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Ontogeny of trichomes in taxa of genus *Plantago* L. subgenus *Plantago*

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Abstract

The development of three types of headed hairs has been studied: 1) hairs with a unicellular stalk and a head divided vertically into two cells, 2) bottle-like hairs, 3) morel-like and two types of headless hairs: a) with a characteristic 2-3-celled base, b) without the characteristic base in six representatives belonging to 4 sections of the genus *Plantago* L. The bottle-like and the morel-like hairs may have originated from the hairs with a unicellular stalk and a head divided vertically into two cells. The *Plantago* sections characterized by the presence of the bottle-like and morel-like hairs are probably evolutionally younger than the sections characterized by the presence of hairs with a unicellular stalk and a head divided vertically into two cells.

Key words: genus Plantago L., hair ontogeny

INTRODUCTION

According to published data, headed as well as headless hairs originate in various plants from one epidermal cell, the so-called initial cell (Inamdar and Patel 1971, Heinrich 1973, Jain and Singh 1973, Singh et al. 1974, Gangadhara and Inamdar 1977, Gupta and Murty 1977, Seithe 1979, Bory and Clair-Maczulajtys 1980, Inamdar and Rao 1981, Pridgeon 1981, Mathew and Shah 1983, Sahu 1984, Jose and Inamdar 1988). In the early stages of their development, initial cells are similar to other epidermal cells (Jain and Singh 1973). Later they distinguish themselves by size, shape, cytoplasm density and cell nucleus size (Jain and Singh 1973, Singh et al. 1974, Gupta and Murty 1977, Inamdar and Rao 1981, Jose and Inamdar 1988). Hypodermal cells may also be

involved in the origination of hairs (Gangadhara and Inamdar 1977, Bory and Clair-Maczulajtys 1980).

According to Uphof (1962) trichomes "start their development with the formation of a papilla which in the glandular hair is clavate or at least more or less rounded at the tip, in the non-glandular ones usually acute". No such difference was observed in the study of Inamdar and Patel (1971) in *Vahlia,* Singh et al. (1974) in *Salvia* or Gupta and Murty (1977) in *Ononis*.

The development of hairs usually already takes place in the germinal stage (Bory and Clair-Maczulajtys 1980, Danilova and Kashina 1987). Seite (1979) and Seithe and Anderson (1982) noticed that during the further development of a plant the hairs may lengthen but the number of cells of which they are built does not change.

After the fulfilment of their functions the secretory trichomes degenerate and are replaced by non-secretory ones (Horner and Lersten 1968). The hairs may detach in a place characteristic for every type leaving so-called traces on the epidermis consisting of a basal cell only or also including one or more of the first stalk cells, sometimes a fragment of the first stalk cell (Uphof 1962, Edmonds 1982, Andrzejewska-Golec and Świętosławski 1988, 1989).

The studies on the ontogeny of hairs in representatives of such genera as *Solanum* and *Rhododendron* allowed Seithe (1962, 1978, 1979) setup interesting hypotheses concerning phylogeny. According to Seithe (1978) there is no marked difference between the first stages of the ontogeny of some headless hairs and the glands in the taxa of the genus *Rhododendron*. From this he concluded that the taxa with these hairs are related to themselves. He drew the phylogenetic tree of the chori subgenerum.

The ontogeny of hairs in the representatives of *Plantago* has not been studied yet.

MATERIALS AND METHODS

I have examined the development of hairs in the following taxa of the genus *Plantago*:

Sectio *Coronopus* DC.

1. *Plantago coronopus* L. subsp. *cupani* (Coimbra),
2. *Plantago maritima* subsp. *borealis* (Lange) Blytt-Dahl (Copenhagen),

Sectio *Novorbis* Decne

3. *Plantago myosuros* Lam.

Sectio *Arnoglossum* Decne

4. *Plantago lanceolata* L.

Sectio *Leucopsyllium* Decne

5. *Plantago lundborgii* Sparre (Copenhagen),
6. *Plantago aristata* Michx. (Copenhagen).

The seeds were sown on Petri dishes covered by filter paper wetted with tap water. The young seedlings were grown on Petri dishes. The material was examined from the moment of sowing untill the appearance of the first leaves. The cotyledons, hypocotyl, epicotyl and first leaves were used. Cross-sections of the above mentioned plant parts, crushed preparations, or peeled epidermis were examined. The samples were fixed in an aqueous solution of chloral hydrate or in an ethanol solution of Sudan III. Light microscopic figures were drawn with the use of Abbe's apparatus.

