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On the “reduction” of terminal bud in seedlings of some papilionoid legumes

With 7 Figures

Summary

Morphological and anatomical structure of seeds and seedlings of *Securigera securidaca* (L.) DEGEN. & DOERFL. and several other members of Loteae tribe [*Ornithopus sativus* BROTT., *Lotus tetragonolobus* L., *Tripodion tetraphyllum* (L.) FOURR. and *Hymenocarpus circinnatus* (L.) SAVI] was studied.

Development of the plumule, cotyledons, shoots system and main root of the seedlings are described with special attention to the vascular system. In cotyledonary axils, serial buds early appear and develop that makes identification of the main shoot rather difficult. However, the apical bud and normally developed main shoot were found in all examined species. DORMER's (1945) idea on the reduction of the main bud and COMPTON's (1912) supposition on extra-axillary branching of epicotyl into equivalent shoots were disproved.

Introduction

Seedlings and juveniles of many Loteae s.l. (incl. Coronilleae) form very rapidly and almost simultaneously several elongated shoots (e.g., WYDLER 1856; LUBBOCK 1892; COMPTON 1912; JAHN 1974), however their number and size may vary depending on the taxonomic position of plant and environmental conditions. DORMER (1945) came to the conclusion that in annuals *Scorpiurus vermiculatus* s.l., *S. muricata* L. s.l., *Lotus tetragonolobus* L. and *Securi-*

Zusammenfassung

Über die „Reduktion“ der Terminalknospe der Keimlinge einiger papilionoider Leguminosae

Morphologische und anatomische Strukturen an Samen und Keimlingen von *Securigera securidaca* (L.) DEGEN. & DOERFL. und einigen anderen Taxa der Tribus Loteae [*Ornithopus sativus* BROTT., *Lotus tetragonolobus* L., *Tripodion tetraphyllum* (L.) FOURR. und *Hymenocarpus circinnatus* (L.) SAVI] wurden untersucht. Die Entwicklung der Plumula, der Keimblätter, Sprosssysteme und Hauptwurzeln von Keimpflanzen wird unter besonderer Berücksichtigung der Leitbündelsysteme beschrieben. In den Keimblattachsen erscheinen und entwickeln sich die Serialknospen früh, was die Identifikation des Hauptsprosses sehr erschwert. Die Terminalknospe als ein sich vollständig entwickelnder Hauptspross wurde in allen untersuchten Arten nachgewiesen. Die Vorstellungen DORMERS (1945) über eine Reduktion der Hauptknospe sowie von COMPTON (1912) über die außeraxillare Verzweigung des Epikotyls in gleichwertige Sprosse werden widerlegt.

gera securidaca (L.) DEGEN. & DOERFL. none of those shoots had relation to the activity of embryo plumule (here and below nomenclature is after GREUTER et al. 1989). Before DORMER, seedlings of *L. tetragonolobus* were studied by WYDLER (1856) who came to the same conclusion. However, DORMER did not cited WYDLER's publication. DORMER (1945) noted, that the shoots were arranged between cotyledons in a distinct order on early ontogeny stages, and the order was correlated with the anatomical structure of plant axis. According to

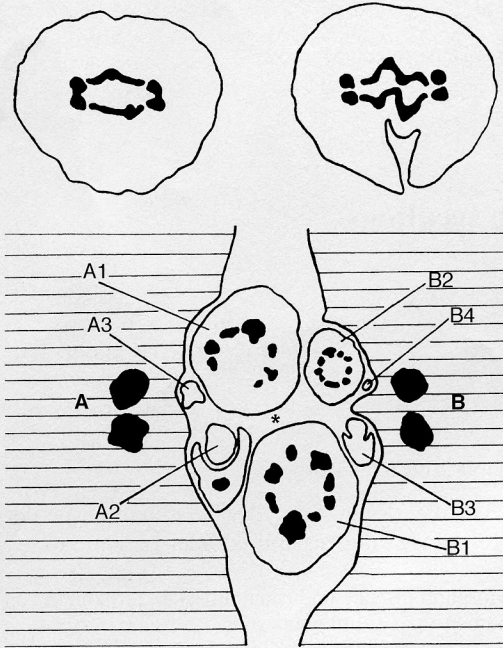


Fig. 1
Schematic drawings of a series of cross sections of *Lotus tetragonolobus* L. seedling (after DORMER 1945)

