Developmental Studies on the Leaf and the Extra-Axillary Bud of *Histiopteris incisa*

RYOKO IMAICHI

Faculty of Agriculture, Tamagawa University, Tamagawa-Gakuen 6-1-1, Machida-shi, Tokyo 194

Anatomical and developmental studies have been made of *Histiopteris incisa* in order to obtain a reasonable interpretation of the so-called extra-axillary bud. Single, or rarely two extra-axillary buds arise on the lateral side of the petiolar base. The branch trace appears to depart from the basiscopic margin of the leaf trace. At the earliest stage of the leaf initiation, the leaf apical cell is cut off in one of the prismatic cells of the shoot apical meristem. The leaf apical cell, then, cuts off segments successively to form a well-defined group of derivatives. On the other hand, a well-recognized cell group called “outer neighboring cell group”, onc, is found adjacent to the abaxial boundary of the derivatives of the leaf apical cell. This group of cells does not originate directly in the mother cell of the leaf apical cell. The primordium of the extra-axillary bud is always initiated in the superficial pillar-shaped cell layer of onc. The leaf primordium may consist of two parts, the distal part derived from the leaf apical cell and the basal part from the adjacent cells including onc. These facts suggest that the extra-axillary bud is of foliar nature.

Key words: Dennstaedtioid fern — Developmental morphology — Extra-axillary bud — Leaf primordium — Shoot apex.

So-called extra-axillary buds are located on the lateral or abaxial side of the petiolar base in most dennstaedtioid fern genera, *Dennstaedtia, Histiopteris, Hypolepis, Paesia*, etc. This type of bud was called “petiolar shoot” by Troop and Mickel (1968), because the branch trace comes from the petiolar bundle not departing directly from the stele of the stem. The extra-axillary bud has been interpreted either as the weaker shank of an unequal dichotomy of the rhizome (Bower, 1923) or as the phyllogenous branch (Goebel, 1928; Troll, 1937).

The author has observed the extra-axillary bud in *Hypolepis punctata* (Thunb.) Mett., which is formed at the base of the leaf primordium (Imaichi, 1974). In the present investigation, special attention has been concentrated on the initiation and development of the extra-axillary bud in *Histiopteris incisa*, which exhibits a similar branching pattern in the petiole to *Hypolepis punctata*, in order to obtain basic information for the interpretation of the petiolar branching in relation to other branching patterns in ferns.

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Materials and Methods

The rhizomes of *Histiopteris incisa* (Thunb.) J. Sm. were collected in the Izu Peninsula. The materials were fixed with Craf I solution for 24 hr (Sass, 1958). Then, they were dehydrated in n-butyl alcohol series and embedded in paraffin. Serial longitudinal or transverse sections of the shoot apex were cut at a thickness of 8 μm, and stained with Delafield’s hematoxylin, safranin, and fast green. The longisections were cut in such an orientation as to include the following three portions in the median plane of section; the center of the shoot apical meristem, the youngest leaf primordium and its extra-axillary bud, as indicated by a line in Fig. 1. The vasculature of rhizome was observed by removal of epidermis and cortical tissue by use of tweezers and needle under a dissecting microscope. The stripped vascular bundles were bleached and then stained with safranin.

Observations

Gross morphology

*Histiopteris incisa* has an underground or surface creeping rhizome, 5–10 mm in diameter. The rhizome does not branch dichotomously, but the extra-axillary bud often grows as a lateral shoot so as to make up a complex shoot system (Fig. 2). Leaves are arranged in two rows on the dorsal side of the rhizome. On the apical dome, the new leaf primordia appear at a divergence angle of approximately 90 degrees (Fig. 3). The basal part of the leaf is covered with brown scales, and numerous adventitious roots exist mainly in this region, as in the case of *Hypolepis punctata* (Imaichi and Nishida, 1973).

Usually only one extra-axillary bud is found at the lateral side of the base of a petiole. In many cases, the leaf and the bud seem to arise at the same position on the rhizome (Fig. 4). Sometimes the bud emerges on the petiole 5–10 mm above the level of the leaf insertion, as in *Hypolepis punctata* (Fig. 5). In a few instances, the bud does not protrude from the petiole, but directly from the rhizome (Fig. 6). The second extra-axillary bud is rarely found in this species, and, if present, is located on the side opposite to the first one on the petiolar base (Fig. 7).

Vascular system of the shoot

The rhizome of *Histiopteris incisa* has a solenostelic stele, in which a leaf gap (lg) is formed at the departure of the leaf trace (Figs. 8, 9A and 10A). In addition, there are one or more narrow perforations (p) in the leaf trace. The vasculature of a young and small-sized specimen with a fairly thin rhizome is shown in Fig. 8. Although the extra-axillary bud of this specimen seems to have arisen directly from the rhizome (cf. Fig. 6), the branch trace departs from the basiscopic margin of the leaf trace remaining in the cortex of the rhizome. The petiolar bundle (pb) is U-shaped in transection, without further division into small strands. The vasculature of a young but somewhat larger specimen with a bud protruding from the petiole above the level of the leaf insertion (cf. Fig. 5) is shown in Fig. 9. The leaf trace consists of three strands so that