The development of three types of headed hairs was observed: 1) with a unicellular stalk and a two-celled head, 2) bottle-like, 3) morel-like and two types of headless hairs: a) consisting of several cells with a characteristic base, b) consisting of several cells without a characteristic base.

RESULTS

All of the observed hair types originate from a single initial cell which differs from other epidermal cells in its size, shape, cytoplasm density, with a well-visible, large cell nucleus — similarly as in the hairs present in the representatives of other genera (see: Introduction). It was not possible to find the initial cell in some species. According to Seithe (1978, 1979), who studied the ontogeny of hairs in taxa of the genus *Rhododendron* and the representatives of *Solanaceae*, this is frequently the case.

The initial cell of the observed types of headed hairs is smaller than the surrounding cells and it is usually located in a slight hollow cave of the epidermis. The initial cell of the observed headless hairs is bigger than the surrounding epidermal cells and juts out of them.

THE DEVELOPMENT OF HAIRS WITH A UNICELLULAR STALK AND A HEAD DIVIDED VERTICALLY INTO TWO CELLS (FIG. 1)

These hairs are common in the genus *Plantago* (Vesque 1885, Unger 1926, Andrzejewska-Golec and Świętosławski 1987, 1988, 1989).

The initial cell was observed only in *P. myosuros* (Fig. 1A). Numerous initial cells appeared on cotyledons of this plant on the second day after sowing; on the third day the two-celled stage consisting of a basal cell and an apical cell was formed (Fig. 1B). Both cells had dense cytoplasm and a large cell nucleus. The apical cell was characteristically bent. On the fifth day, well-shaped hairs with a head divided into two cells (Fig. 1D) and the numerous hairs in the three-celled stage (Fig. 1C) could be noticed. During several of the following days a gradual decrease of the number of three-celled hairs was noticed. The first leaves appeared on the fourteenth day after sowing and they were covered with already well-shaped headed hairs (Fig. 1E).

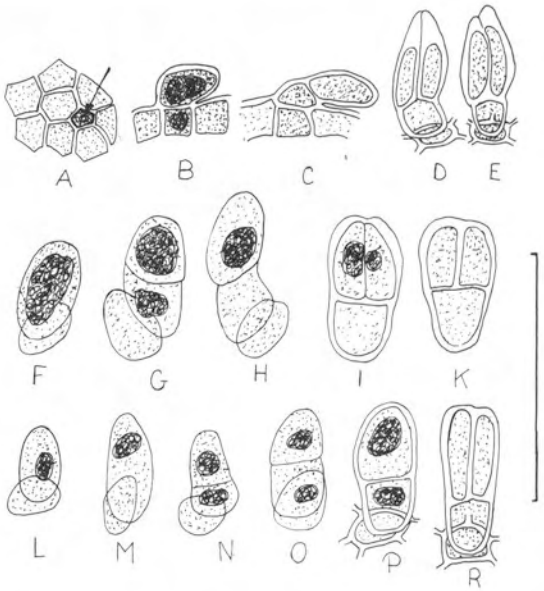

Fig. 1. Development stages of hairs with a unicellular stalk and head divided vertically into two cells on cotyledons: A-E — *Plantago myosuros* Lam., F-K — *Plantago lundborgii* Sparre, L-R — *Plantago aristata* Michx. A — an initial cell (arrow); B, F, L, M — two-celled stage; C, G, H, N-P — three-celled stage; D, I, K, R — developed young hairs on cotyledons, E — developed young hairs on the first leaves. Scale bar 0.1 mm

The development of headed hairs with a unicellular stalk and a two-celled head was similar to the case of cotyledons of the representatives of sectio *Leucopsyllium* (Fig. 1F-R) where the two-celled phase (Fig. 1F, L, M) appeared on the second day after germination and the three-celled stage on the third day (Fig. 1G, H, N-P). During, next 3-5 days the hairs reached the same size and number of cells of the hairs as in florescent plants (Fig. 1I, K, R).

The development of headed hairs with a unicellular stalk and a head divided vertically into two cells in the genus *Plantago* taxa observed by me takes a course similar to the development of this type of hairs in *Labiatae* and *Moraceae* (Singh et al. 1974, Gangadhara and Inamdar 1977, Danilova and Kashina 1987).

THE DEVELOPMENT OF BOTTLE-LIKE HAIRS (FIG. 2)

These hairs are characteristic of taxa of the sectio *Coronopus* (DC.) Dietrich (Andrzejewska-Golec and Świętosławski 1987).

