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Floral Organogenesis of *Titanotrichum oldhamii* (Gesneriaceae)

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Abstract: Floral organogenesis of *Titanotrichum oldhamii* (Hemsl.) Soler., the only species in the genus and endemic to East Asia, was observed under SEM. We found that the development of calyx, corolla and androecium belongs to pentamerous pattern. They come respectively from primordia of calyx, corolla and androecium, and all differentiated from the flower primordium. The zygomorphism of corolla and androecium is derived from quicker growth of the upper lip of corolla and delay in development of the staminode. Initiation of sepal primordia and their development are not consistent in order; the order of initiation is from adaxial central primordium, abaxial two primordia and finally lateral two primordia, while the order of development is first adaxial central sepal, lateral two and finally abaxial two. Sepals are valvate in flower bud. Initiation of corolla lobe primordia and their development are consistent in order, i.e. first abaxial central lobe (central lobe of the lower lip), lateral two (lateral two lobes of the lower lip) and finally adaxial two (two lobes of the upper lip). The aestivation of corolla is imbricate, and the order from outside to inside is the central lobe of the lower lip, lateral two of the lower lip, and finally two of the upper lip or lateral two lobes of the lower lip, two of the upper lip and central one of the lower lip. Stamen primordia are alternate to the corolla lobe primordia, with the anterior two primordia later than the posterior two in initiation; staminode primordium is simultaneous with the posterior two in initiation, but smaller, and opposite to the adaxial carpel (upper lip of stigma). Compared to the patterns of floral organogenesis of *Rehmannia* (Scrophulariaceae), *Whytockia* and *Rhynchoglossum* (Gesneriaceae), the present authors found that the floral organogenesis is diverse and does not form two distinct patterns among these four genera. Based on the results we tend to consider that the conventional demarcation between the Scrophulariaceae and Gesneriaceae using number of ovary locules (two vs one) and placentation (axile vs parietal) is questionable.

Key words: Gesneriaceae; *Titanotrichum*; floral organogenesis

The genus *Titanotrichum*, belonging to the subfamily Cyrtandroideae in the family Gesneriaceae, forms a monogeneric tribe, Titanotricheae Yamazaki ex W. T. Wang, with a single species, *T. oldhamii* (Hemsl.) Soler., which is endemic to East Asia and distributed in Fujian, S. Zhejiang and Taiwan in China, and Ryukyu in Japan^[1-3].

Since Forbes and Hemsley^[4] described this species in 1890 in the genus *Rehmannia* (*R. oldhamii* Hemsl.) of the Scrophulariaceae with a question mark, its systematic position has been controversial. Solereder^[5] established a new genus, *Titanotrichum*, to accommodate the species, *T. oldhamii* (Hemsl.) Soler. and placed it into the Gesneriaceae (Cyrtandroideae: Didymocarpeae) together with *Rehmannia*. In 1949 Sealy^[6] considered the genus *Titanotrichum* more closely related to *Isoloma* (= *Kohleria*) and *Naegelia* (= *Smithiantha*) in the subfamily Gesnerioideae than to the subfamily Cyrtandroideae. Burt^[7] kept *Titanotrichum* in Gesneriaceae, but removed *Rehmannia* back to the Scrophulariaceae, whereas Kvist and Pedersen^[8] considered the genus under study more closely related to the Scrophulariaceae than to the Gesneriaceae. Wang *et al.*^[1,9] established a new monotypic tribe for the genus, tribe Titanotricheae, in

Gesneriaceae, and arranged the tribe after the tribe Klugieae. Based on sequences of cpDNA gene *ndhF* of the Gesneriaceae, Smith *et al.*^[10,11] was still not certain of the systematic position of *Titanotrichum*, considering that the genus is relatively close to Gesneriaceae, in which it is more closely related to Cyrtandroideae than to Gesnerioideae. Observed in the present work was floral organogenesis of the genus *Titanotrichum* with the aim of providing evidence on ontogeny to resolve its phylogenetic position.

1 Materials and Methods

The material for this study was collected in August of 2000 and 2001 from Yongchun County, Fujian Province, China. The voucher, LI Zheng-Yu and ZOU Xiu-Hong 11327, is preserved in the Herbarium of Institute of Botany, the Chinese Academy of Sciences (PE). Inflorescences at different stages of development were fixed in FAA. After being soaked in 95% alcohol for over 24 h floral apex was peeled off from the material. The obtained apex or flower buds were stepwisely dehydrated with absolute alcohol and iso-amylacetate. The material was critical point-dried with CO₂, mounted, coated and observed under a SEM Hitachi S-800. Ovaries were fixed in FAA, and sections (6-10 μm in thickness) were prepared

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according to the conventional paraffin method and were stained with safrannin-fast green.

2 Results

2.1 Inflorescences

The genus *Titanotrichum* is a perennial. Rhizomes possess fleshy scales. Stems are unbranched. Basic unit of inflorescences is a cyme, on which usually only the terminal flower developed, while lateral ones reduced (Fig. 1), and thus the cyme seems to have a single flower. However, sometimes both the terminal and one of lateral flowers developed. A number of cymes formed a reduced panicle, which appeared racemose. By opening bracts and bracteoles, flower primordia and flower buds at different stages were found irregularly arranged on an inflorescence axis, which became nearly pyramidal in shape, and was covered with multicellular hairs (Figs. 2, 3).

