

Biomorphology of Veronicas of Russia and neighbouring states

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Summary: Shoot structures, shoot systems and inflorescences of 140 species and intraspecific variety, ontomorphogeny, seasonal development of 23 model species of *Veronica* L., and the shrub structure of *Hebe andersonii* Lindl. have been studied. Universal and principal modules in plant structure could be singled out and described. The terms “architectural model”, “shoot formation model”, “module” and “metamere” are discussed. Shoot formation models of perennial and annual Veronicas are characterized. Ways of vegetative growth and reproduction are described. On the basis of the synthetical approach a system of *Veronica*-life forms has been suggested and the supposed initial life form of *Veronica* is characterized. Possible tendencies and modi of life form transformations are outlined. Ways of formation of terminal inflorescences, perennial herbs and annual plants are discussed. On the basis of analogies in structures of shoot systems of perennial and annual Veronicas, a conclusion is drawn that the law of homologous rows in hereditary mutability acts in shoot formation.

Zusammenfassung: Sprossaufbau, Sprosssysteme und Infloreszenzen von 140 Arten, intraspezifische Variabilität, Ontomorphogenese und saisonale Entwicklung bei 23 Modellarten von *Veronica* L. und der Aufbau des Strauches von *Hebe andersonii* Lindl. wurden untersucht. Universal- und Grundmodelle des Aufbaus der Pflanzen wurden herausgehoben und beschrieben. Die Begriffe „architektonisches Modell“, „Modell der Triebbildung“, „Modul“ und „Metamere“ sind besprochen. Die Modelle der Triebbildung bei den mehr- und einjährigen Veronica-Arten werden charakterisiert. Die Arten des vegetativen Wachstums und der vegetativen Vermehrung sind beschrieben. Auf der Basis des synthetischen Ansatzes wird ein System der Lebensformen von *Veronica* entwickelt und die vermutliche Ausgangs-Lebensform der Gattung *Veronica* beschrieben. Die Tendenzen und Modi der Veränderungen der Lebensformen werden dargelegt. Wege der Bildung des Terminalblütenstandes bei Mehr- und Einjährigen werden besprochen. Auf Grund der Analogien im Bau der Triebssysteme der mehr- und einjährigen Veronica-Arten wird abschließend festgehalten, dass das Gesetz der homologen Reihen in der vererblichen Veränderung der Triebbildung eine Rolle spielt.

Keywords: biomorphology, module organization, architectural models, shoot formation models, inflorescences, life forms, system and evolution of life forms, *Veronica*

The genus *Veronica* L. (Scrophulariaceae) within the territory of the former USSR is represented by 184 species, divided into 9 sections: *Labiatooides* Wettst., *Pseudo-Lysimachium* Koch., *Beccabunga* (Hill.) Griseb., *Veronica*, *Veronicastrum* Koch., *Stenocarpon* Boriss., *Alsinebe* Griseb., *Alsinooides* Koch. and *Diplophyllum* (Lem.) Walp. (YELENEVSKY 1978). A lot of new species and subspecies have been described recently (TSVELEV 1982; KLINKOVA 1993; SENNIKOV 1995). In this paper the structure of the species is accepted in the size, suggested by YELENEVSKY (1978). The locations of Veronicas are different within the described territory. Species of subsections *Veronica*, *Montanae* Boriss. ex A. Jelen., *Calycinæ* Benth., *Urticifoliae* Boriss. ex A. Jelen., *Multifloræ* Benth., *Canae* (Yamazaki) A. Jelen. are found in light forests and the edge of forests. *V. linariifolia* Pall. ex Link., *V. spicata* L., *V. incana* L. (section *Pseudo-Lysimachium*), *V. teucrium* L., *V. jacquinii* Baumg., *V. prostrata* L. (section *Veronica*) are found in steppes and forest-steppes, and annual plants of subsections *Pellidosperma* (E. Lehm.) Stroh and *Alsinebe* in southern steppes. *V. chamaedrys* L., *V. serpyllifolia* L., and some annual species are considered to be weeds. Species of the *Orientalis* Wulff. subsection and many

annuals are found in highland-xerophil groups of plants in the mountains of Ancient Midland. Plants of the *Petraeae* Benth. subsection and *V. armena* Boiss. et Huet (*Armeno-persicae* Riek subsection) are highland petrophytes. *V. gentianoides* Vahl. (section *Veronicastrum* Koch.) occurs in all zones of the Caucasus mountains. *V. bellidioides* L., *V. alpina* L. (subsection *Alpinae* Benth.) *V. aphylla* L. (subsection *Aphylla* (Rompp) Stroh) are found in pratulum alpinum. Species of the *Carpathicae* A. Jelen. subsection (section *Veronica*) and *Fruticulosae* Benth. (section *Veronicastrum*) grow in rocky areas. Some species like *V. campylopoda* Boiss. (E. Lehm.) Stroh occur in deserts.

In spite of an arid environment in several cases, Veronicas are not xerophytes. They are flowering and bearing fruits in early spring and refer to mesophytes, ephemerae and semiephemeroid plants. Hygro- and hydrophytes of the *Beccabunga* section are found in different natural zones and are marked by a considerable height amplitude. According to RAMENSKY (1938) Veronicas have two life strategies: they are explorer or patients. As an example, *V. chamaedrys* is a very stress-tolerant species (GRIME et al. 1988).

Inflorescences are one of the most important diagnostic characters of *Veronica*. Depending on the position of partial inflorescences (racemes), shoots are traditionally divided into acrobotryose with terminal racemes (species of sections *Pseudo-Lysimachium*, *Veronicastrum*, *Alsinebe*, *Alsinooides* (except *V. filiformis* Sm.), *Diplophyllum*) and pleurobotryose with lateral racemes (species of sections *Veronica* and *Beccabunga*). False terminal racemes can be found in *V. teucrium* and *V. urticifolia* L (SELL 1964 a, b, c; YELENEVSKY 1978).