Lower scheme illustrates a section made above the cotyledonary node. Two cotyledons (A and B; shaded areas) are shown only partially. Black areas are vascular bundles. According to DORMER's (1945, 1946) interpretation, A1, A2, and A3 is a series of shoots developed from serial buds in the axil of the cotyledon A, B1, B2, B3, B4 is a series of shoots developed from serial buds in the axil of the cotyledon B. An asterisk indicates the position of the reduced main shoot according to DORMER's interpretation. In our interpretation, B1 is the main shoot, while two series of axillary shoots are A1–A2–A3 and B2–B3–B4.

DORMER, near cotyledonary node two vascular bundles deviate from the vascular cylinder of hypocotyl towards each cotyledon, and above the stele becomes bent, with several constrictions, then it forms individual steles of separate shoots. A group of shoots of successive orders that can be named primary, secondary, tertiary, etc., is associated with each cotyledon. The smaller and younger the shoot is, the closer is it to the cotyledon. The line connecting the bases of the shoots of increasing order (and age) forms a zigzag (Fig. 1).

As far as known, seedlings from herbaceous plants possess axillary shoots due to rather early branching in cotyledonary and other lower nodes of the main shoot. In Leguminosae, serial buds of descending type often occur in axils of leaves, including cotyledons (e.g., GULENKOVA 1974). The line that can be drawn through the bases of shoots developed from serial buds is zigzag, because the shoots deviate from the middle line in turn sometimes to the right, sometimes to the left.

DORMER (1945) noted a great similarity in arrangement of shoots in the seedlings of *Securigera*, *Scorpiurus* and *Lotus tetragonolobus* and the shoots which arise from serial buds of cotyledons in many other legumes with well developed main shoot. As a result, DORMER concluded that two mentioned groups of shoots are associated exactly with the serial buds situated in cotyledonary axils. As far as, there were no traces of terminal bud activity in the centre of the seedling, between two biggest shoots, the author postulated complete reduction of the plumule in studied species.

LUBBOCK's data (1892) on the seedling structure of *L. tetragonolobus* correspond well with DORMER's description: "stem ... dividing into four immediately above and between the cotyledons, ... two branches take the lead and are the strongest" (p. 419). However, LUBBOCK considers as possible also another explanation, according to which one of the two leading shoots is the main, and the others appear in cotyledonary axils. According to COMPTON (1912), in *Securigera varia* (L.) LASSEN, "the epicotyl consists at first of two stems, each with its own leaf system, borne without special relation to the position of the cotyledons" (p. 51), and in *Scorpiurus vermiculatus* "Three or four epicotyledonary branches arise at the node, as well as axillary buds borne on the short cotyledon tube" (p. 47).

As DORMER (1946) considered, reduction of the terminal bud in seedlings is a very rare phenomenon in seed plants. He compares the investigated species with *Welwitschia mirabilis*, whose main shoot finishes its development after giving birth to only two eophylls.

The genera *Scorpiurus* and *Coronilla* were usually placed in the tribe Coronilleae or in the subtribe Coronillinae of the tribe Hedysareae, *Lotus* was referred to Loteae and *Securigera* was