Early phases of bottle-like hair development on cotyledons in the representative of this section — *P. coronopus* subsp. *cupani* — are similar to the developmental stages of hairs with a unicellular stalk and a head divided

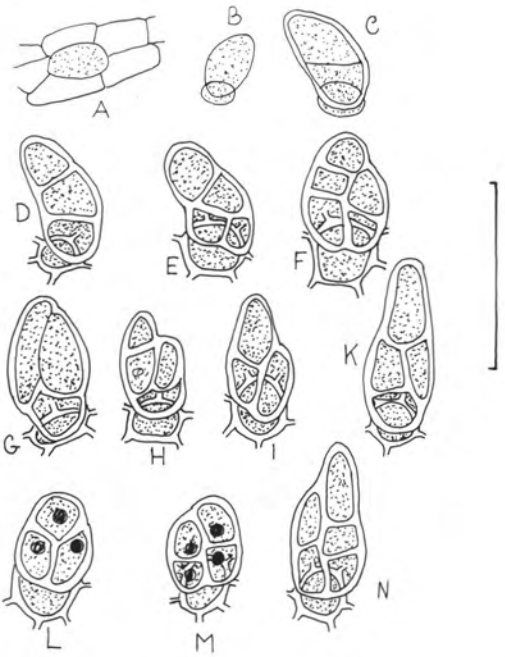

Fig. 2. Development stages of bottle-like hairs on cotyledons of *Plantago coronopus* L. subsp. *cupani*. A — two-celled stage — surface view, B — two-celled stage — side view, C — three-celled stage, D — four-celled stage, E-N — next stages. Scale bar 0.1 mm

vertically into two cells. I observed the two-celled stage on the second day after sowing (Fig. 2A, B) and the three-celled stage on the third day (Fig. 2C). These stages are similar to the analogical development phases of hairs with a unicellular stalk and a head divided vertically into two cells. Yet, the four-celled stage of a bottle-like hair (Fig. 2D) does not resemble a developed hair with a unicellular stalk and a two-celled head. In the case of the bottle-like hairs the first division of a unicellular head takes place in the transverse plan.

THE DEVELOPMENT OF MOREL-LIKE HAIRS (FIG. 3)

These hairs are characteristic of the taxa of sectio *Maritima* Dietrich and *Arnoglossum* Decne (Andrzejewska-Golec and Świętosławski 1987, 1989).

On cotyledons of *P. maritima* (Fig. 3A-K) the two-celled stage was observed two days after the germination (Fig. 3A). On the turn of the second and third day, the three-celled stage originated as the result of vertical cell division (Fig. 3B). On the third day the head was divided horizontally (Fig. 3F) or vertically (Fig. 3C), in the latter case the head resembled a developed hair with a unicellular stalk and a head divided vertically into two cells. A morel-like hair was formed as the result of further horizontal and vertical divisions (Fig. 3D, E, G-K).

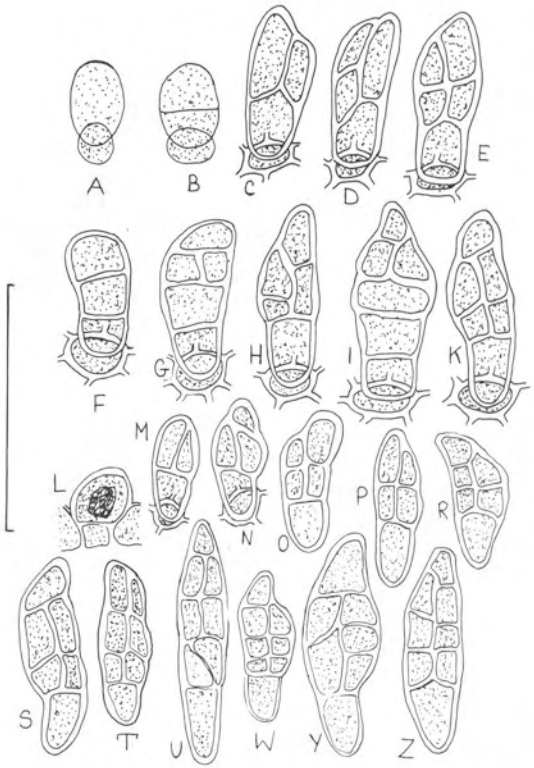

Fig. 3. Development stages of morel-like hairs on cotyledons (A-U) and on the first leaves (W-Z): A-K — *Plantago maritima* L. subsp. *borealis* (Lange) Blytt-Dahl, L-Z — *Plantago lanceolata* L. A, L — two-celled stage, B — three-celled stage; C, F, M — four-celled stage; D, G, H, N-Z — next stages; E, K — developed young hairs. Scale bar 0.1 mm

