# Noboru HARA*: Early ontogeny and malformation of *Ginkgo* leaves

## 原　襄*: イチョウの葉の初期発生と奇形

The *Ginkgo* leaf is usually divided into two major lobes, each of which in turn is further dissected into segments. The leaves of the long shoot, especially of epicormic shoots usually have a deep sinus between lobes but there are, however, some leaves which have scarcely any sinus at all (Fig. 1; Critchfield 1970, Foster & Gifford 1974, Hara 1981). Hara (1980) studied the early ontogeny of leaves of epicormic shoots and reported that the basic plan of the *Ginkgo* leaf is principally formed not by a flabellate dichotomy, but should rather be considered to be formed cruciately, at least until the stage of the second bifurcation.

The author has found various malformed leaves on epicormic shoots of a *Ginkgo* tree at the Botanical Gardens, University of Tokyo. In the present study some of the forms of malformed leaves will be reported and the early ontogeny of the leaf primordia of such shoots will be described using a scanning electron microscope (SEM). The deduced ontogenetic process of such malformed leaves will be discussed.

**Materials and methods** Most of the specimens of malformed leaves were obtained in 1980 from epicormic shoots of a female tree of *Ginkgo biloba* L. at the Koishikawa Botanical Gardens, University of Tokyo, Tokyo. The remainder were collected at the Hongo Campus, University of Tokyo. As a comparison, some materials of normal leaves were collected from a tree at the Komaba Campus, University of Tokyo, and some seeds were also collected at the same campus. Shoot tips for SEM micrographs were collected in April 1981, fixed in Craf Ⅲ, dehydrated in ethyl alcohol, critical-point dried and coated with gold. The SEM micrographs were prepared on a Hitachi S-405 SEM set at 15 kv.

**Observations**

Gross morphology of the malformed leaf: Various leaves from epicormic shoots of the tree in the Botanical Gardens are described here. Some leaves

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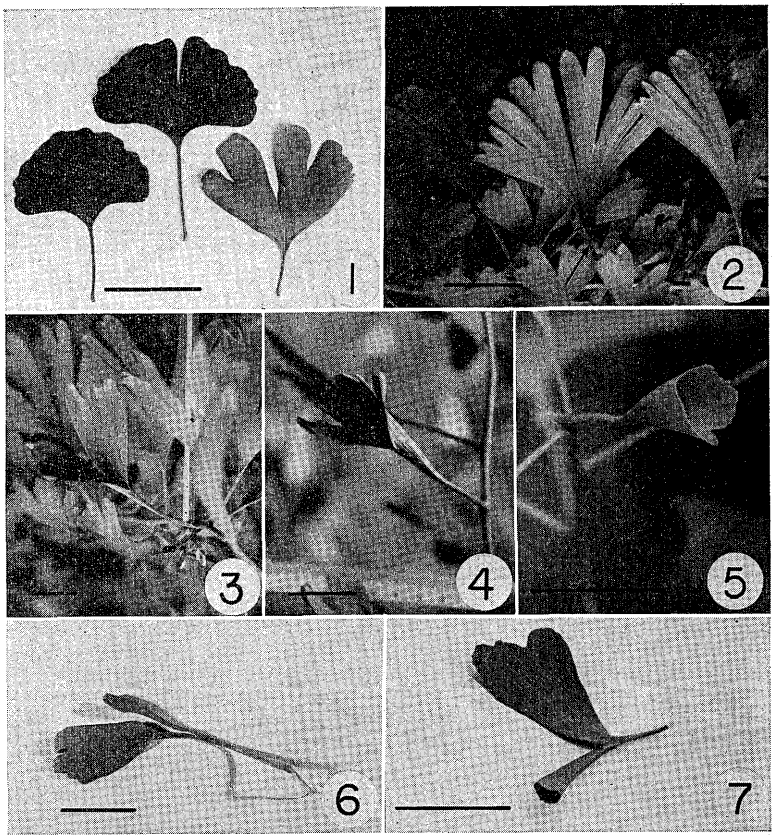
showed extremely deep sinuses, although such sinuses are not characteristic of malformation. The connecting region between the lamina and the petiole of such leaves is cup-shaped, as shown by the arrow in Fig. 2 and is called the 'cup-shaped lamina base' in the present study (although it is very small in the case of Fig. 2). The leaves shown in Fig. 3 and Fig. 4 also clearly have cup-shaped lamina bases.