being included either in Loteae, or in Coronilleae. DORMER (1946) was one of the first, who suggested to consider all genera of Coronilleae as a part of Loteae tribe, using as an important argument the similarity in seedling structure in *Securigera*, *Scorpiurus* and *Lotus tetragonolobus*. The majority of taxonomists support now the DORMER's suggestion. It was confirmed by data of both comparative morphology (in a broadest sense), and molecular systematics (POLHILL 1981, 1994, LASSEN 1989; LISTON 1995; DIEZ & FERGUSON 1996; TIKHOMIROV & SOKOLOFF 1997; DOYLE et al. 1997; ALLAN & PORTER 2000). Therefore, the correctness of this joining seems to be convincing. On the other hand, the facts of lacking terminal bud which were also cited in more recent publications (e.g., JAHN 1974, DUKE & POLHILL 1981, POLHILL 1989; ALLAN & PORTER 2000) need further investigations. As a matter of fact, side by side with "unusual" seedling, marked by DORMER, seedlings with well developed terminal bud were described in Loteae (TROLL 1964). And what is more, according to TROLL's data, in annual *Tripodion tetraphyllum* (L.) FOURR., as well as in *Securigera*, *Lotus tetragonolobus* and *Scorpiurus*, several shoots arise between cotyledons with only one of them having markedly bigger size, which is correctly considered by TROLL (1962) as the main (Fig. 2).

In order to obtain more exact information on the lacking plumule in some Loteae we have conducted a morphological and anatomical study in *Securigera securidaca* (one of the species studied by DORMER), as well as in several other members of Loteae s.l.

Materials and methods

The seedlings of *Securigera securidaca* (L.) DEGEN. & DOERFL., *Ornithopus sativus* BROT., *Lotus tetragonolobus* L., *Tripodion tetraphyllum* (L.) FOURR. and *Hymenocarpus circinnatus* (L.) SAVI grown from seeds in the greenhouse of the Botanical Garden of Moscow State University and in the laboratory of Orel State University were studied. The seeds were kindly supplied by Jardin Botanique National de Belgique; Jardim Botanica de Universidade de Lisboa; Botanischer Garten der Universität Bern; Botanischer Garten der Technischen Hochschule Aachen; United States Department of Agriculture, Agricultural Research service, Plant Genetics Research Unit. Anatomical structure of seeds as well as 4-, 12-, 15- and 20-days seedlings was analysed on transverse

and longitudinal sections, made by hand with razor, followed by mounting in glycerine. For SEM investigations the material was dehydrated in an alcohol series and acetone and subsequently critical-point dried.

Results

The structure of seeds and seedlings of *Securigera securidaca*

Mature seeds of *S. securidaca* retain rather wide layer of endosperm with reserve protein, have big (c. 7 mm) curved embryo morphologically differentiated into embryo shoot, containing hypocotyl, two large fleshy cotyledons with plumule possessing a leaf primordium between them, and a radicle with pileorhiza.

In cotyledons as well as in the axillar part of embryo, a procambium system is well developed by the beginning of germination (after six-hours soaking in water). Cotyledon blades have distinctly differentiated anatomical structure. Epidermal cells on the adaxial and abaxial sides are small, with dense cytoplasm, thin pectin rich walls, stomata lacking. Uniform seven-layer mesophyll consists of closely arranged short palisades. In the middle part of the cotyledon, up to 17 vascular strands starting to differentiate can be observed. That structure of cotyledonary blades seems to be connected with their storing and haustorial functions which they realise on early ontogeny stages.

The terminal bud and the main shoot were observed in all examined seedlings (Figs. 3, 4). Successive stages of main bud development are illustrated in Fig. 5.

On the first or second day from the beginning of seed soaking, a radicle at first appears freeing itself from the seed coat, giving rise to the main root. In two-days seedlings, root hairs arise near the top of the radicle. After the radicle, a hypocotyl elongates, by the third day dragging out of the seed cotyledonary blades and lifting them up to the soil surface.

Axial organs from the four-days seedlings with non-divergated cotyledonary blades keep primary structure of the central cylinder (Fig. 6). The main root is tri- or tetrarch. Cortex contains 11 or 12 layers of cells, single-layer exoderm and endoderm with Caspary cingula. In the absorption zone, the root is covered by rhizoderm consisting of long light absorbing root hairs.

