



MORPHOLOGICAL DEVELOPMENT OF PETALS IN RANUNCULACEAE

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The petals, or the honey-leaves, are of great divergence in morphology in Ranunculaceae, i. e., tubular, bilabial, cup-shaped, flat, concaved or scaled at the base, with or without spur or succate. The previous observations showed that although the petals differ in mature morphology, they showed great similarity in the early development stage. The petal primordia are all hemispherical, rounded and much smaller than the sepal primordia, a relatively long plastochron exists between the last sepal and the first petal and differentiate into a blade and a short stalk. Thus, we assumed that the different morphology of the mature petals might be due to the morphological repatterning of petals in the development. To prove the hypothesis, the morphological development of the petals from 22 species from 20 genera, recovering all ten petalous clades and the major morphological types, in Ranunculaceae was observed by scanning electron microscope (SEM).

The young petal undergoes the following developmental stages to the mature petal after it differentiates into blade and stalk. In the first stage, a depression appears at the base of the blade and the nectary tissue will appear in the depression in the later development. In the second stage, two bulges appear at the base of the depression that makes the petal bilabial and the bulges will be the upper lip of the petal and thus the blade will be the lower lip. In the third stage, two bulges become larger and fuse with one another at first and then fuse with the margins of the blade in each side, or each of the bulges fuses with the margin of the blade at first and then fuses with one another, or the bulges stop further growth and the depression

deepened to form the succate or the spur. In the fourth stage, the lips, the two fused sides and the stalk growth in different speed.

The divergence of development of different petals happens mainly in the third and the fourth stages and less divergence in the second and then the first stages. For example, a tubular petal of *Helleborus thibetanus* undergoes the following developmental stages: a depression appear at the base of the blade, then two bulges appear at the base of the depression, and then the bulges fuse with one another to form the upper lip, the upper lip fuses with two margins of the blade that makes the petal oblique cup-shaped, the growth speed of the upper lip is faster than the two fused sides and that of the later is faster than the lower lip that makes the petal to be tubular; a spurred petal of *Aquilegia yabeana* undergoes the following developmental stages: a depression appears at the base of the blade, then two bulges appears at the base of the depression, the depression deepens to form the spur and the bulges stop further growth.

According to the molecular systematic results, the genera in two basal most clades, *Glaucidium* and *Hydrastis*, are apetalous. *Coptis* and *Xanthorrhiza* are in the next basal most clade, the petal in this clade only has, or sometimes not clear, the depression at the base of the blade and the nectary tissue appears in the depression and the petals in these genera are not bilabial. The rest of the genera form the core Ranunculaceae in which two bulges appear at the base of the depression. The appearance of the bulges can be considered as a key innovation and let the petals get the diverged potential in morphology and finally resulted in the divergence of the genera.

The development processes of the petals in different petalous clades, or even in different petalous genera in the same clade, are different. The bulges might be lost in *Consolida* clade, in this case, the spur is well developed, or only one bulge appears in *Ranunculus* and *Nigella* clades, or both the bulges and the depression might be lost in *Adonis* which has the flat petals without nectary tissue.

The growth of the bulges which becomes the upper lip of the petal or the depression which becomes the succate or the spur can result in the hidden of the honey from the nectary tissue and thus can increase the difficulty for the nectar foraging pollinators and avoiding the non nectar foraging insects and then increase the pollination efficiency and increase the adaptability to different nectar foraging insects.