2.2 Floral morphology

A mature flower is of a relatively large bract and 1-2 bracteoles at the base (Fig. 4). Flowers are bisexual, zygomorphic, with five nearly equal sepals, corolla infundibuliform-tubular, limb two-lipped, upper lip two-lobed, lower lip three-lobed; fertile stamens four, all inserted at the base of corolla tube, didynamous, one staminode on adaxial side; anthers two-locular, longitudinally dehiscent, filaments dorsifixed; disc inferior; ovary superior, one-locular with two parietal placentae, stigmas two, posterior one minute, anterior one lingulate, entire.

2.3 Initiation and development of calyx primordia

At the top sect of inflorescences collected in mid August we found flower buds and cyme primordia with size getting gradually smaller upwards, and arranged in all directions (Fig. 3). When cyme primordia near the top of inflorescence became oblate and apex flattened with a size about 51 μm in diameter lateral flower primordia could not be seen (Fig. 5). As the terminal flower primordium became spherical and its apex swelled upwards, two bracteole primordia different in size differentiated on lateral sides and the lateral flower primordia had just appeared

(Fig. 2). Subsequently, the bracteole primordia elongated and flattened, becoming ovate bracteoles (Figs. 6, 7). The floral apex continued to swell upwards, and one of two protuberances, whose cells tightly arranged, occurred at a 90° angle to the bracteoles. They are the abaxial sepal primordia (Figs. 8, 9). Soon after a smaller rounded protuberance differentiated on opposite (adaxial) side, i.e. adaxial sepal primordium, and then lateral two sepal primordia arose at inner side of the two bracteoles (Figs. 10, 11). As the sepal primordia continued to develop, adjacent ones united only at the very base. The sepal primordia flattened, elongated and laterally expanded, gradually becoming separate and ovate sepals in a primary state in the order: adaxial one, lateral two and finally abaxial two (Figs. 10-12). Sepals continued to elongate and curved inwards, and gradually covered the centre of floral apex. Margins of adjacent sepals were close to each other, and thus calyx aestivation was valvate. From epidermal cells grew rounded and verrucose protuberances, which developed into multicellular hairs (Figs. 13, 14).

2.4 Initiation and development of corolla lobe primordia

When all the sepals had formed but their indumentum had not differentiated, the flower bud reached a size of 143-200 μm in diameter. By opening such a flower bud with sepals removed, it could be found that the floral apex slightly swelled but then flattened, and gradually became pentagonal, 94-125 μm in diameter. As the five sides swelled upwards simultaneously the five angles alternate to sepals expanded and swelled, forming small rounded protuberances (Figs. 11, 15), whose top enlarged rapidly and became corolla lobe primordia in such an order: first abaxial central lobe primordium, abaxial lateral two and finally adaxial two (Figs. 16-19). The pentagonal meristem continued to grow and became circular, forming an initiative state of corolla tube (Figs. 20-23). The abaxial central primordium first flattened, elongated and widened, becoming deltoid (central lobe of

