of cone scale	Number of seeds	% in total	Germinated seeds	Germination %	Reproductive potential in %*
8th pair	0	0.0	0	0.0	0.0
7th pair	20	4.6	1	5.0	0.2
6th pair	49	10.8	7	14.3	1.5
5th pair	69	15.3	22	32.0	4.9
4th pair	81	17.8	29	35.8	6.4
3rd pair	88	19.4	33	37.5	7.3
2nd pair	94	20.6	27	28.7	5.9
1st pair	57	11.5	13	22.8	2.6
Total	458	100.0	132	28.8	28.8

* Reproductive potential = % in total seeds × germination % × 100

It is evident from this table that the germination rate of the seeds on each scale is related to their positions on the cone as well as to the number of seeds on each scale. In general the reproductive potential of the middle pairs of scales is higher than those of the basal and terminal pairs.

DISCUSSION

1. Ovule scale and seed scale

In most conifers the shape, structure, and arrangement of seed scales on mature cones are very different from the ovule scales in the strobili at flowering time. The morphology of the strobilus is more stable than that of the mature cone. When the strobilus is differentiated on a plant all the internal and external conditions genetically required for flowering must be sufficient. In other words the variation range for the strobili to form is very limited. The shape, size, structure, and arrangement of ovule scale on the strobilus are more reliable than the matured cones. The reason that previous taxonomists have neglected the importance of the young strobili and paid more attention to the matured cones, is perhaps because the cones are more easily obtainable and easier to preserve. But the morphology of the cones and the seed scales on the cone are different from tree to tree, from place to place and from year to year. The previous classification of conifers based upon cones and seed scales should be revised along with investigations into the developmental morphology of the strobilus.

2. The arrangement and number of ovule scales on strobili

It has been known by taxonomists that the arrangement of the scales "follows that of the foliage-leaves" (Rendle, 1956). In Cupressaceae the ovule scales are arranged in decussating whorls. The number of scales in this kind of a strobilus should of course be in even numbers. In the following table the number of scales of some genera in Cupressaceae are recorded.

Table 7. Numbers of ovule scales on strobili in some genera of Cupressaceae

Genus	No. of species	No. of scales	Reference
Callitris	12	even	Dallimore & Jackson, 1923
*Cupressus**	13	even	D. & J., Sargen, 1896; Ohwi, 1965; Bentham & Hooker, 1883
Chamaecyparis	5	even	Bailey, 1949; Rehder, 1953, 1954
Fokienia	1	even	D. & J.
Libocedrus	7	even	D. & J., Sargent, Bailey, Rehder
Tetraclinis	1	even	D. & J.
Thuja	5	even	D. & J., Bailey, Rehder
Juniperus	6	even	Sargent
Juniperus	3	odd	Sargent

* Including *Chamaecyparis* in some literature.

From my investigation (Table 3) the number of ovule scales in *Ch. formosensis* is 7–8 pairs and in *Ch. obtusa formosana* is 4–5 pairs.

The earliest record concerning *Chamaecyparis* from Eastern Asia was by Siebold and Zuccarini in Flora Japonica in 1870. In their descriptions of three species under the name *Retinispora* (*Chamaecyparis*) the number of ovule scales were 8–10 for *C. obtusa*, 10–12 for both *C. pisifera* and *C. squamosa* (Siebold & Zuccarini, 1870). But in the Japanese literature, the number of ovule scales in *Ch. obtusa* has been recorded as 7–9 by Shirasawa (1900) and as 10–11 in *Ch. formosensis* by Matsumura (1961). In the description given by Shirasawa, he states that "the seed scales are woody, peltate, 7 or 9, the central one solitary and the other scales opposite". Evidently Shirasawa counted the central rudimentary growing point as a seed scale, since this piece is very similar to the sterile scales on mature cones. (Plate II-E. & F.).

I have found some mature cones in *Ch. formosensis* with a short twig growing from the central piece (however no such cones have been observed in *Ch. obutsa formosana*). From Plate II-G. the new growth of this central growing point with two sterile scales below is clearly seen. In addition, this new growth from a mature cone is not uncommon in other conifers (Plate II-H. & I.). In my opinion the rudimentart central piece is probably an evolutionary evidence of a stem apex. On this shortened stem the megasporophylls (the ovule scales) are arranged closely to form a female strobilus (Aase, 1915; Florin, 1954; Worssdell, 1900). If the growing point of the stem had not changed completely or this rudimentary growing point had been stimulated by internal substances of the twig (especially on the juvenile trees), it could be redifferentiated from the rudimentary state into normal growth (Esau, 1960). In the evolutionary trend the more differentiated character (such as the central piece in *Ch. obtusa formosana*) should be the more advanced one. *Ch. formosensis*, owing to the rejuvenescence of the central piece in strobilus and the more scales in a strobilus, should be the more primitive one of the two species.

According to the above discussion the numbers of ovule scales of a strobilus in these two species of *Chamaecyparis* should be 7–8 pairs (14–16 scales) in *Ch. formosensis* and 4–5 pairs (8–10 scales) in *Ch. obtusa formosana* (at least they should be in even numbers).