VOULF (1915), RÖMPP (1928), YAMAZAKI (1957), HAMANN (1958), SELL (1964c), KAGARLITSKAYA (1981), TSVELEV (1982) describe terminal racemes to be primary in a species, YELENEVSKY (1978) considers lateral racemes as primary. STAUFFER (1965) presents an initial inflorescence of Veronicas as a composite raceme with leaves and both, lateral and terminal ordinary racemes. All mentioned authors analyse inflorescences separately, in isolation from the vegetative part of a shoot.

From the positions of modern Russian and foreign morphology structure of shoot systems of 140 species *Veronica* L. and 33 species *Hebe* Commers. ex Juss., ontomorphogeny, seasonal development of 23 model species of Veronicas and shrub structure of an aeroxylous frutex *Hebe andersonii* Lindl. have been studied.

Characterizing life forms of Veronicas, SEREBRYAKOV (1962, 1964) defined them as a peculiar look (habit) of a group of plants, including their overground and underground organs – underground shoots and root system as an ontogeny resulting from their growth and development in certain environment. Historically this habit appears under certain ground and climate conditions and reflects adaptation to them. From the ecological-coenotic viewpoint life forms are nothing but ability of a plant to adapt to the whole complex of location and settling in new places. Dynamics of the life forms is expressed in seasonal rhythm of the plant development. That is why SEREBRYAKOV also defined a life form as a habit, connected with development rhythm and adapted to present and past environmental conditions (SEREBRYAKOVA 1972). The vegetative organs of a plant, mainly their shoots and shoot systems, play the major role in the architectonics of life forms (SEREBRYAKOV 1962). SHIK (1951) describes laws of life form development more distinctly when explaining her understanding of development rhythm as a sum of growth, form building and development of plants in changing environmental conditions.

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This traditional approach is not always helpful when one gives a detailed description of life forms of Veronicas and compares them. This is connected with ways of growth, fragmentation degree, peculiar features of shoots and shoot structures and especially with structures and arrangement of inflorescences in shoot systems. The synthetic approach of SHORINA (1994) to description of *Veronica* biomorphs is based on various classifications, each of them reflecting a certain aspect of organism-environment relations. The complementary principle is recognised by modern biology (BEGON et al. 1989). From the one hand, it allows to characterize and compare biomorphs using a wider range of characters, from the other hand – to build the life form hierarchy of plants in a genus, based on not only biomorphological but other characters. When describing shoot systems, we have made a try to join various classifications of biomorphs and various characters. Some of them are based on biomorphological indices, while the others – on phytocenotic ones. That is why it is necessary to explain the accepted approaches and terminology.

Inflorescence structure

The physiognomic, structural and rhythmologic approaches, described in detail by KUZNETSOVA (1985 a, b, 1987, 1991), are applied to characterize inflorescences: the physiognomic approach – to description of particular inflorescences, the structural approach, developed by TROLL (1954, 1956, 1964), – to total description of inflorescences and the rhythmologic approach – to description of intercalary inflorescences. As early as in 1930s GOEBEL (1931) mentioned anthoclades (blooming branches), synflorescences (amalgamated inflorescences) and whole blooming plants of annuals in addition to the notion “inflorescence” in its traditional understanding (raceme, ear etc.). The fact had been taken little notice of, until TROLL’s works appeared. TROLL (1954, 1956, 1964) gave a profound analysis of inflorescences. He wrote: “... we shouldn’t dwell upon inflorescences as such. It is important to connect them with the whole structure of a vegetative body and describe them accordingly”. This very approach to inflorescence analysis, treating an inflorescence as part of a whole complex, i.e. a shoot, seems to be correct and acceptable.

Traditionally inflorescences are subdivided into apical (terminal) and laterate (axillary). In addition to them PARKIN (1914), followed by IMS (1964), distinguished intercalary inflorescences. According to PARKIN (1914), an distinguished intercalary inflorescence is part of a perennial axis (it may be annual with Veronicas), whose apex keeps growing after blooming and losing laterate shoots. The inflorescence of this type is an amplification (floral) zone of a shoot with monopodial growth. One shoot may have several of such zones, often coinciding with current twigs. Covering leaves, whose axils contain flower-bearers, may alter into bracts. It is this zone, that, according to PARKIN (1914), is an intercalary inflorescence. At the same time he describes amplification zones, which are not specialized and have laterate inflorescences (di- or pleiochasia) in foliage leaves axils (*Drimys axillaris* Forst.), and all transitions from them to a typical bracteosa intercalary inflorescence (*D. winteri* Forst, *D. piperita* Hook. f. etc.). Pseudoterminal inflorescences can be found in this genus as well. In this case the growth of a primary shoot stops after a typical bracteosa inflorescence has been formed, which, in its turn, dies off after fruiting and the further growth is provided by a bud under the inflorescence. The intercalary type of inflorescences is evident but, surprisingly, it was not accepted by botanists. As KUZNETSOVA (1987) justly remarks, intercalary and pseudoterminal inflorescences are widely spread in nature. The existing divergence of

terminology causes inconveniences when they are described and compared. It prevents from seeing unity in various arrangements of flowers. That is why it is reasonable to treat intercalary inflorescences as an independent group. According to PARKIN (1914), intercalary inflorescences of Veronicas are non-specialized amplification (floral) zones, where particular inflorescences (simple bracteose racemes) are in axils of foliage leaves. According to TROLL (1954, 1956, 1964), this is a proliferated inflorescence. Intercalary inflorescences of Veronicas coincide with current twigs and are found between two vegetative sections of an elementary shoot, i.e. a shoot formed during one period of growth (GROUDZINSKAYA 1960). Hypogeal parts of shoots of perennial Veronicas stay alive within different periods – from part of their vegetation period up to one to three or four years. Within this period the shoots of species in the *Veronica* subsection may grow and bloom annually. Even one-season hypogeal shoot parts of these Veronicas form vegetation sections placed over inflorescences. These sections are sometimes rather long with many metameres. The place of intercalary inflorescences depends on position of shoots. Plagiotropic and cormus anisotropus shoots, lying flat after blooming, have them in the middle of the current twig (Fig. 1). Flowering of plants having such shoots is an intermediate stage in development of elementary shoots. Polycarpics with monocarpic shoots have one amplification zone; those with di- and oligocarpic shoots – one on each elementary shoot.