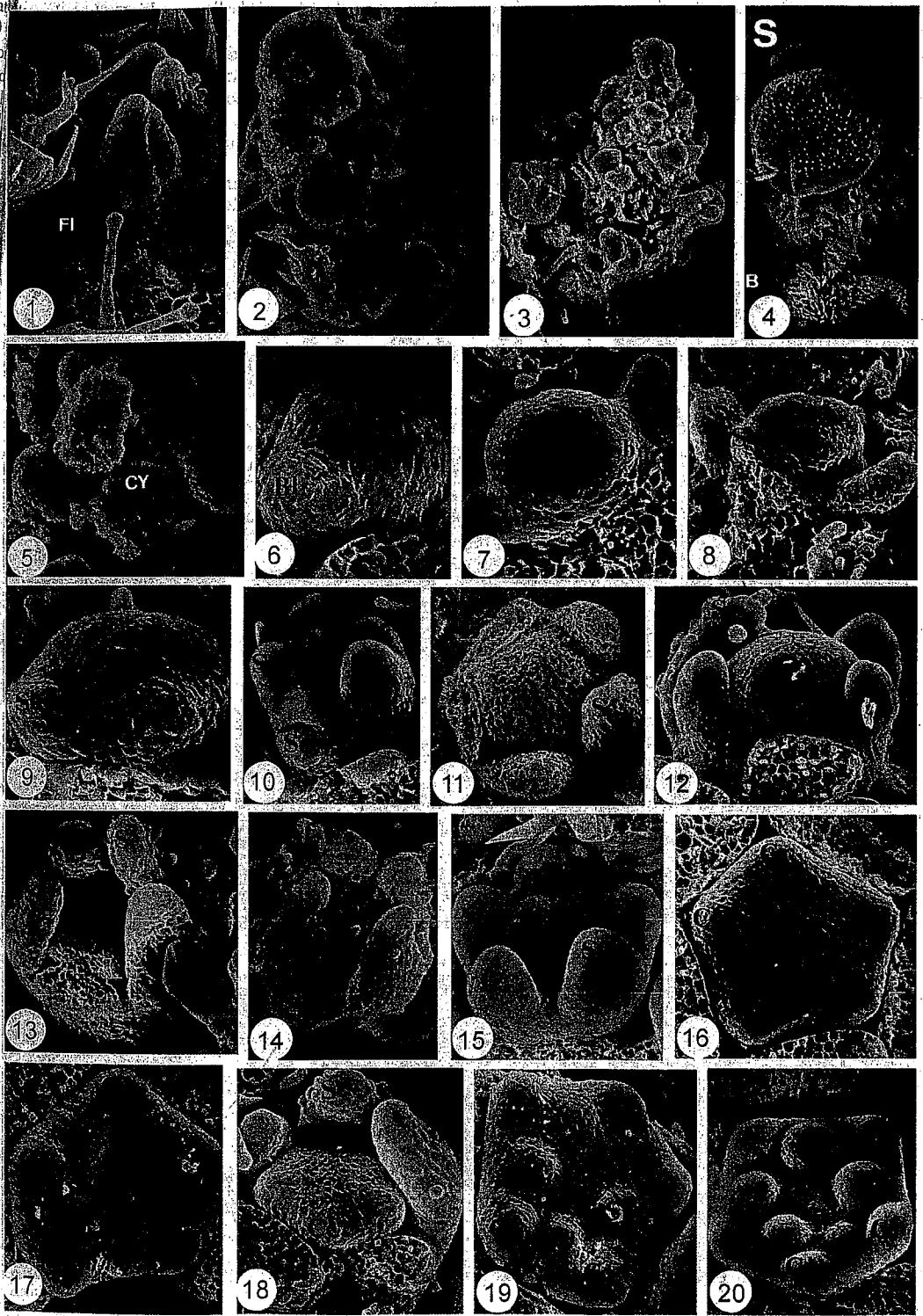
Figs. 1-20. SEM observations on morphogenesis of inflorescences and floral organs. 1. A cyme, showing the well developed apical flower and reducing primordium of a lateral flower, $\times 150$. 2, 3. Apical part of an inflorescence, showing floral primordia at different developmental stages and irregularly arranged. 2. $\times 120$. 3. $\times 48$. 4. A floral bud, showing a bract, two bracteoles and sepal, $\times 12$. 5-9. Initiation of floral primordium and calyx primordia. 5. Apical part of an inflorescence, showing cyme primordia, $\times 240$. 6. Showing bracteoles primordia, $\times 420$. 7. Flattening of bracteole primordia, and upward swelling of floral apex, $\times 240$. 8. Showing primordia of bracteoles and abaxial two sepals, $\times 210$. 9. Primordia of two abaxial sepals, $\times 300$. 10-14. A flower, showing development of sepals. 10, 11. Adaxial sepals, abaxial two sepals at early stage, and flattened pentagonal centre of floral apex. 10. $\times 150$. 11. $\times 240$. 12-14. Sepals at late stage of development, showing verrucose protuberances on the dorsal side and valvate aestivation. 12. $\times 210$. 13. $\times 180$. 14. $\times 120$. 15-19. A flower, showing order of initiation of corolla lobe primordia and stamen primordia. 15. Pentagonal floral apex swelling upwards, $\times 180$. 16-18. Floral apex with sepals removed. 16. Showing corolla lobe primordia at an early stage, $\times 240$. 17. Showing corolla lobe primordia at a later stage, $\times 210$. 18. Initiation of abaxial central corolla lobe primordium and abaxial lateral two. 19. Showing primordia of corolla lobes, posterior stamens and staminode, $\times 210$. 20. A flower, showing order of development of corolla lobe primordia and fertile stamen primordia: abaxial central lobe of corolla first flattening, then abaxial two lateral and finally adaxial two; anterior stamen primordia rapidly growing and slightly larger than posterior stamen primordia, and staminode primordium retarding in development, $\times 150$.

Abbreviations: B, bract; Bl, bracteole; Cb, abaxial lateral lobe primordium of corolla or abaxial lateral lobe of corolla; Cc, abaxial central lobe primordium of corolla or abaxial central lobe of corolla; Cd, adaxial lobe primordium or adaxial corolla lobe; CY, A cyme primordium; F, floral primordium or floral apex; Fl, reducing primordium of a lateral flower; I, inflorescence; S, sepal or sepal primordium; Sa, anterior stamen primordium or anterior stamen; Sb, abaxial sepal primordium or abaxial sepal; Sc, adaxial center sepal primordium or adaxial center sepal; Sd, adaxial lateral sepal primordium or adaxial sepal; Sn, staminode primordium or staminode; Sp, posterior stamen primordium or posterior stamen.

2). Subsequently, the bracteole primordia elongated and flattened, becoming ovate bracteoles (Figs. 6, 7). The floral apex continued to swell upwards, and one of the protuberances, whose cells tightly arranged, occurred at 10° angle to the bracteoles. They are the abaxial primordia (Figs. 8, 9). Soon after a smaller rounded protuberance differentiated on opposite (adaxial) side, the abaxial sepal primordium, and then lateral two sepal primordia arose at inner side of the two bracteoles (Figs. 10, 11). As the sepal primordia continued to develop, the sepal primordia united only at the very base. The sepal primordia flattened, elongated and laterally expanded, gradually forming separate and ovate sepals in a primary order: adaxial one, lateral two and finally abaxial one (Figs. 10-12). Sepals continued to elongate and gradually covered the centre of the floral primordium. Margins of adjacent sepals were close to each other, thus calyx aestivation was valvate. From epistichous position, the sepals grew rounded and verrucose protuberances, developed into multicellular hairs (Figs. 13, 14).