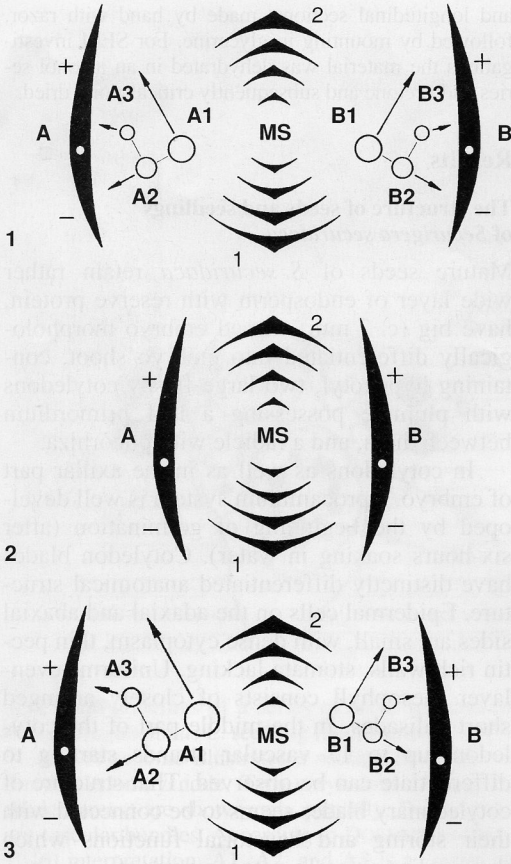


Fig. 2

Diagram 1 of the seedling of *Tripodium tetraphyllum* (L.) FOURR. (after TROLL 1964): MS is the main shoot; 1 and 2 are the first and the second eophyles; A and B are the somewhat asymmetrical cotyledones (cf. "+" and "-" poles); A1–A3 and B1–B3 are shoots developed from two series of axillary buds (one series was in the axil of the seedling A, and another was in the axil one of the seedling B). We believe that seedlings of all members of Loteae tribe demonstrate essentially the same structure. Two principal deviations can be observed, namely, suppression of axillary shoots (up to a type illustrated on diagram 2, as in some perennial species), and more intensive development of shoots in the axil of one of two cotyledons (as in *Securigera securidaca* and *Lotus tetragonolobus*, illustrated on diagram 3).

Epidermis of hypocotyl consists of a single layer of closely arranged cells with thick outer walls; the cuticle is wavy; stomata are numerous. Root structure continues unchanged through the major part of the hypocotyl. The transition

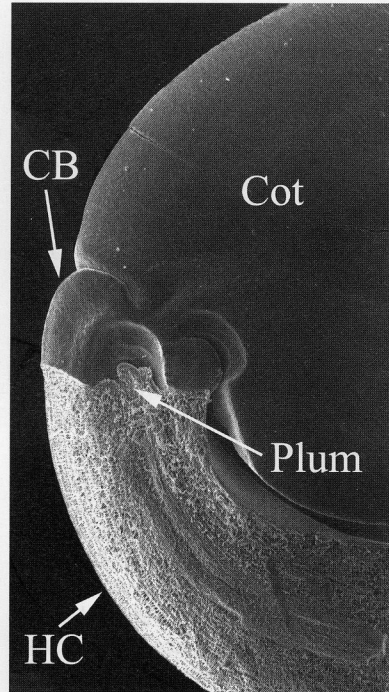


Fig. 3

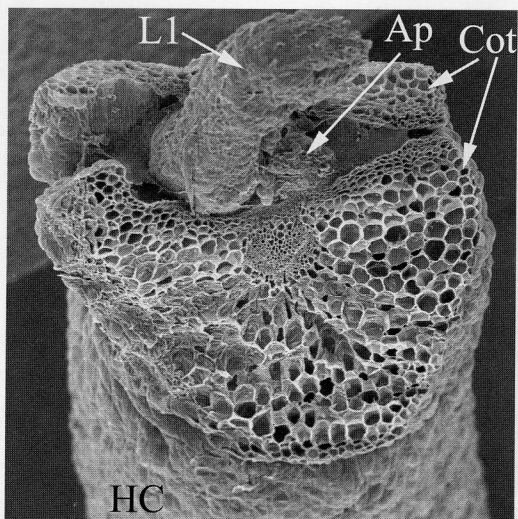
A sagittal section of one-day seedling of *Securigera securidaca*, $\times 30$ (SEM). Note asymmetry of the cotyledon

CB – basal part of the cotyledon; Cot – cotyledon blade; HC – hypocotyl (dissected); Plum – plumula

from exarch xylem to endarch one passes near the cotyledonary node. However, in contrast to the main root, the hypocotyl possesses a distinct central strand of parenchyma.