Another problem is whether the lowest pair of scales with a transitional form between the scale leaves and true ovule scales can be counted as ovule scales. In observations on young strobili and matured cones of these two species, ovules are found in some of the first pair of scales although their shape is similar to the scale leaves.

3. The number of ovules and their arrangement in the scale

The period between pollination and fertilization is very long (Baird, 1953; Coulter & Chamberlain, 1910; Konar, 1960; Lawson, 1904, 1909; Miyake, 1908; Saxton, 1910; Wong, 1948). It has been said that the development of the female strobilus after the pollination may be independent of the fertilization process (Allen, 1942a; Saxton, 1909). Thus in a mature cone we find normal full seeds, empty seeds, undeveloped ovules, and even seeds with unfertilized haploid embryos. When we say that certain species has some seeds on each scale, what kind of seeds are being referred to? It has been seen in the tables mentioned above that the number of ovules or seeds in each scale is always variable according to the different positions of the scales on the strobilus. How can we maintain that the seeds are always of the same number on every scale of the cone? Moreover, the previous investigators have not only stated that there is a definite number of seeds in every scale, but have also used this definite number to distinguish the genera *Cupressus* (with over 5 seeds in each scale) from *Chamaecyparis* (with less than 5 seeds) (Harlow & Harrar, 1937; Liu, 1960).

For the purpose of classification and identification of *Chamaecyparis* the numbers of seeds per scale in mature cones is less reliable than the number of ovules on each ovule scale of the strobilus.

As shown in Table 4 the normal number of ovules per scale in the two species of *Chamaecyparis* of Taiwan are always in even numbers, and these seeds are arranged in two opposite rows on each scale. In fact, these even numbered ovules of some species in the genus *Chamaecyparis* has long been recorded (Plate I-F. G. & H.) and the dichotomous arrangement of the ovules has been supported by the anatomical study of many investigators (Aase, 1915; Worssdell, 1900). It is not known that why investigators abandoned the valuable characters of ovules and of the strobili and selected the variable characters of the seeds and mature cones for their basis of the classification of the conifers.

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Explanation of Plates

Plate I.

A. Ovule scales of a female strobilus of ***Chamaecyparis formosensis***, with different numbers of ovules on each scale; A-1, one of the first pair, ...A-7, of the seventh pair.

B. Ovule scales of a female strobilus of ***Ch. obtusa*** var. ***formosana***, with different numbers of ovules on each scale; B-1, one of the first pair, ...B-5, two sterile scales of the fifth, the last pair, with a rudimentary central piece between them.

C. One of the ovule scales of a matured strobilus of ***Ch. formosensis***, with five ovules in two rows (a. the pollination fluid of the matured ovules).

D. One of the ovule scales of ***Ch. obtusa*** var. ***formosana***, with four ovules in two rows.

E. Compression of the cone scales of ***Ch. obtusa*** var. ***formosana*** with two triangular seeds in the corners.

F. Ovule-scale of ***Ch. thyoides*** of N. America with two ovules on the base (from Sargent).

G. Ovule-scale of ***Ch. nootkatensis*** of N. America with four ovules in two rows (from Sargent).

H. Ovule-scale of ***Ch. lawsoniana*** of N. America with six ovules in two rows (from Sargent).

Plate II.

A. Female strobilus of ***Ch. formosensis*** on blooming at 9:00 A.M. The numbers 1, 2, 3, ... are the ovules on the different pairs of scales in ascending order. The ovules on lower scales matured early and the pollination drops were larger. (×625).

B. The same strobilus at 11:30 A.M. in the same day, 30 minutes after artificial pollination. All the pollination drops of visible ovules were dried up. (×625)

C. Matured cones of ***Ch. obtusa*** var. ***formosana*** (left) and ***Ch. formosensis***, showing the imbricately compression of cone scales. (×16)

D. Triangular seeds of ***Ch. obtusa formosana***. (×100)

E. and F. Central piece (the rudimentary growing point) of a dried cone with sterile scales on both sides of ***Ch. obtusa*** var. ***formosana*** (E) and ***Ch. formosensis*** (F). (×100)

G.-I. Rejuvenile central pieces of matured cones of ***Ch. formosensis*** (G), ***Cryptomeria japonica*** (H), and ***Cunninghamia lanceolata*** (I). (G.×16, H.×1/4, I.×1/4)

J. Two seed scales of ***Ch. formosensis*** with eight seeds each, including the full, the empty or/and the undeveloped seeds. (×2)

Plate I

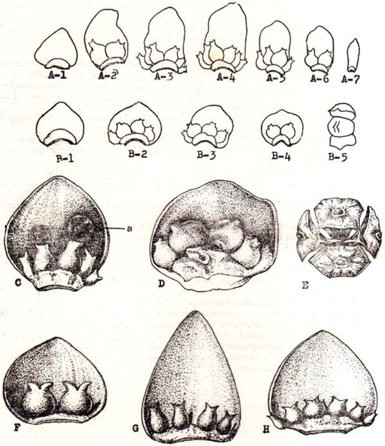

Plate II