Initiation and development of corolla lobe primordia. After all the sepals had formed but their indumentum was not differentiated, the flower bud reached a size of 1.5 mm in diameter. By opening such a flower bud, it was found that the floral primordium was well rounded but then flattened, and gradually became pentagonal, 94-125 μm in diameter. As the five angles of the floral primordium simultaneously expanded and swelled, forming small protuberances (Figs. 11, 15), whose top enlarged into five corolla lobe primordia in such an order: central lobe primordium, abaxial lateral two (Figs. 16-19). The pentagonal primordium continued to grow and became circular, forming the corolla tube (Figs. 20-23). The central lobe primordium first flattened, then swelled, becoming deltoid (central lobe of

the corolla), showing the well developed apical flower bud. The floral primordia at different developmental stages are shown in Figs. 1-12. 1-5. Initiation of floral primordia, ×240. 6. Showing bracteoles primordia, and abaxial two primordia of sepals. 10, 11. Adaxial sepals, abaxial two sepals. 12-14. Sepals at late stage of development, ×180. 14. A flower, showing the well developed apical flower bud, ×180. 15-18. Flower bud showing corolla lobe primordia at a later stage, ×180. 19. Showing primordia of corolla lobes, posterior and fertile stamen primordia: abaxial central lobe of corolla; Cc, abaxial central corolla lobe; CY, A cyme primordium; Sa, anterior sepal or sepal primordium; Sa, anterior lateral sepal primordium or adaxial center of stamen; Sa, posterior stamen primordium or posterior

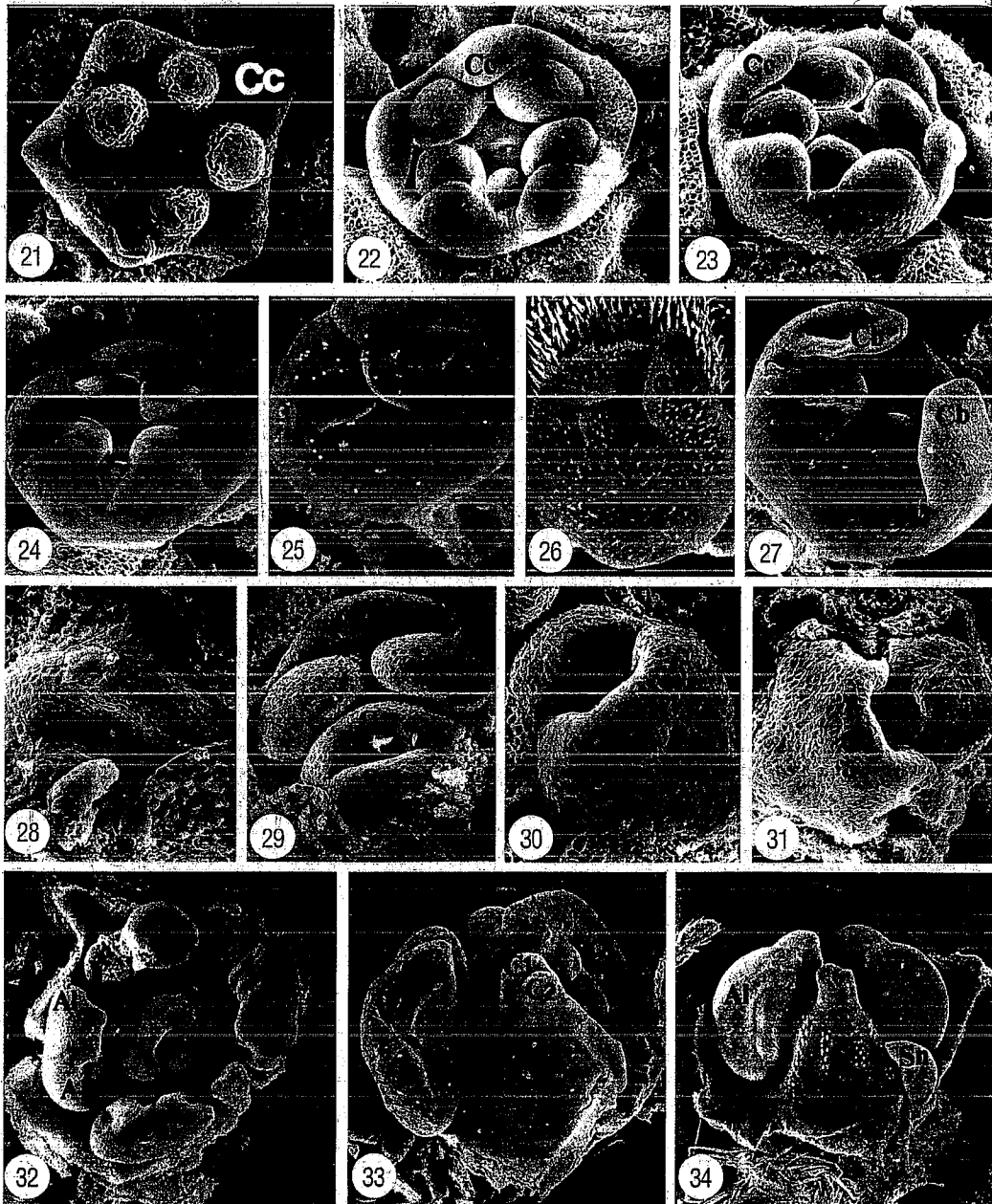


the lower lip). This was followed by abaxial lateral two primordia (lateral two lobes of the lower lip), and finally adaxial two lobe primordia (Fig. 21). Therefore, initiation of the primordia and their subsequent development of corolla lobes were consistent in order.