Orthotropic shoots have intercalary inflorescences on their apices. The monopodial growth of a shoot continues after an inflorescence is formed and shoot tops always have several metameres of the second vegetation section. Their internodes are usually shorter and their leaves smaller in size. In fact this is an apical inflorescence but morphologically it still remains intercalary (Fig. 1). The term apical (upper) intercalary inflorescence may be offered to characterize such inflorescences. It reflects both its position on a shoot and formation of a second, though small, vegetation section in a current twig. This intercalary inflorescence differs from an apical one, which continues a shoot axis. An ability of apical meristems to form organs, in the latter case, results in an apical (terminal) inflorescence. At the end of the monopodial shoot growth leaf embryos develop to the stage of bracts, while axillary buds generate single flowers, but not particular inflorescences or more complex shoots. Generation of an inflorescence in such cases is the final stage, the end of the initial shoot life term; so inflorescences of this type might be called final. Depending on their ramification inflorescences may be simple or complex. Shoots with simple intercalary inflorescences are usually referred to as “single flowers in axils”. Depending on the structure of the primary axis apex, double racemes may be homoeothetical and heterothetical (FYODOROV & ARTYUSHENKO 1979). Homoeothetical racemes s. str. are one of the types of polytelic inflorescence (TROLL 1964). Its primary axis doesn't end in a cluster, while its inflorescences are only particular inflorescences (FYODOROV & ARTYUSHENKO 1979). Unlike apical intercalary inflorescences, homoeothetical racemes do not have a second vegetative section. In fact, inflorescences of all pleurobotryous Veronicas are homoeothetical racemes (in the wide sense), for both intercalary and apical intercalary inflorescences are formed by only lateral particular inflorescences. In order to define those double inflorescences of Veronicas, which are on shoot apices, the term ‘homoeothetical racemes s.str.’ may be used. Particular racemes are generated by axillary buds of all metameres of this inflorescence while an apical bud is formed on a shoot apex. Complex inflorescences, whose primary axis ends in simple racemes, may be referred to as heterothetical inflorescences (FYODOROV & ARTYUSHENKO 1979).

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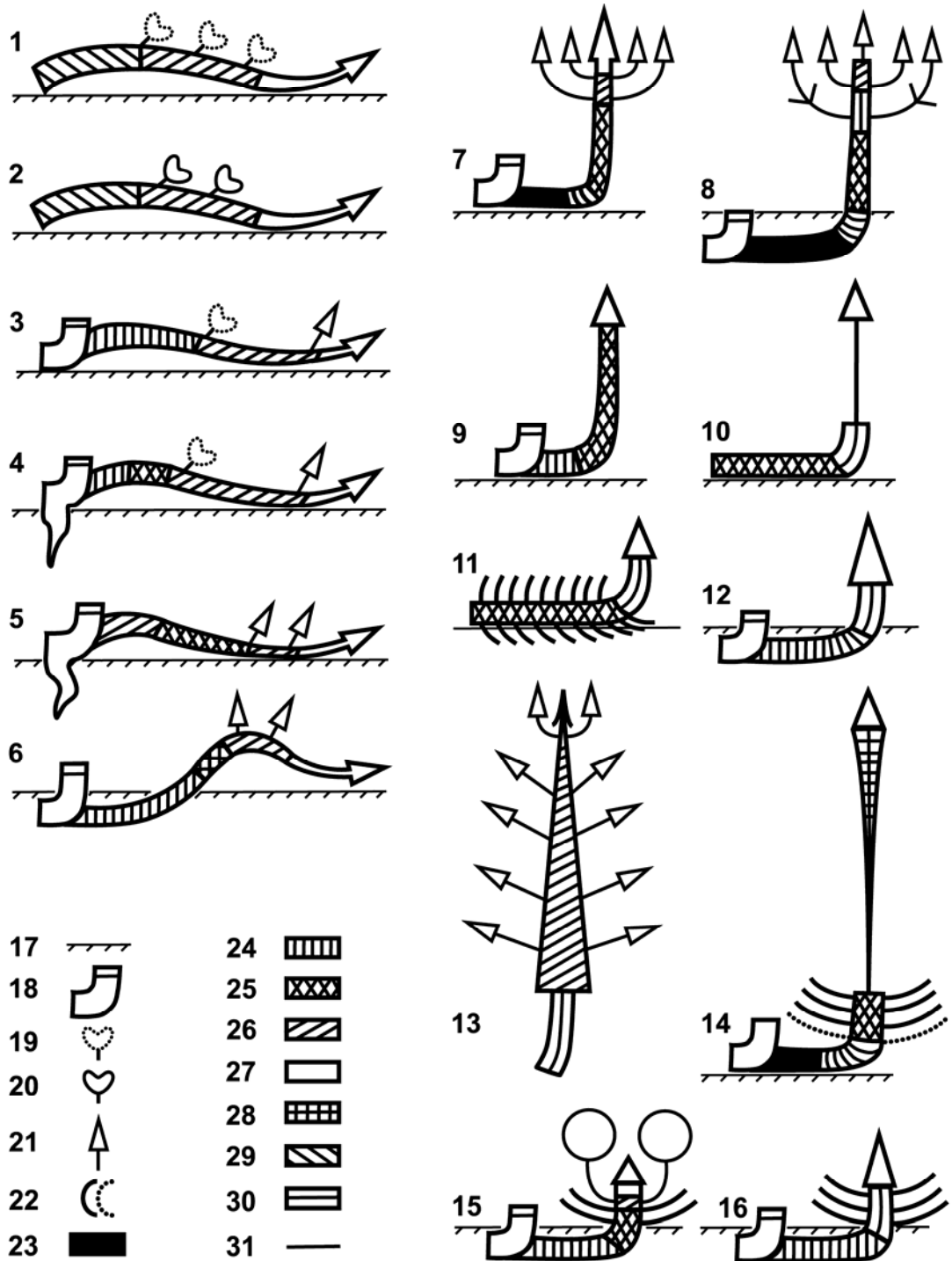