The leaf shown in Fig. 5 was found in 1982 on a seedling grown from a seed collected at the Komaba Campus, University of Tokyo. This leaf has a completely cup-shaped lamina. On the tree at the University of Tokyo Botanical Gardens there were also several young cup-shaped leaves on epicormic shoots in spring, but only a few mature cup-shaped small leaves in summer and autumn. Some young cup-shaped leaves developed in summer into leaves such as shown in Figs. 3 and 4, but only few became precociously mature cup-shaped small leaves. The latter were usually found on sylleptic short shoots grown on epicormic shoots. Furthermore, there were found two cup-shaped half-leaves at the Hongo Campus (Fig. 6) and the Botanical Gardens (Fig. 7). A half of such a leaf has a flat laminal part with the other half being cup-shaped. The flat laminal part shown in Fig. 6 has a cup-shaped base such as the cup-shaped lamina base of the leaf in Fig. 3.

Early ontogeny of the leaf primordium: The early ontogeny of the leaf primordium of normal leaves from a tree at the University of California, Berkeley has been studied using the SEM (Hara 1980). In the present study the author has tried to confirm the results obtained in the former study and compare the leaf development of normal leaves to that of malformed leaves. The specimens for the present study were obtained at the Komaba Campus, University of Tokyo. As in the previous study, the leaf primordium obtained in Tokyo shows successive bifurcations (Fig. 8). The second bifurcation occurs cruciately, that is, at approximately a right angle to the first. Thus, the abaxial surface of the lamina is derived from the outer surface of the leaf primordium and the adaxial surface is derived from the depressed inner surface formed by the first and second bifurcations of the primordium.

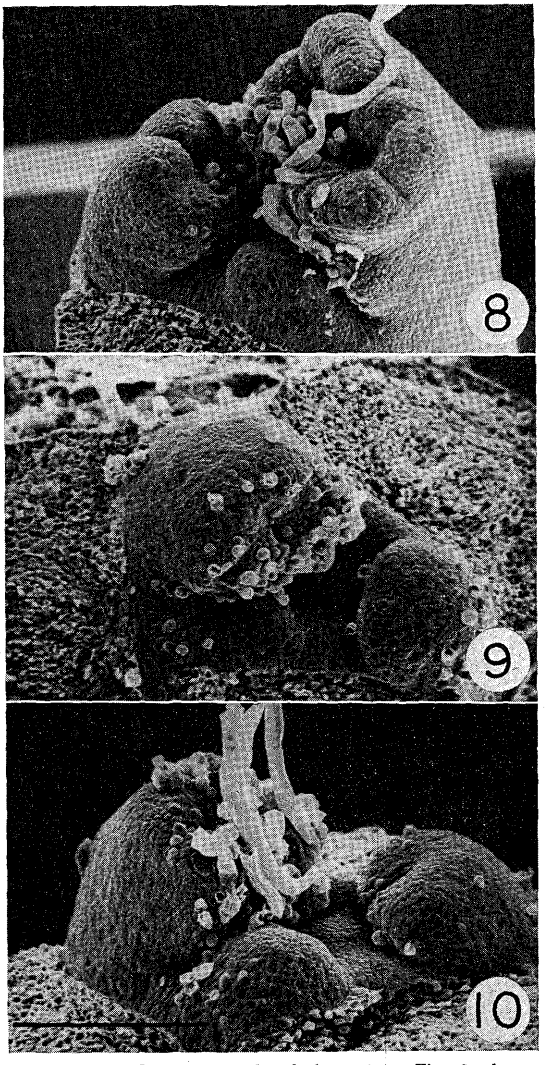
The shoot tips from epicormic shoots of the tree in the Botanical Gardens are shown in Figs. 9 and 10. The principal plan of the development of the leaf primordium seems to be almost the same as that of the normal primordium shown in Fig. 8 in that the primordium shows successive bifurcations. However,