When the five corolla lobe primordia all differentiated and became deltoid, they became rounded at the top.

At this time the lobes gradually curved inwards and as the corolla tube arose high and high they gradually enveloped the central part of the floral apex. Simultaneously, the adaxial two lobes grew obviously more quickly than the abaxial three, and thus corolla zygomorphism appeared (Figs. 22 - 24).

As corolla tube continuously elongated, and corolla



lobes grew, wider developed into a corolla aestivation from outside to lateral two and adaxial two lobes central one (F parts grew rapidly as long as the elongated up to open

2.5 Initiation of primordia

Initiation of corolla lobes was similar to that of the latter. I the abaxial lateral two three oblate primordia: following enlargement of the small round abaxial centre of primordia height at corolla lobe primordia time, the diameter was maintained (Fig. 21). Inwardly elongated horizontally and formed in

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At this time the lobes gradually curved inwards and as the corolla tube arose high and high they gradually enveloped the central part of the floral apex. Simultaneously, the abaxial two lobes grew obviously more quickly than the adaxial three, and thus corolla zygomorphism appeared (Figs. 22-24).

As corolla tube continuously elongated, and corolla



lobes grew, widened and curved inwards, the flower bud developed into a size of 0.6-1.8 mm in diameter. The corolla aestivation, as we observed, is imbricate; we saw from outside to inside: the abaxial central lobe, abaxial lateral two and finally adaxial two (Figs. 25, 26) or the adaxial two lobes, abaxial lateral two and finally abaxial central one (Fig. 27). Thereafter, when all the floral parts grew rapidly and the corolla tube reached five times as long as the limb, the gynoecium and androecium also elongated up to the corolla limb and the flower is ready to open.

2.5 Initiation and development of androecium primordia

Initiation of stamen primordia took place later than that of corolla lobe primordia and they were alternate to the latter. In between the adaxial two lobe primordia and the abaxial lateral two lobe primordia and in between adaxial two lobe primordia but more inwardly occurred three oblate protuberances. They are two posterior stamen primordia and one staminode primordium (Fig. 17). Following enlargement of the three primordia, the other two small rounded protuberances occurred on lateral sides of abaxial central corolla lobe primordium but closer to the centre of the floral apex. These were anterior two stamen primordia (Fig. 19). When the corolla tube enlarged in height and width and reached a diameter of 60 μ m, the corolla lobe primordia began to differentiate, and the stamen primordia continued to enlarge into spherical. At this time, the anterior stamen primordia (ca. 60 μ m in diameter) were slightly larger than the posterior two (ca. 54 μ m in diameter), while the staminode primordium maintained the smallest (ca. 36 μ m in diameter) (Figs. 20, 21). As the corolla lobe primordia flattened and curved inwards, the fertile stamen primordia flattened and elongated into nearly spherical (Figs. 22-24), and then horizontally elongated. Soon they sank into a slit at surface and constricted in the middle. Thus anther locules and connective differentiated, and the prototype of anthers had formed, becoming oblong, 300 μ m in length and 165 μ m in width, whereas the staminode primordium developed

much later and grew slowly, becoming rectangular, only 54 μ m in length and 41 μ m in width (Fig. 32).

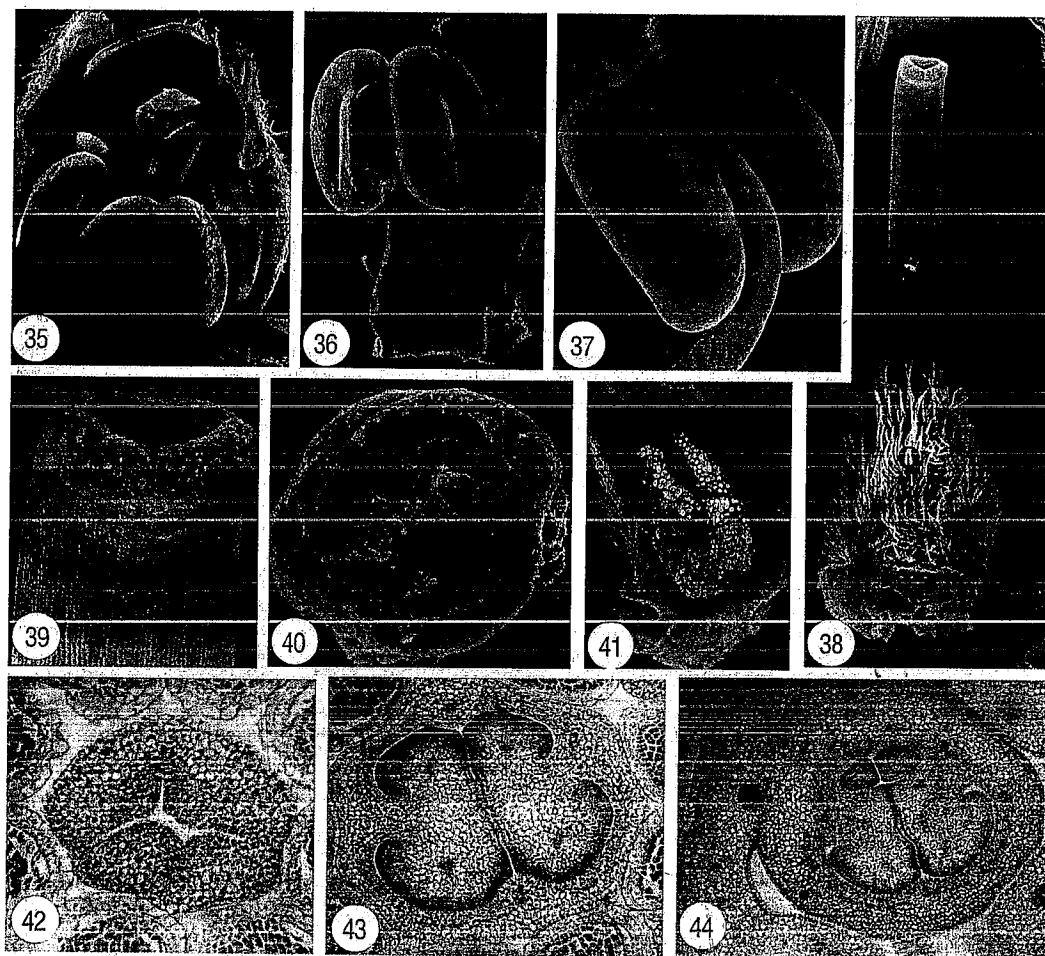
As anther locules elongated right downwards and widened, the sunken slit became even more remarkable and anther locules ellipsoid (Fig. 33); the staminode flattened into lamellate, 0.6 mm long, without an obvious filament (Fig. 34). Filaments of the fertile stamens departed from near the base of corolla tube and were dorsifixed. Owing to relatively slow growth of the anterior stamens the four fertile stamens became didynamous and free at the top (Figs. 35-37).