Figure 1. Structure of *Veronica* shoots: 1 – *V. officinalis*, 2 – *V. filiformis*, 3 – *V. umbrosa*, 4 – *V. multifida*, 5 – *V. prostrata*, 6 – *V. chamaedrys*, 7 – *V. jacquinii*, 8 – *V. longifolia*, 9 – *V. pinnata*, 10 – *V. serpyllifolia*, 11 – *V. telephifolia*, 12 – *V. macrostemon*, 13 – *V. anagallis-aquatica*-hydrophyte, 14 – *V. gentianoides*, 15 – *V. bogosensis*, 16 – *V. schmidtiana*; 17 – ground level, 18 – residuous, 19 – fruit of previous years, 20 – fruit of current year, 21 – simple racemes, 22 – leaves. Shoot zones: 23 – low inhibition, 24 – innovation, 25 – middle inhibition, 26 – vegetative-generative, 27 – of second vegetative growth, 28 – undeveloped generative, 29 – vegetative, 30 – amplification, 31 – upper inhibition. Additional roots are not shown.

More complex inflorescences may be triple or multiple racemes. These synflorescences are formed by particular inflorescences and paracladia which have up to 3 branches. GOEBEL (1931) wrote that such an inflorescence could make a whole annual plant, “a flowering plant”.

Thus, the following terminology is acceptable to characterize inflorescences. According to their location on a shoot, inflorescences of *Veronica* may be intercalary, apical intercalary, homoeothetical s.str. and apical racemes. The intercalary inflorescences of *Veronica* are always frondose, the apical intercalary inflorescences are frondoso-frondulose and the apical ones are frondoso-frondulosa-bracteose, frondulosa-bracteose and bracteose. The apical inflorescences may be simple terminal and complex: double, triple and multiple racemes. The complex racemes are homoeothetical and heterothetical. SELL (1964 a, b, c) and YELENEVSKY (1978) mentioned in their works, that homoeothetical racemes could become heterothetical racemes when pseudoterminal inflorescences are formed. And vice versa, heterothetical complex racemes can become homoeothetical, which is peculiar to many genera and species (MARESQUELL & SELL 1965; KOUZNETSOVA 1985 a, b, 1991, 1998; NECHAYEVA 1957; NECHAYEVA, VASILEVSKAYA & ANTONOVA 1973).

Variety of shoots

As an apical meristem of *Veronica* shoots never become a flower and can grow for several years, it may be treated as monopodial. As distinct from GATSOUK (1974), we refer here lateral axillary inflorescences as well. To characterize *Veronica* shoots according to the length of their life cycle, number of bloomings and fruitings and growth direction, SEREBRYAKOV's ideas (1952) for analysis of monocarpic shoots can be applied. The length of monopodial growth defines a shoot type and zones of its structure. It also correlates with the shoot location.

Plagiotropic shoots – monopodial oligocyclic oligocarpic – grow for more than two years and bloom more than two times. They are dicyclic dicarpic; dicyclic monocarpic; winter monocarpic. Functionally shoot parts are different. That is why several zones of their structure are determined (SAVINYKH 1979, 1981). The vegetative zone is a shoot section before the first inflorescence. The vegetative-generative zone is a shoot section from the first to the last inflorescence. The second vegetative growth zone is the last vegetative section in a shoot structure. The vegetative-generative zone includes several amplification zones, divided by vegetative sections. The latter is formed within two vegetation periods, after an intercalary inflorescence is generated during the first vegetation period and before the next intercalary inflorescence is formed during the second vegetation period. An intercalary inflorescence is the vegetative-generative zone with monopodial monocarpic shoots.

Cormus anisotropus shoots, lying flat after blooming and rising a little when a vegetative proximal section is formed, are dicyclic or winter with an intercalary inflorescence. According to the terminology by TROLL (1964) and MOUSINA (1976), the following zones are defined in their structure (SAVINYKH 1998): the lower inhibition zone – a basal shoot section with dormant (resting) buds, ensuring vegetative spreading and nourishment; the innovation zone – a shoot part with innovation (renewal) buds; the middle inhibition zone – an epigeal shoot part without sylleptic sprouts; the intercalary inflorescence and the second vegetative growth zone. As such shoots have peculiar structure and only one blooming and fruiting it is reasonable to name them monopodial monocarpic.

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Orthotrop-monocarpic shoots are defined according to the length of a vegetative assimilating shoot phase (SEREBRYAKOVA's term, 1947) and an internode length. Tricyclic and dicyclic monocarpic shoots are of the rosette and semirosette types. Analysing structures of orthotrop-monocarpic shoots of Veronicas BORISOVA & POPOVA (1990) defined the lower inhibition zone, the innovation zone, the middle inhibition zone, the amplification zone, the upper inhibition zone (several metameres with vegetative leaves under the main inflorescence in a synflorescence) and the inflorescence. These zones are marked in different ways in different species. Not all of them have marked middle and upper inhibition zones. But semirosette shoots have an undeveloped generative zone, i.e. a shoot section between an innovation zone and an inflorescence, whose leaf axils have embryonic inflorescences with few flowers and separate flowers, which usually remain undeveloped (SAVINYKH 1998).

Geophytes have the initial phases of shoot development in the ground. With some of them, such as *V. spuria*, the basal part – the geophilic shoot part which is to become an element of sympodial rhizome (*V. teucrium*) – will die off up to the innovation zone. That is why long monocarpic shoots with a one-season epigeal part may be not only monocyclic but also di- and tricyclic (depending on the length of bud phase and hypogeal germination stage).

Orthotrop-monocarpic shoots of Veronicas, especially those with terminal, double, homoeo- and heterothetical and apical intercalary inflorescences correspond with monocarpic shoots of seasonal climate herbs, as understood by SEREBRYAKOVA (1952). That is why only those Veronica shoots with functional structural zones and a life cycle ending in blooming and fruiting are defined as monocarpic proper as distinct from monopodial monocarpic shoots with intercalary inflorescences.