Figs. 1-7. Fig. 1. Normal leaves. Fan-like leaf (left), leaves dissected into two segments (middle) and four segments (right). Scale=ca 5 cm. (After Hara 1981). Fig. 2. Leaf dissected into several segments with extremely deep sinuses. There is a small cup-shaped lamina base (arrow). Scale=ca 5 cm. Figs. 3, 4. Leaves with a cup-shaped lamina base: Fig. 3, the inside of the leaf is seen from the upper side of the leaf; fig. 4, the inside is seen from the lower side of the leaf. Scale=ca 3 cm. Fig. 5. Cup-shaped leaf on a seedling. Scale=ca 3 cm. Figs. 6, 7. Cup-shaped half-leaves. Half of the lamina is cup-shaped and the other half of the leaf has a cup-shaped base in fig. 6 and is normal in fig. 7. Scale=ca 3 cm.

the furrows produced by bifurcations are more shallow than those of the normal primordium. The depression is also shallow, at least in the early ontogenetic stages as shown in Figs. 9 and 10.

**Discussion** Watari (1936) described cup-shaped *Ginkgo* leaves from the Hongo Campus and reviewed papers concerned with such leaves. However,




Figs. 8-10. SEM micrographs of shoot tips. Fig. 8, shoot tip of an epicormic shoot of a tree that forms normal leaves. Figs. 9 and 10, shoot tips from a tree that is likely to form malformed leaves. Primordium in fig. 8 shows cruciate bifurcations with deep furrows. Shoot tips in figs. 9 and 10 show cruciate bifurcations with shallow furrows. Scale=ca 300 $\mu$m.

there has been no study which has reported in detail on the ontogenetic process of the malformed leaf. In this report the process of the malformed *Ginkgo* leaf is correlated to that of the normal leaf. The author attempts to explain the presence of various forms of malformed leaves of *Ginkgo*, observed in the present study, from the ontogenetic process of cruciate bifurcations.

The normal leaf is formed as follows (cf. Fig. 8, Fig. 11A; Hara 1980). The first and second bifurcations occur successively which result in the formation of furrows on the primordium. The furrows are clearly seen in the apical view of the primordial lamina. The furrow, which is formed by the first bifurcation, becomes deep on the adaxial side forming the typical pattern of the dorsiventral lamina.

By deduction then, the cup-shaped leaf shown in Fig. 5 and Fig. 11D could be formed if the lamina

sector of the primordium did not separate at the adaxial side; and the malformed leaf shown in Fig. 3 and Fig. 11B could be formed if the lamina sector was incompletely separated at the adaxial side. Such a leaf as shown in Fig. 4 and Fig. 11C might be produced. In this case, of course, the furrow on the adaxial side of the primordium would not be deep, but that on the abaxial side would be relatively deep.

The cup-shaped half-leaves shown in Figs. 6 and 7 show that even half of a leaf can form a cup-shape. The development of such leaves is shown in Fig. 11E.

It was suggested by Hara (1980) that the basic plan of the *Ginkgo* leaf is

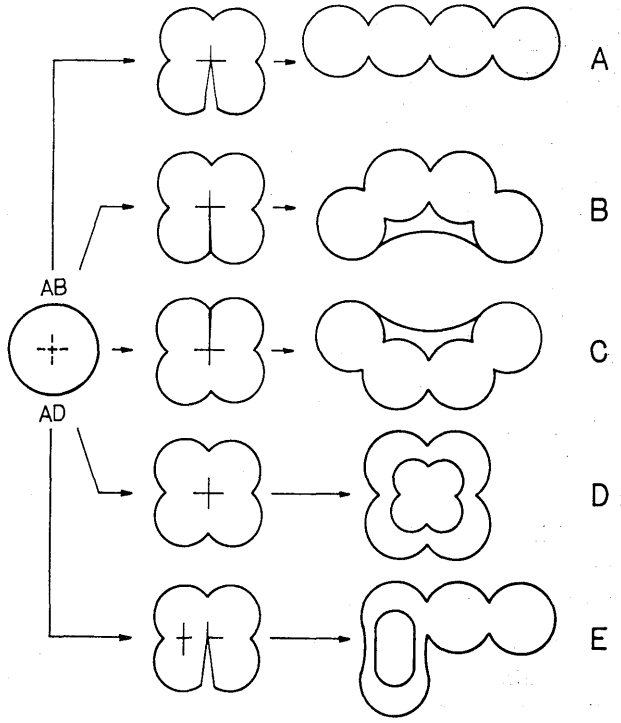



Fig. 11. Diagrams (as seen from above) of the deduced ontogentic processes of the lamina. A circle on the left represents the primordium at a very early stage. A: the development of the normal leaf (discussed in Hara, 1980). B-E: the development of malformed leaves. AB, abaxial; AD, adaxial.