2.6 Initiation and development of gynoecium primordia

The gynoecium primordium was derived directly from the central meristem of the pentagonal floral apex. When the corolla lobe primordia flattened and curved inwards, and the stamen primordia began to differentiate, the centre of the floral apex swelled upwards and subsequently sank at the very centre, forming a arched depression (Fig. 22). The depression continued to sink and enlarged into a nearly orbicular hole, which divided the central part of the pentagonal floral apex into two unequal meristem regions, with the abaxial region much larger than the adaxial one, and two carpel primordia thus began to differentiate (Figs. 23, 24, 28). As the carpel primordia widened below and arose upwards above, and the meristem in the hole continuously differentiated, the adaxial and abaxial sides of each carpel primordium grew at different rates and thus they became arched (Figs. 29-31). When the two carpel primordia enlarged at the base and grew upwards, they became conical and gradually constricted into unequally two-lipped at the top. At this time, ovary and stigma had formed, but style had not initiated yet (Figs. 32, 33).

As verrucose protuberances occurred on the outer wall of the ovary and gradually developed into multicellular hairs, the gynoecium continued to constrict at the top, and due to intercalary growth the top grew upwards rapidly up to the corolla limb in height, forming a cylindrical style (Figs. 34, 35, 38). In a transverse section, margins

Figs. 21-34. - SEM observations on morphogenesis of inflorescences and floral organs. 21. Continuous flattening and elongating of abaxial central lobe of corolla, four fertile stamens primordia and delayed development, and staminode primordium, $\times 210$. 22-24. Inwards curving corolla lobes; adaxial lobes slightly longer than the others, corolla tube, fertile stamens starting flattening, central arched slit (hole) of flower primordium dividing meristem into two unequal regions, and two carpels at early stage of development. 22. $\times 120$. 23. $\times 132$. 24. $\times 90$. 25, 26. A flower bud, showing aestivation from outside to inside: abaxial central lobe, abaxial lateral two and finally adaxial two, indumentum on the outer surface of corolla. 25. $\times 72$. 26. $\times 24$. 27. A flower bud, showing aestivation from outside to inside: adaxial two lobes, abaxial lateral two and finally abaxial central one, $\times 18$. 28-31. Early development of two carpel primordia. 28. Further sinking of meristem, starting differentiation, $\times 150$. 29. Sinking area forming a hole; carpels becoming arched in shape; anterior stamens growing horizontally; slit between anther locules starting separation, $\times 240$. 30. Two carpels growing upwards; and their margins starting separation, $\times 180$. 31. Two carpels growing quicker on dorsal side than on ventral side, thus both becoming u-shaped, $\times 180$. 32-34. Development of androecium and gynoecium. 32. The abaxial carpel rapidly growing and slightly enveloping margins of the adaxial carpel, making the top of carpels unequally 2-lipped; fertile stamens growing horizontally, anthers sinking longitudinally and anther locules had differentiated; staminode getting lamellar, $\times 60$. 33. Anther locules longitudinally elongating; conical and unequally 2-lipped stigma constricted near the top, $\times 30$. 34. Developing fertile stamens and staminode, and verrucose protuberances and indumentum on the outer surface of ovary, $\times 18$. Abbreviations: Al, anther locule; Cl, abaxial carpel; C2, adaxial carpel; Cb, abaxial lateral lobe primordium of corolla or abaxial lateral lobe of corolla; Cc, abaxial central lobe primordium of corolla or abaxial central lobe of corolla; Co, connective; Sn, staminode primordium or staminode.