Veronicas form shoot systems of different structures on one monopodial shoot because of the differences in the length of their growth period. These shoot systems can be called the mature monopodial shoot system (MMSS) (SAVINYKH 1979, 1981). This system is akin to the cormus formativus shoot system of shrubs – CFSS (MAZURENKO & KHOKHRYAKOV 1977), substitution complex of *Dactylis glomerata* L. (BOLOGOVA 1993) and relates to the retaining monopodial shoot complex (according to GATSOUK 1994). MMSS is different from CFSS, because in the first case the shoot flowers while the cormus formativus shoot usually doesn't. Separation of these two structures makes it possible to add time parameters, namely biological time, to the space signs when they are compared. That is why it is necessary to compare life forms of Veronicas on the basis of not only shoot structure in mature generative age but also structure of shoot systems, formed on it.

Vegetative mobility

It is probable that ontomorphogeny has greatly influenced the changes in life forms during their evolution. Shoots cannot live endlessly. The maternal plant divides into a number of daughter ones as the parts connecting them die off. This happens at different age and intervals from the beginning of ontogeny. So ontogeny speed is the criterion in analysing life forms of Veronicas. Ontogeny speed is correlation of an individual structure and its age by the time it has achieved this age. The smaller the time index, the higher the ontogeny speed. What is taken into consideration, when plants with vegetative expansion are concerned, is the age when fragmentation begins. That is why phases have been not only defined but correlated with the age of individuals to characterize ontomorphogeny.

The approaches of RABOTNOV (1969) and SMIRNOVA et al. (1976) are helpful when vegetative reproduction type, degree of fragmentation and vegetative expansion intensity are described. Three biomorph types have been defined according to the vegetative expansion type and degree of influence on the environment (SMIRNOVA et al. 1976): monocentric, feebly marked polycentric, strongly marked polycentric. Mature individuals of monocentric species have roots, shoots and innovation buds concentrated in one centre, the latter being the multiplication centre of the individual at the same time. The monocentric type is mainly presented by plants of which vegetation expansion is not characteristic.

Strongly marked polycentric biomorphs have several or many strongly marked centres of environmental influence (e.g. partial bushes). Each of such centres is a place where roots, shoots and innovation buds are located. These are relatively autonomous individuals as they are normally connected with each other by specialized multiplication roots – communication rhizomes or roots of soboliferous plants.

Feebly marked polycentric biomorphs have several multiplication centres, but they are so close or, vice versa, so far from one another, that they are hardly made out. The latter type is akin to non-centric biomorphs (SHORINA's term (1981)), when centres of environmental influence are impossible to define.

The above mentioned biomorph types are different in fragmentation degree. Fragmentation is a process when some parts of individuals become autonomous which leads to their separation and independent life (SMIRNOVA et al. 1976). This process is marked differently in different biomorph types. SMIRNOVA offers the following parameters to describe it: degree of specialization, time, degree of separation. As a result the following variants of fragmentation are defined: a) specialized and non-specialized; b) early and late; c) full and partial. Fragmentation, typical of species, having no specialized multiplication shoots, may be called non-specialized. Specialized fragmentation is typical of species, which have specialized organs for vegetative multiplication developing in ontogeny: communication rhizomes, stolons, basal vegetative plagiotropic parts of anisotropic shoots. Partial fragmentation is expressed in relative autonomisation of certain plant parts: shoots and their groups. Full fragmentation means vegetative reproduction, whenever it takes place in ontogeny.

RABOTNOV (1969) defined 3 vegetative reproduction types of perennial herbs within the fragmentation period. The first type, at the end of a long life cycle, is a senile particulation – a senile collapse which does not lead to rejuvenation. Normal particulation, when the vegetative descendants partially rejuvenate, takes place in the middle of a long life cycle. The most specialized type of fragmentation is called juvenile particulation, when reproduction is made by strongly rejuvenated vegetative diaspores.

In this case particulation is equal to vegetative reproduction. NOUKHIMOVSKY's (1997) point of view seems to be more correct. He treats particulation as a means of vegetative reproduction or a means that makes vegetative reproduction possible, particulation being a process and vegetative reproduction being its result.

The vegetative reproduction types, mentioned by RABOTNOV (1969), point at the ontogeny period of this process. But a vegetative reproduction type should also define completeness and characteristic means of this process. That is why the beginning of fragmentation period should be treated as the basis to compare vegetative reproduction types of life forms. In many

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species of *Veronica* fragmentation begins in mature generative age or just on the eve of it, this being various for various species. So to compare ontogeny speed of perennial plants age periods are defined (RABOTNOV 1950; URANOV 1975), according to the biological time scale.

Structure of individuals as “module organized”

Treating plants as modular organisms (BEGON et al. 1989) allows to study their structures as a series of naturally repeating elements. KOUZNETSOVA (1995) has worked out the requirements for such structural elements: they are easily found on a plant and easily distinguishable. In her opinion, those structural elements are instruments of morphological plant analysis. This conforms to the idea of ESAU (1980) about “dismemberment of a plant body into sections and the typology of those sections as a logical and convenient way to study a plant, focusing on the structural and functional specialization of separate plant sections. Though one shouldn't treat this way as the only possible in order to have a clear view of a plant as a single whole”.

There have been several attempts to define structural units of a plant body (GATSOUK 1974, 1994, 1995; SHAFRANOVA & GATSOUK 1994; KOUZNETSOVA 1995). They got various names in the above mentioned works. SEREBRYAKOV (1952, 1962, 1964) was the first to define such units as the monocarpic shoot, annual shoot, skeleton axis and partial shrub. Later on the following terms were added: the leading shoot system, ramification shoot system (KHOKHRYAKOV 1975, 1981), 12 collaterally subordinated units – from the metamere s.str. to the genet (GATSOUK 1974, 1994), replacement shoot complex of cereals (BOLOGOVA 1993), monopodial polycarpic shoot (MIKHAILOVA 1972), monopodial skeleton shoot sympodial system of monopodial skeleton axes (PETOUKHOVA 1977) etc.