S. securidaca has unilacunar, one- or two-traced cotyledonary node. In both cases cotyledons have three bundles in the base: the central and two lateral ones. In one-trace node, two lateral cotyledonary bundles fuse with median one and come into central cylinder as a single strand. In two-trace node, the central cotyledonary bundle bifurcates, and each of two branches fuses with one of the two lateral cotyledonary bundles. The last type is the most characteristic for Leguminosae while the one-trace node was reported only for several species as a rare type of structure (SMITH 1981).

In *S. securidaca*, as well as in some other legumes, some seedlings have triarch root structure, while the others have tetrarch one

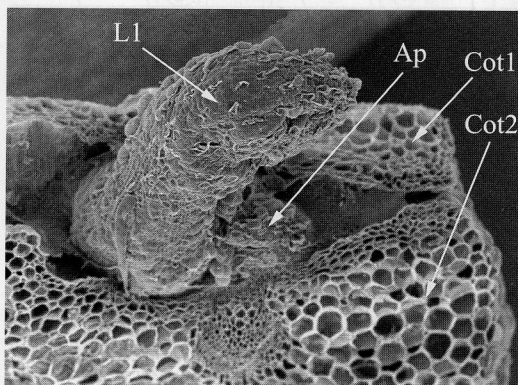


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Fig. 4

A five-days seedling of *Securigera securidaca* with both cotyledons removed, $\times 75$ (1) and $\times 150$ (2) (SEM)

Ap — apex of the main shoot; Cot — cotyledon base; HC — hypocotyl; L1 — first eophyll of the main bud



2

(COMPTON 1912). When the root structure is tetrarch, two large double collateral bundles are prominent at the level of the cotyledonary node. These are the cotyledonary traces. Collateral bundle in the intracotyledonary plane is a trace of the first leaf of the main shoot, i.e., its median bundle (Fig. 6). Vascular bundle of the second leaf of the main shoot contains only protophloem elements. Just below the cotyledonary node, protoxylem strands start to deviate from trace of each cotyledon towards intercotyledonary plane. A bit lower, they fuse with each other and with the xylem of the first eophyll trace (Fig. 6). If intercotyledonary exarch protoxylem does not develop on the side of the second eophyll, the triarch root structure is formed.

The anatomical structure of hypocotyl of four-days seedlings illustrates well the activity of terminal bud meristem, while axillary cotyledonary buds are absent.

The cotyledons structure gradually changes in relation to their function. They convert from storing organs into assimilating ones. Two outer layers on adaxial side of blade remain palisades while others, expanding and increasing intercellular space, form spongy mesophyll.

In 10–12-days seedling with separating from each other and rapidly growing cotyledon blades and increasing first leaves, the cambium activity in hypocotyl and then in the root can be observed. The initiation of cambium activity is linked with activation of main shoot apical meristem. Together with unrolling of new leaves on the main shoot, the numbers of vascular bundles increases up to 4–6 at the cotyledonary node level and up to 6 at elongating epicotyl. On this stage, the cotyledons are not strongly opposite but slightly moved from each other by short mesocotyl.

The activation of cambium is linked also with formation of buds in axils of cotyledons and, later, of the first leaf. After the main bud, some additional buds appear in axillary complex forming a descending series. In 15-days seedling, up to three buds can be observed in the axil of each cotyledon. The main axillary bud of the lower cotyledon starts up to grow and develops into a shoot a bit earlier than the bud in the axil of the upper cotyledon. The first leaf of each lateral shoot, in contrast to the lowest leaf of the main shoot, as a rule, possesses five but not three leaflets, as the latter. The main shoot, retaining leading position, in