principally formed not by a flabellate dichotomy, but should rather be considered to be formed cruciately, at least until the stage of the second bifurcation. The form of the cup-shaped half-leaf found in the present study is further suggestive that the basic plan of the *Ginkgo* leaf is formed cruciately even through the stage of the third bifurcation.

From a tree at the Botanical Gardens, University of Tokyo, which forms malformed leaves of various types, leaf primordia with relatively shallow furrows have been observed on the shoot tips of epicormic shoots. Such shallow furrows of the primordia might be correlated to cuu-shape formation. The shallowness in the early stage of ontogeny might be correlated to retardation of vertical separation which then forms a different pattern of the dorsiventral lamina. However, dissected lamina sectors of such leaves are able to grow actively in a relatively late stage of ontogeny to form extremely deep sinuses, because a number of fully developed, extremely dissected leaves such as shown in Fig. 2 were found. The formation of the complete cup-shaped leaf such as shown in Fig. 5 seems to be correlated to precocity. As far as the present study is concerned, the mature cup-shaped leaves seem to be the ones which have failed to elongate the dissected lamina sectors during a relatively late stage of ontogeny.

Thus, the process of the malformed leaf formation in *Ginkgo* can be deduced from the ontogenetic process of the primordium of the normal leaf. Also, the forms of the malformed leaves seem to reflect the ontogenetic process of cruciate bifurcations.

In the present study, the deduced morphological process of malformed *Ginkgo* leaves was discussed. Although Maekawa (1948) discussed the dichotomy of *Ginkgo* in correlation to the cup-shaped leaf, there may be a need to study much more before an adequate discussion on the phylogeny of *Ginkgo* can be made, and the dichotomy in *Ginkgo* should be compared to that in the primitive vascular plants.

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**Literature cited**

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イチョウの奇形葉についてはすでに多くが知られているが，本研究ではおもに東京大学理学部付属植物園のイチョウの'ひこばえ'に生じた奇形葉を観察した。盃状葉 (Fig. 5)，葉身の半分が盃状になった半盃状葉 (Figs. 6, 7)，葉身基部が盃状になった基部盃状葉 (Figs. 3, 4) が観察された。このような奇形葉を生じやすいひこばえの茎頂付近を走査型電子顕微鏡で観察したところ，奇形葉の発達過程は十字二又分枝状に発達をする正常な葉の発達過程に関連が深いと推察することができた。

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□杉本順一：**静岡県植物誌** (SUGIMOTO, J.: Flora of Shizuoka Prefecture) 814 pp., 4 pls. 1984. 第一法規出版株式会社. ¥12,000. 著者が60年以上にわたって自ら踏査して集めた資料を基にした待望の書が出版された。静岡県は海岸から高山まで，また地質的にも多岐にわたる環境下にあって豊富な植物相が見られ，富士，箱根，伊豆など古くから多くの学者によって調査されている地域をふくみ，これをまとめることは至難な仕事であるが，一方学問的には最も興味ある地域の一つである。本書にはこれまで記録された約4800の高等植物が網羅され，その全部に要をえた記載がつけられ，県内の産地がかなり詳しく記されている。筆者は周知のように，静岡県だけでなく日本の植物全体について広い知識と長い経験をもち，文献にも落ちなく目を通しており，その同定に信頼性が高く，フローラとして大切な細かい変異を初め専門家が知りたいと思うデータがうまくとりいれられている。いわば静岡県産高等植物の戸籍原簿というべきものである。今後開発などによって失われる植物も増えるであろうし，新しい研究によって分類方式や学名などが変ることがあっても，日本植物の進化や変遷など歴史的考察を必要とする研究に適確な基礎資料を提供する不朽の書である。高齢の著者が戦災により大切な標本をすべて失われた不幸をのりこえて，残された記録と新たに集められた資料をここに集大成された熱意に対し敬意を表したい。 (原　寛)