The general words to define them are metameres, modules, blocks. The English word “block” has 14 meanings in Russian (OZHEGOV 1987). It is too vague. It can hardly be used to name specific structural parts. The term “metamere” (from the Greek “meta” = between, after and “meros” = part) is used both – in broad and narrow sense. In the broad sense, a metamere is any element of a plant structure, which is repeated (SHAFRANOVA 1980). Metamerism is a morphological reflection of the rhythm of plant growth and formbuilding, i.e. reiteration of structural elements along the shoot axis (elementary metameres) and, in a broader sense, in a system of shoots. Metameres may be of various levels: from a shoot to a partial shrub (SHAFRANOVA 1980; WHITE 1979, 1984). In the broad sense a metamere and a module mean the same. The Latin word “modullus” has three meanings: measure, rhythm and melody; an architectural module is a scale of proportionality. According to “The dictionary of foreign words” (LEKHINA & PETROVA 1954), a module is a unit of measure, a part of a building serving to make it proportional. PREVOST (1967) says that a module is a simple unit of a shoot structure with determinated growth – a shoot. This is a narrow understanding of the term. In the broad sense the term “module” coincides with the term “metamere”. Modulation is a repetition of similar structural elements – modules – in the architectural model of a plant. In a broader sense modulation and metamerism are treated similarly (PREVOST 1978; HALLE 1986). The term “module” is more suitable for biomorphological analysis. In addition to morphological peculiarities – in the meaning rhythm, melody – it also reflects rhythmic peculiarities of shoot systems growth.

Thus, modules are structures, naturally repeated in a plant body, making a single whole (metameres as defined by SHAFRANOVA 1980, 1981); module growth units (BEGON et al.

1989) may be of various ranks (MARFENIN 1999). Modules of plants may vary from a metamere s.str. as an elementary unit of a shoot to a partial shrub, innovation shoot system and a whole monocentric plant. This approach makes it possible to compare similar, homologous growth structures during the ontogeny of an individual and plants of different other biomorphs.

ARBER's conception of a shoot (1950) – “a shoot as a single whole”, including its vegetative and reproductive parts, i.e. inflorescence, all these included in the notion module – seems most correct. When biomorphs are compared at various levels of their shoot systems, the following modules can be defined in structures of *Veronica*.

One-axis (GATSOUK 1994) or monopodial (SAVINYKH 1979) shoot: formed during the period of monopodial growth, within activities of one meristem. Laterate inflorescences are included in it. GATSOUK's terms are accepted to name modules.

Long-living one-axis shoot complex (GATSOUK 1994), mature monopodial shoot system (SAVINYKH 1979): a system of shoots, formed during monopodial growth of a one-axis shoot.

Shoot axis complex of one visible order (GATSOUK 1994): a shoot system, formed on the basis of a whole one-axis shoot or its part.

To compare their biomorphs we define in structures of *Veronicas* the elementary, universal and principle modules. **The elementary module** is a metamere s.str.

The distinctive feature of the universal and principle modules as compared with the formerly used units (GATSOUK 1974, 1994; SHAFRANOVA 1980, 1981) is time parameters, included in them: length of monopodial growth and length of a shoot life. The notion universal means many-sided, covering many things (OZHEGOV 1987) and general (FROLOVA 1986). We see **the universal module** as an elementary biomorphological unit of a shoot system. This is, first of all, a one-axis shoot, formed as a result of activities of one apical meristem. The universal character of this module makes it suitable to use when characterizing organisms and organs of individuals, at all stages of their development, when biomorphs are compared. A one-axis shoot changes during its ontogeny. It is vegetative in the pre-generative period, vegetative-generative in the generative period and again vegetative in the post-generative period. It is different at different stages of development, especially with oligocyclic monocarpic shoots of rosette and semi-rosette herbs. Different species have different structures, which depends on their ecology, biology and biomorph types. Besides different shoot parts are included into the structure of the perennial body of a plant. But the universal module – a one-axis shoot – is the result of activity of one meristem, and this is the feature, according to a structural unit, singled out when biomorphs are compared.

Monocarpic monopodial shoots have various structures depending on the inflorescence type, structure and position of innovation buds and the time when innovation shoots appear. In vegetatively fixed dwarf semishrubs it is a one-axis shoot. In many herbs, especially those having a cormus anisotropus and orthotropic shoots, innovation shoots are formed at the time of flowering and fruiting and the inflorescences are, as a rule, complex. That is why a disjunctive system (MAMEDOVA 1985) is formed on the basis of a one-axis monocarpic shoot towards the end of its life before its epigeal parts die off. The disjunctive system is made of

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partial inflorescences, sometimes paracladia, and innovation shoots. The system is named disjunctive because lateral shoots are divided by the middle inhibition zone. This system is identical to the skeleton monopodial shoot system and the system of a cormus amplificandi (GATSOUK 1970) or the long-living one-axis shoot complex (GATSOUK 1994) and the mature monopodial shoot system as we understand it. This system may be treated as a universal module of long-shoot herbs with a cormus anisotropus and orthotropic shoots, because it is an elementary biomorphological unit.

The word “principle” is understood as the most important, the main, something that makes a basis and is the essence of a thing (OZHEGOV 1987). The principle module is a structure defining a biomorph type. **The principle module** is a time-and-space structure, forming on the basis of a whole universal module or its part and naturally repeated in mature generative individuals. The peculiar features of the principle module as a structural-biological unit are as follows:

1. It is formed on a base and within a period of life of a whole universal module or its part.
2. It is found in mature generative individuals.
3. It is naturally repeated in mature generative individuals.
4. It depends on the position of shoots.
5. As a complex it defines a biomorph type.

Thus, the principle module is an elementary biomorphological type of an individual. Perennial plants in mature generative age are, as a rule, a sum of principle modules and may be called multimodule organisms. Vegetative annual plants, annual plants and monocentric herbs are formed by one module and may be called monomodule ones. The last idea does not imply, that no smaller modules can be defined within their structures, and confirms the fact that modules may differ in degree and complexity of generalization.