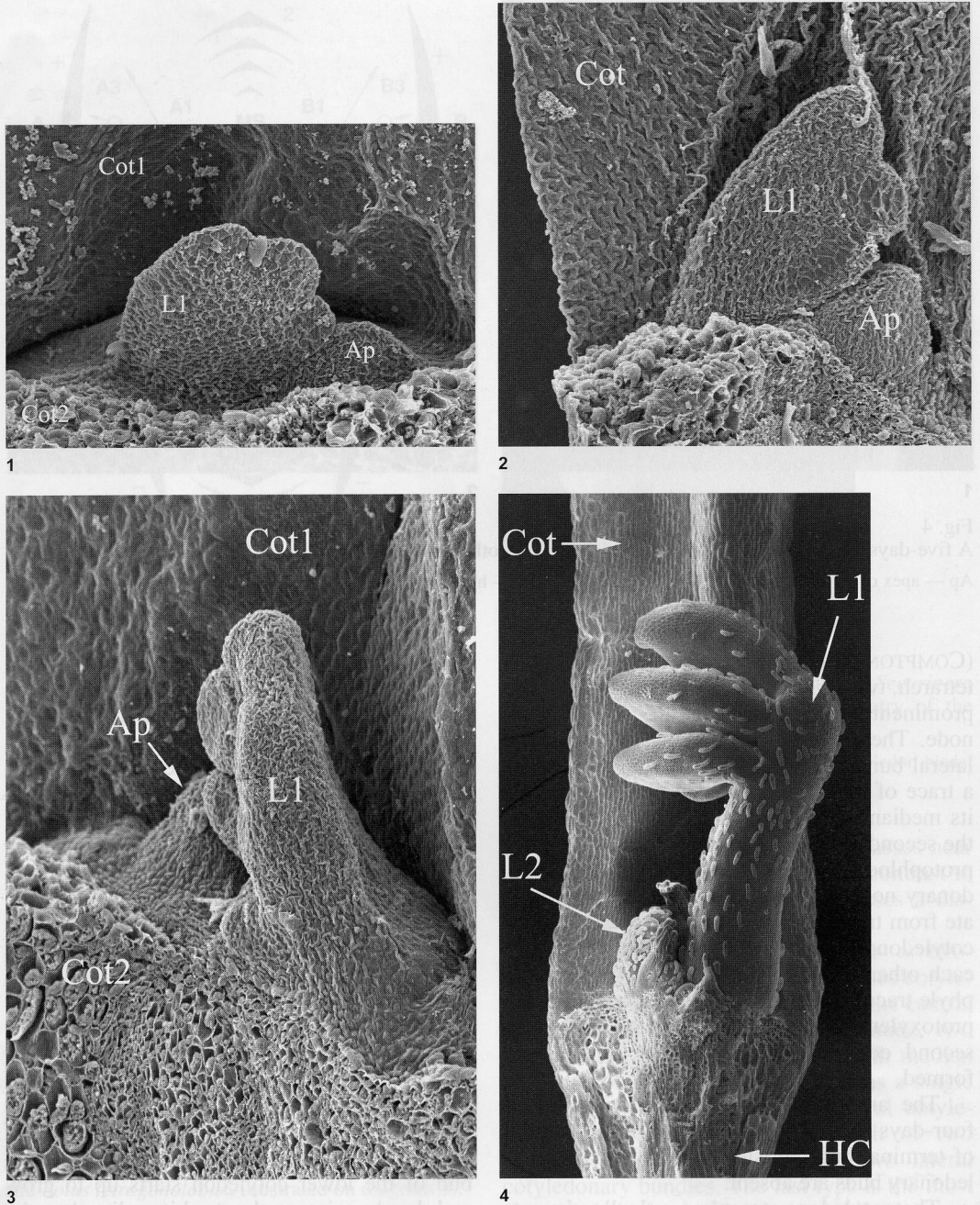
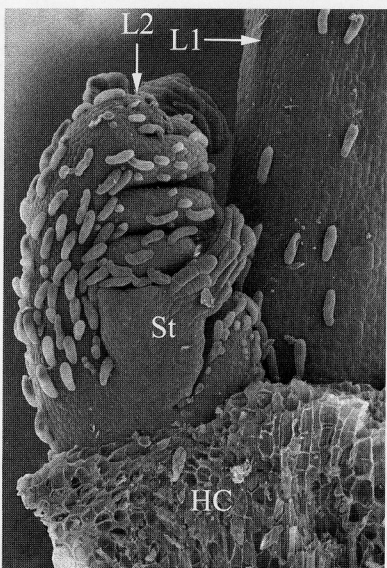