The development of the hairs of cotyledons of *P. lanceolata* was similar (Fig. 3 L-Z). The two-celled hair stage could already be observed on the day after sowing (Fig. 3L). On the fifth day hairs built of 4 cells similar to the hairs with a unicellular stalk and a two-celled head appeared (Fig. 3M). On the sixth day I observed hairs with a 3-4-celled head (Fig. 3N-P) and on the eleventh day, with a 5-celled head (Fig. 3R, S). The head underwent further divisions and on the 16th day it had 6-8 cells which is as many as in hairs of florescent plants. The first leaves which appeared on the 14th day had well-developed hairs. I did not observe morel-like hairs on hypocotyls or on epicotyls.

Shah and Kachroo (1975) described the development of hairs with a unicellular stalk and a multicellular head in some representatives of the family *Moraceae*. Weberling (1977) described the ontogeny of hairs with a stalk of several cells and multicellular head in *Sambucus racemosa*. The development of these hairs was similar to the stages of morel-like hairs in *Planiago maritima* observed by me.

THE DEVELOPMENT OF HEADLESS HAIRS WITHOUT A CHARACTERISTIC BASE (FIGS. 4, 5)

Initial cells could be observed on cotyledons on the second day after sowing (Fig. 4A, B). On the fourth day, 2-4-celled hairs appeared (Fig. 4C-G), on the fifth, 5-6-celled hairs (Fig. 4H, I). Thus, they had the same number of cells as in florescent plants. The first leaves had headless 1-3-celled hairs (Fig. 5A-C). On the fourth day after the spreading of the first leaves, 4-5-celled hairs could be observed (Fig. 5D, E) and on the sixth day, 6-celled hairs (Fig. 5F). There were no hairs on the hypocotyl or the epicotyl.

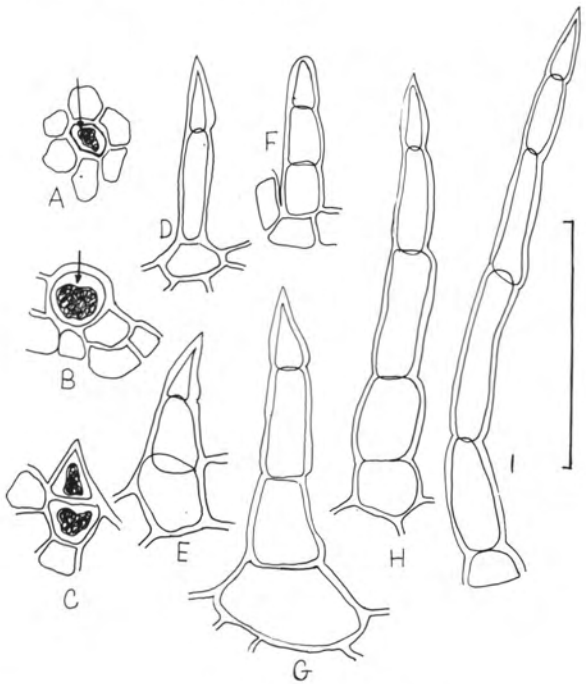

Fig. 4. Development of headless hairs on cotyledons of *Plantago myosuros* Lam. A, B — an initial cell (arrows), C — two-celled stage, D-I — young hairs. Scale bar 0.1 mm

THE DEVELOPMENT OF HEADLESS HAIRS WITH A CHARACTERISTIC BASE (FIG. 6)

On the first and second day of germination the initial hair cells were observed on cotyledons (Fig. 6A, B). They were cone-shaped. The initial cell division into a basal and apical cell took place on the third day (Fig. 6C, D). On the fourth day, the large apical cell was divided vertically into two cells (Fig. 6E, G). During the next several days, further divisions took place resulting in the formation of a hair with 2(3)-celled base (Fig. 6F, H, I-L).