The principle plant modules are various. With herbal prostrate chamaephytes, creeping perennial herbs this is a system of plagiotropic shoots of the 3rd and 4th orders of ramification. It is identical with a long-living one-axis shoot complex according to GATSOUK (1994). With a multi-barreled tree it is its top (ANTONOVA & LAGOUNOVA 1999), with a single-barreled tree it is a branch of its stem (ANTONOVA & LAGOUNOVA 1999), with shrubs it is the cormus formativus system (MAZOURENKO & KHOKHRYAKOV 1977), with dwarf semishrubs it is the innovation shoot system (MAZOURENKO & KHOKHRYAKOV 1977). With monocentric herbs with orthotropic shoots and short vertical rhizomes it is a monocarpic shoot (a one-axis shoot by GATSOUK 1994). In the last case the principle module coincides with the universal module. With long rhizome herbs the principle module is a partial shrub (a shoot complex of rooting on the territory according to GATSOUK 1994). The long-living one-axis shoot complex seems to be an intermediate structure, which may be both, a universal module (a disjunctive system of a one-axis shoot) and a principle module (with creepers and trailers). It demonstrates stages of module transformation during their evolution.

Architectural models and models of shoot formation

The term “architectural model” was first used by HALLE & OLDEMAN (1970) to describe shoot systems of tropical trees. It means a form or strategy of growth becoming apparent in a combination of morphological signs, that does not always depend on ecology but depends on the size of a plant. It has often been analysed in dynamics and statics within recent years

(MARKOV 1990). From the viewpoint of static morphology an architectural model is a result of a growth programme, a result of a complete genotype realization in a corresponding construction of an individual when there are no hindrances to growth. From the viewpoint of dynamical morphology an architectural model is a scheme, plan, a genetic programme of growth, which defines an order of architectural phases in the shoot body structure of a plant (HALLE & OLDEMAN 1970; HALLE et al. 1978). When characterizing shoot formation features of perennial herbs in a seasonal climate in analogy with the ideas of the French scientists, SEREBRYAKOVA (1971, 1977, 1979, 1981, 1987) defined the following architectural models: the monopodial model with long shoots, the sympodial model with long shoots, the sympodial semirosette model, the monopodial rosette model. Later SEREBRYAKOVA concluded that the architectural models of trees and herbs are not identical. That is why she offered the term “a model of shoot formation” for perennial herbs (SEREBRYAKOVA 1979, 1981, 1987): inherited shoot formation type, characteristic of a plant species and depending on meristem activity and types of branching. The names of shoot formation models are the same: the monopodial model with long shoots, the sympodial model with long shoots, the sympodial semirosette model, the monopodial rosette model. It is evident, that not all the combinations of signs are present. For example, the sympodial rosette model is absent. This shoot type was pointed out by GOLUBEV (1965).

With short-lived and annual plants an architectural model, shoot formation models and the morphological structure type are close to the notion “architecture” defined by MARKOV (1990). When architecture is described such signs as a root system type and metamerism are taken into consideration in addition to the specific signs of an architectural model and shoot formation model. That is why the architecture of short-lived plants is a structural plan of a whole individual. It is built by putting in order and coordination of metameres of various ranks (phytomeres, modules etc.) in space. The metameres of various ranks are repeating subunits, changing for special functions and reflecting environmental conditions in their proportions (MARKOV 1990).

In all the cases the plant body is built according to the programme of the genotype, which is realized by the total meristem activities during the growth process independently of ecological conditions. Independence is the ability to keep morphological signs of species constant, including the type of growth, only the number, proportion and (or) size of repeated elements of the construction being changed (HALLE & OLDEMAN 1970).

Models of shoot formation should be distinguished from architectural models. A model of shoot formation is an inherited formation type, a technology of **shoot** formation of herbs (SEREBRYAKOVA 1979, 1981, 1987). Similar to a life form, it is defined by the structure and peculiarities of shoot formation in mature generative age. Apparently, variations of shoot parts and whole shoots could appear on the basis of an architectural model during adaptation to environment. The results are various shoot formation models and different herb types. Later various shoot formation models and even new life forms could appear on the basis of one shoot formation model, which was caused by changes of internode length, way of growth, shoot position, character of leaves (green or scaly), peculiar features of flower-bearing plants etc.

According to SEREBRYAKOVA (1987), shoot formation models are, as a rule, not adaptable, which seems to be rather argueable. Monopodial long-shoot herbs mainly dwell in shady and

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humid places. Sympodial long-shoot herbs – in open and drier places: those are steppe and meadow plants and early spring plants with a special growth rhythm identical to the growth rhythm of deciduous forest perennial herbs. Rosette herbs dwell in dry steppes, highlands and tundra. Thus, we are convinced, that shoot formation models are adaptable. The adaptation is reflected in various internode length and different ways of growth. BELL & TOMLINSON (1980) define adaptation architecture for creeping plants, stressing the fact, that it is impossible to speak about architectural models proper without mentioning adaptability of a morphological construction. We think, that variations in shoot formation models is a definite level of adaptation to the environment. Thanks to it, the range of possibilities for broader realization of the biotype conditions becomes greater: “a state of dynamic balance between an organism and environment is achieved, while the organism preserves its features and ability to live in changing environmental conditions” (the state of homeostasy according to SHILOV 1997). This state is achieved in accordance with the rule of two adaptation levels (SHILOV 1997). The first level is characterized by general stabilization of separate functional parts and whole organisms in most general and stable environmental parameters. The second level is characterized by additional appliances, the result of labial reactions, preserving relative constancy of the first level, while there are environmental changes in biocoenosis. Apparently, shoot formation models of herbs arose out of the first adaptation level, while their variants – out of the second one. The two processes could be parallel but independent, or they could happen at different time periods.

Widening of signs is taken into consideration, when shoot formation models are characterized, and the growing number of their variants only is convenient when separate life forms of closely related species are compared. It may be used as an instrument only when biomorphs are compared. In the opposite case the term “a variant of the shoot formation model” will be close to the definition of a life form. But still there is a positive moment about defining variants of shoot formation models. It may be stated, that various life forms arise on the basis of one shoot formation model, the way of their formation in one big taxon is defined, it is possible to determine that shoots of various flowering plant groups develop according to the same model.