Fig. 5
Successive stages of main bud development of *Securigera securidaca* (SEM)

1 — one-day seedling, $\times 380$; 2 — two-days seedling, $\times 300$; 3 — three-days seedling, $\times 300$; 4 — six-days seedling, $\times 50$;
5 — eight-days seedling, $\times 150$

Ap — apex of the main shoot; Cot — cotyledon; HC — hypocotyl (dissected); L1, L2 — the first and the second eophylls of the main bud; St — stipule



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 zu Fig. 5 (5)
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this age may be slightly moved to the side, retaining leading position, in this age may be slightly moved to the side as a result of rapid expansion of axillary complex of the lower cotyledon.

In juveniles (20–25-days seedlings), as well as in elder plants of *S. securidaca*, axillary shoot of the lower cotyledon and the main shoot often have the same height and equal number of metamers and leaves. In preferable condition some additional buds in serial complexes may realise together with the main bud. Each consequent shoot in axillary complex somewhat retards from the preceding one, it is usually shorter and less foliated.

In some cases we observed early basitonic branching of the main shoot as a result of development of axillary bud of lower assimilating leaf (Fig. 7). This process retains realisation of serial buds of cotyledons.

Revealing of the main shoot could be often rather difficult in adult plants of *S. securidaca*. That could lead to a wrong opinion, that two equivalent "main" shoots or, according DORMER (1946), two shoots developed from axillary buds of cotyledons, may occur in plants of early stages of development. A study of ana-

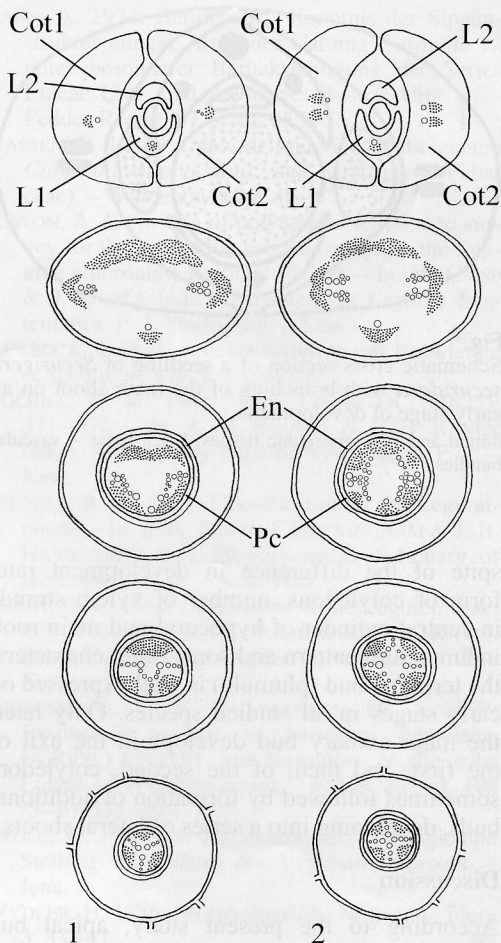


Fig. 6
 Schematic drawings of two series of cross sections of four-days seedlings of *Securigera securidaca*

1 — triarch root structure; 2 — tetraarch root structure
 Cot1, Cot2 — cotyledons; En — endoderm; Pc — pericycle;
 L1, L2 — the first and the second eophylls of the main bud.
 Phloem is shown as dotted areas.

tomical structure of vascular system on late-ontogeny stages supplies a few useful informations. Revealing of the original appearance of each shoot becomes more difficult due to strong secondary thickening of the hypocotyl.

Seedlings of other members of the Loteae s.l.