Figs. 35-44. 35-39. SEM photographs of floral organs. 35. A flower bud with sepals removed to show adaxial corolla lobes, one abaxial lateral lobe, fertile stamens, style and stigma, $\times 12$. 36. Fertile stamens, showing subulate filaments; $\times 15$. 37. Fertile stamens, showing dorsifixed anthers, $\times 12$. 38. Gynoecium, showing ovary, style and stigma, $\times 12$. 39. Enlargement of stigma shown in Fig. 38, $\times 48$. 40, 41. Transverse and longitudinal sections of ovary, showing two parietal placentae. 40. $\times 12$. 41. $\times 21$. 42-44. Transverse sections of ovary 5 mm long and embedded in wax, showing one locule and two parietal placentae from near the base to near the top. 42. Near the top, $\times 128$. 43. At the middle, $\times 64.5$. 44. Near the base, $\times 51$.

Abbreviations: Fi, filament; O, ovary; ST, style; St₁, abaxial stigma; St₂, adaxial stigma.

of two carpels had fused to form a syncarpous ovary, protruded inwards and reflexed, so that they did not fuse at the centre and thus formed a one-locular ovary (Fig. 40). In the longitudinal section the placentae with numerous ovules extended from the base to the top of ovary without formation of central septum (Fig. 41). Consecutive transverse sections of a flower 5 mm long and embedded in wax show that margins of the two carpels completely fused and protruded inwards to nearly the centre but reflexed, and thus they did not fused there. Therefore, two-carpellary ovary still maintained one-locular, with two parietal placentae (Figs. 42-44).

3 Discussion and Conclusion

3.1 The structure of stigma

Wang *et al.*^[1] and Li and Kao^[3] considered that the genus *Titanotrichum* had two-fid stigma with the anterior segment lingulate and shallowly two-lobed. Our investigation shows that the two carpels maintain free at the apex from initiation (Figs. 33, 34). Their apices are always free and have never fused at all the stages of development. We also found that the carpels constrict only near the top and their apices become unequally two-lipped. As intercalary growth takes place in the constricted region the

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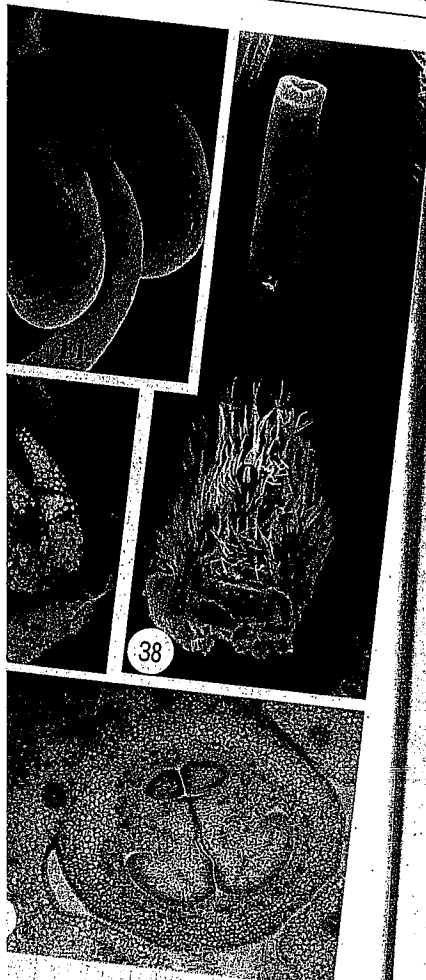


Fig. 37. Fertile stamens, showing part of stigma shown in Fig. 38, $\times 48$. 40, $\times 21$. 42 - 44. Transverse sections of ovary to near the top. 42. Near the top, $\times 128$.

Conclusion
Stigma
 Li and Kao^[3] considered that the stigma is two-lobed with the anterior margin shallowly two-lobed. Our investigation shows that the stamens and carpels maintain free at the apex (Fig. 34). Their apices are always free at all the stages of development. The carpels constrict only near the apex and become unequally two-lipped. As a result, the stigma in the constricted region the-

style differentiates and elongates, and the stigma continues to differentiate till its maturity, but no further division is found for the lower segment (Figs. 35, 38, 39). This pattern of development is consistent with that of *Rehmannia glutinosa* revealed by WANG Yin-Zheng and his co-workers (WANG Yin-Zheng's unpublished data).

3.2. Anthers always free

Wang et al.^[11] and Li and Kao^[3] consider that anthers of the four fertile stamens connate at the top in pair, but the present study shows that the anthers are always free from their initiation to maturity.

3.3. The initiation and development of primordia of calyx, corolla and androecium

It was found in the present investigation that in the genus *Titanotrichum* sepals are free and all derived separately from different sepal primordia, which are connected to each other laterally only at the very base, and thus they are connate only at the very base (Fig. 14). According to initiation and size of the sepal primordia, the initiation order of sepal primordia is from abaxial two sepal primordia: adaxial one and finally to adaxial two (Figs. 7 - 9), while their development order is from adaxial sepal, lateral two and finally to abaxial two (Figs. 10 - 14). According to the present observations, initiation and development of corolla lobe primordia are consistent in order, i. e. first abaxial central lobe, abaxial lateral two and finally adaxial two (Figs. 16 - 24). Aestivation of corolla is found to be imbricate: from outside to inside abaxial central lobe, abaxial lateral two, and finally adaxial two (Figs. 25, 26), or abaxial lateral two lobes, adaxial two and finally abaxial central lobe (Fig. 27). The posterior stamen primordia are earlier than the anterior ones in initiation, but they are simultaneous in development; the staminode primordium is simultaneous with the posterior stamen primordia in initiation, but smaller and delayed in development. Finally, the staminode is without differentiation of anther and filament, and is lamellar in structure, only 0.75 mm long (Figs. 19 - 23).