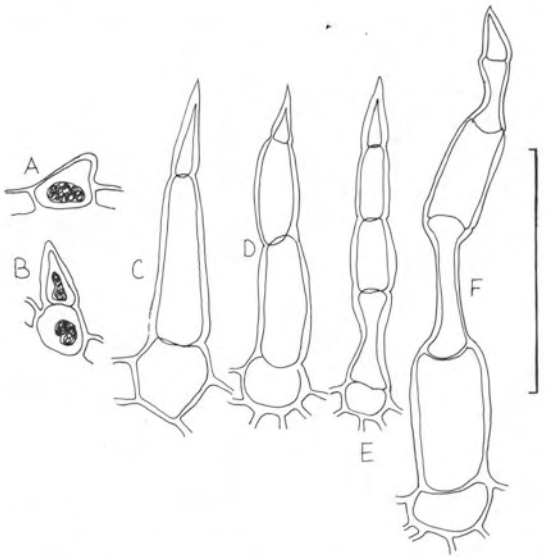

Fig. 5. Development stages of headless hairs on the first leaves of *Plantago myosuros* Lam. A — an initial cell, B — two-celled stages, C-F — young hairs. Scale bar 0.1 mm

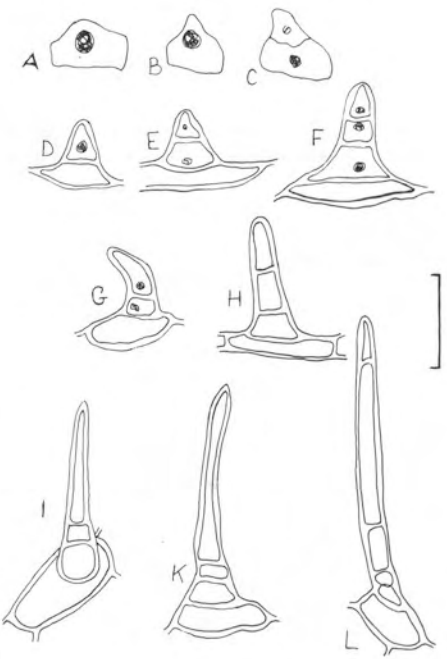

Fig. 6. Development stages of headless with two-three-celled base hairs on cotyledons of *Plantago aristata* Michx. A, B — initial cell, C, D — two-celled stage, E-L — young hairs. Scale bar 0.1 mm

DISCUSSION

Analysis of the development of headed hairs (observation of the first stages) in three types of representatives of the genus *Plantago* let us suppose that bottle-like and morel-like hairs may originate from hairs with a unicellular stalk and a head divided vertically into two cells or that all of the three types have a common origin (Fig. 7). The *Plantago* taxa characterized by the presence of the headed hairs of a more complicated structure eg. sectio *Coronopus* DC. sensu Dietrich (bottle-like hairs), *Maritima* Dietrich ana *Arnoglossum* Decne (morel-like hairs) are probably evolutionally younger than taxa characterized by the presence hairs with a unicellular stalk and a head dividend vertically into two cells.

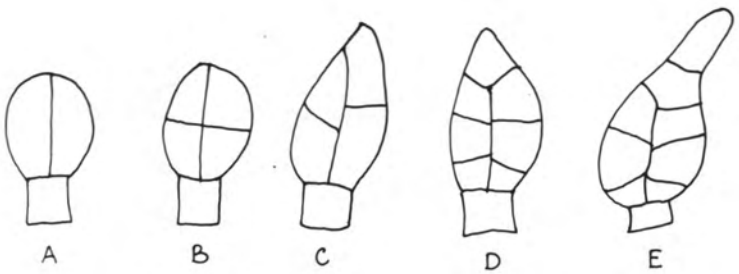

Fig. 7. Diagram of filogenetic stages the headed hairs of the taxa of the genus *Plantago* L. A — hair with head divided vertically into two cells, B — hair with four-celled round head, C — hair with four-celled conical head, D — morel-like hair, E — bottle-like hair

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Ontogeneza włosków u taksonów rodzaju Plantago L., podrodzaju Plantago

Streszczenie

Zbadano rozwój 3 typów włosków główkowych (z jednokomórkowym trzonkiem i główką podzieloną pionowo na dwie komórki, buteleczkowatych i smardzowatych) oraz 2 typów włosków bezgłówkowych (z kilkukomórkową nasadą i bez nasady) u 6 przedstawicieli czterech sekcji rodzaju *Plantago* L. Włoski buteleczkowate i smardzowate mogły powstać z włosków o jednokomórkowym trzonku i główce podzielonej pionowo na dwie komórki. Prawdopodobnie sekcje *Plantago*, charakteryzujące się obecnością włosków buteleczkowatych i smardzowatych, są ewolucyjnie młodsze od sekcji, dla których typowa jest obecność włosków z jednokomórkowym trzonkiem i główką podzieloną pionowo na dwie komórki.