Morphological and anatomical study of seedlings and juveniles of other annuals of Loteae s.l. (incl. Coronilleae) led to similar results. In

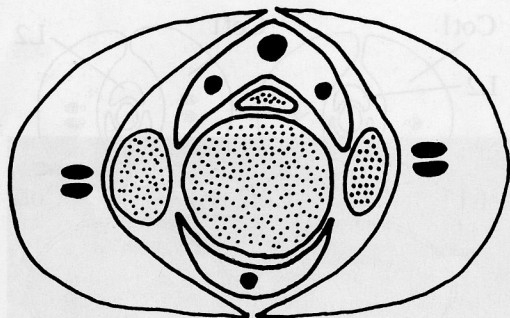


Fig. 7

Schematic cross section of a seedling of *Securigera securidaca* with branching of the main shoot on an early stage of development

dotted areas – meristematic tissues; black areas – vascular bundles

spite of the difference in development rate, form of cotyledons, number of xylem strands in central cylinder of hypocotyl and main root, indumentum pattern and some other characters, the terminal bud (plumule) is well expressed on early stages in all studied species. Only later, the main axillary bud develops in the axil of the first, and then, of the second, cotyledon, sometimes followed by formation of additional buds, developing into a series of lateral shoots.

Discussion

According to the present study, apical bud which gives rise to normally developed main shoot was revealed in all examined species. Development of the main shoot metamers (i.e., epicotyl and one or two leaf primordia) passes ahead of the formation of axillary complexes of cotyledons. Only as far as some new leaf primordia arise, axillary buds began to appear. Firstly, a bud arises in axil of each cotyledon, as well as lower eophyll, and only when vascular cambium is formed, additional buds develop, which give rise to descending series. Their formation seems to be related to prolonged activity of axillary meristem. Sometimes, cotyledons are separated by short mesocotyl. Development of the shoot from the main bud in the lower cotyledon axil usually passes faster than in the upper cotyledon axil, and the first axillary shoot quickly reaches the same dimensions as the main one. As far as the main

shoot is often moved to the side, the two shoots (i.e., main and lateral one) became very similar to each other. This fact could be one of the reasons for DORMER's (1945) conclusion on the absence of the main bud and for COMPTON's (1912) supposition on extra-axillary branching of epicotyl into equivalent shoots.

Analysis of vascular system of seedlings on late development stages only, as well as investigation of adult plants, seems to make the decision of the question of interest more difficult. However, anatomical study of Loteae members on early developmental stages supported the presence of plumule in all studied species. Indeed, the trace of the main shoot first leaf situated in intercotyledonary plane, fuses with symmetrically bifurcated bundles of both cotyledons, as it should pass, if the shoot really is arisen from the plumule (Fig. 6). Development of axillary shoots is closely related to the activation of cambium. Formation of large array of secondary vascular bundle tissues, in its turn, makes the interpretation of sections on this stage rather difficult.

When axillary complexes of cotyledons develop simultaneously to each other, the main shoot becomes bigger than any of the axillary ones, and can be easily revealed. Just such a variant of development was described by TROLL (1964) in *Tripodion tetraphyllum*. According to our data, relative rate of shoots development may vary, e.g., in *T. tetraphyllum* we have observed seedlings with a lateral shoot that has about the same length as the main one.

Finally, it should be noticed that DORMER, when analysing seedlings of Loteae s.l., could probably proceed from the idea of their radial symmetry. However, the cotyledons in papilionoid legumes, as well as their axillary complexes, are somewhat asymmetrical (SMITH 1981), that can be connected with bilateral symmetry of seed and, in the end, with a campylo-tropous type of the ovule. As a result, the seedling has bilateral structure (Fig. 3), and two shoots developed from the main axillary buds of cotyledons are moved to the same side from cotyledonary plane, that can be seen on the drawing of TROLL (1964): The diagram suggested by DORMER (see Fig. 1), cannot be obtained from TROLL's scheme (see Fig. 2) by simple "elimination" of the main shoot, as far

as on DORMER's diagram two biggest shoots are moved to different sides from cotyledonary plane. Therefore, even these indirect arguments supports the opinion that one of the biggest shoots on DORMER's diagram is really apical but not axillary one.

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