3.4 Comparison with related groups

Most authors^[3,9,12] emphasize number of ovary locules in delimitation between the Scrophulariaceae (two-locular, with axile placentation) and the Gesneriaceae (one-locular, with parietal placentation). The Gesneriaceae is usually one-locular, with parietal placentation, less frequently two-locular, with axile placentation, or two-locular but one locule developed while the other reduced. The observations on floral organogenesis show that in *Rehmannia* of the Scrophulariaceae and *Rhynchoglossum* of the Gesneriaceae ovary changes in number of locules with development from two-locular with axile placentation in the lower part to one-locular with parietal placentation in the upper part^[13] (WANG Yin-Zheng's unpublished data). In *Whytockia* of the Gesneriaceae the ovary is always two-locular with axile placentation from the base to the top^[14,15] (WANG Yin-Zheng's unpublished data). The initiation of carpel primordia in *Titanotrichum* is consistent with that in *Whytockia*, *Rhynchoglossum* and *Rehmannia*. In the genus under study,

however, margins of two carpels primordia curve inwards and fuse, forming a syncarpous ovary, and the margins continue to extend toward the centre, but they do not fuse there, and thus the ovary maintains one-locular, with two parietal placentae (Figs. 28 - 34), and is different from those in the above three genera. The order of development of sepal primordia in *Titanotrichum* is from adaxial sepal to abaxial, and is almost completely consistent with that in *Rehmannia* and *Whytockia*, but different from that in *Rhynchoglossum*, which is simultaneous in development. The aestivation of sepals in *Titanotrichum* is valvate and is similar to that in *Rhynchoglossum* and *Rehmannia*, but different to that in *Whytockia* which is imbricate^[13] (WANG Yin-Zheng's unpublished data).

The order of initiation of corolla lobe primordia in *Titanotrichum* (abaxial central lobe, abaxial lateral two, and adaxial two) is basically similar only to that in *Rehmannia* (WANG Yin-Zheng's unpublished data), and different from that in *Whytockia* and *Rhynchoglossum*, where all the five primordia initiate simultaneously^[13] (WANG Yin-Zheng's unpublished data). At the stage of flower bud the aestivation of corolla lobes in *Titanotrichum* (Figs. 25 - 27) differs apparently from that in *Rehmannia* and *Whytockia*: abaxial two lobes, adaxial two and abaxial central one from outside to inside (WANG Yin-Zheng's unpublished data); no observation has been conducted for *Rhynchoglossum*.

The four genera are different from each other in order of initiation of fertile stamen primordia. In *Whytockia* and *Rhynchoglossum*, they arise simultaneously^[13] (WANG Yin-Zheng's unpublished data), in *Rehmannia* the anterior primordia occur first (WANG Yin-Zheng's unpublished data), while in *Titanotrichum* the posterior ones come first (Figs. 16, 17). With initiation stamen primordia are earlier than corolla lobe primordia in *Whytockia* (WANG Yin-Zheng's unpublished data), but later than those in all the other three genera, which are consistent in this respect.

We understand, based on the observations on floral organogenesis of the above four genera, that floral organogenesis is diverse in the Scrophulariaceae and Gesneriaceae. Relationships between the two families in floral organogenesis are also complex; the four genera do not form two patterns: one in the Gesneriaceae, while the other in the Scrophulariaceae. The delimitation between the two families as conventionally done using number of ovary locules and placentation type is not convincing. The two families need to be further studied in systematics.

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台闽苣苔(苦苣苔科)花部器官的形态发生

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摘要: 在扫描电镜下对台闽苣苔(*T. oldhamii* (Hemsl.) Solereder)进行了花部器官形态发生的观察,为探索该类群的个体发育、类群间的系统发育关系和进化趋势提供依据。研究发现该属植物萼片、花冠和雄蕊发生式样均为五数花类型,它们各自来源于花原基上分化出来的萼片原基、花冠原基和雄蕊原基;花冠与雄蕊的两侧对称性与花冠上唇生长稍快和退化雄蕊原基发育迟滞相关;萼片原基的发生和发育的顺序是不一致的:萼片原基发生的式样为近轴中原基—远轴2原基—2侧原基,发育式样则为近轴中萼片—2侧萼片—远轴2萼片,花蕾时为镊合状排列。花冠裂片原基的发生和发育式样是一致的,即远轴中裂片(下唇中裂片)—远轴2侧裂片(下唇2侧裂片)—近轴2裂片(上唇2裂片)。花蕾期卷迭式为覆瓦状排列,从外向内:下唇中裂片—下唇2侧裂片—上唇2裂片或下唇2侧裂片—上唇2裂片—下唇中裂片。雄蕊原基与花冠裂片原基互生,前方雄蕊原基在发生上稍迟于后方雄蕊原基,后者与退化雄蕊原基几乎同时发生,但较小,并与近轴心皮(或柱头上唇)对生。将该属与玄参科(Scrophulariaceae)的地黄属(*Rehmannia*)、苦苣苔科(Gesneriaceae)的异叶苣苔属(*Whytockia*)和尖舌苣苔属(*Rhynchoglossum*)的花部器官比较发现,这四个属在这方面呈现出多样性和交叉。过去一直按子房室数和胎座类型划分玄参科(子房2室、中轴胎座)和苦苣苔科(子房1室、侧膜胎座)这一做法受到了质疑。

关键词: 苦苣苔科; 台闽苣苔属; 花器官发生

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