Various shoot formation models in one concrete taxon must have arisen on the basis of the common “technology” of a plant body construction. This “technology” might have been the initial architectural model. That is why there is no need to refuse the notion “an architectural model” of herbs as it is understood by its authors (HALLE & OLDEMAN 1970; HALLE et al. 1978) and SEREBRYAKOVA (1977). An architectural model programmes ontogeny of herbs, especially its initial stages. It is not by chance that at the beginning of ontogeny signs of an initial life form arise, which conforms to the biogenetic law by Ernst Haeckel. As a shoot formation model may change during the ontomorphogeny and plants of one taxon may have different models, the variety of the latter in the genus may prove an ability of its initial form for adaptations. So, for one taxonomic group, no bigger than a genus, an architectural model defines the development of ontogeny, it is genetically inherent and sometimes may be for the whole period of a plant life. Shoot formation models are variations, arising on the basis of architectural models of initial forms. They are inherited means of shoot formation.

In order to elucidate relationship between life forms of closely related taxons, it is necessary to disclose common features of their structure. Those will be signs of an architectural model of the initial form – the plan of their body.

All mentioned above was used to characterize model objects. The characterization included the long-living one-axis shoot complex structure, the complex of the one visible order shoot axis, a shoot formation model and description of ontomorphogeny. In addition to morphological data the information about geographical spreading and location of plants was used. Besides, model species were compared with related species, and possible ways of biomorphs origin were compared with palaeographic data. The accepted approach, based on thorough systematic and florogenetic analysis of a genus by YELENEVSKY (1978), may not only explain the evolution of life forms of Veronicas, but also make certain suppositions about the origin of seasonal climate herbs as a whole.

System of life forms of Veronicas

The following signs can be chosen as the basis for making a biomorph system: the number of fruitings of a plant; length of life period; degree of vegetative mobility and influence on habitat; length of life period of epigeal individuals; ways of their spreading; type of hypogean organs; shoot type according to internode length and location in space; inflorescence type; life form type according to RAUNKIAER (1934). Model species are indicated in brackets.

1. Polycarpics

1.1 Perennial plants

1.1.1. Vegetatively immobile monocentric

1.1.1.1. **Dwarf shrubs** aeroxyulous, chamaephytes: long-shoot with anisotropic monopodial oligocyclic di- oligocarpic shoots and double intercalary racemes – species of *Orientalis* Wulff subsection (3)¹.

1.1.1.2. **Dwarf semishrubs** aeroxyulous, chamaephytes

A. Long-shoot: a) with anisotropic dicyclic di-monocarpic monopodial shoots and double intercalary racemes – *V. multifida* (3); b) with orthotropic monocyclic monocarpic shoots and terminal racemes – *V. pinnata* (1,4).

B. Rosette with semirosette anisotropic di-tricyclic monocarpic shoots and terminal racemes – *V. incana* (1).

1.1.1.3. **Herbs**

A. Taproot hemicryptophytes: a) with orthotropic monocarpic shoots and double intercalary racemes – *V. filifolia* Lipsky (3); b) with anisotropic monocarpic shoots and homoeothetical racemes – *V. microcarpa* Boiss.(3); transitional forms, when one species has both lateral and terminal racemes – *V. keborassanica* Czerniak.

B. Rhizoma caespitosa hemicryptophytes

1. With short vertical rhizomes, long epigeal monocarpic shoots and a) homoeothetical racemes – *V. ciliata* Fisch. (5); b) terminal racemes – *V. linariifolia* (1) and *V. pinnata* (1).

¹ The figure in brackets points to sections, where the indicated biomorphs can be found: 1 - *Pseudo-Lysimachium*, 2 - *Beccabunga*, 3 - *Veronica*, 4 - *Veronicastrum*, 5 - *Stenocarpon*, 6 - *Alsinebe*, 7 - *Alsinoidea*, 8 - *Diphlophyllum*.

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2. With short horizontal shoots, long epigeal monocarpic shoots and a) homoeothetical racemes – *V. prostrata* (3); b) terminal racemes – *V. tianschanica* Lincz. (1).

1.1.2. Vegetatively movable plants

1.1.2.1. **Herbal chamaephytes** acentric epigeal creeping with long plagiotropic oligocyclic oligocarpic monopodial shoots and double intercalary racemes – *V. officinalis* (3).

1.1.2.2. **Perennial herbs**

1.1.2.2.1. Undeveloped polycentric hemicryptophytes

A. Long-shoot with anisotropic dicyclic di-monocarpic monopodial shoots and double intercalary racemes – *V. umbrosa* (3).

B. Rosette with short internodes along the whole shoot length and a) double intercalary racemes – *V. bombycina* Boiss. et Kotschy; b) terminal racemes – *V. telephifolia*.

1.1.2.2.2. Developed polycentric

A. With rhizoma epigeogenum

A.1. Long-shoot hemicryptophytes: A.1.1. With anisotropic shoots and upper intercalary inflorescences – *V. jacquinii* (3); A.1.2. With orthotropic shoots and a) homoeothetical and false terminal racemes – *V. urticifolia* (3); b) terminal inflorescences – *V. spuria* (1).

A.2. Upper rosette hemicryptophytes with adscendent anisotropic shoots and a) upper intercalary inflorescences – *V. aphylla* (3); b) terminal racemes – *V. densiflora* Ledeb. (1,5).

A.3. Semirosette hemicryptophytes with adscendent anisotropic monocarpic shoots, terminal and heterothetical racemes – *V. incana* (1)

B. With hypogeogenous rhizomes

B.1. Long-shoot

B.1.1. Chamaehemicryptophytes with anisotropic winter monocarpic monopodial shoots and double intercalary racemes – *V. chamaedrys* (3).

B.1.2. Geophytes with orthotrop-monocarpic shoots and a) upper intercalary inflorescences, homoeo- and heterothetical racemes – *V. teucrium* (3); b) terminal and heterothetical racemes – *V. longifolia* (1).

B.2. Upper rosette hemicryptophytes with anisotropic shoots and a) upper intercalary inflorescences – *V. pyroliformis* Franch. (3); b) upper intercalary and false terminal racemes – *V. bogosensis* Tumadzhanov (3); c) terminal racemes – *V. schmidtiana* Regel (1).

1.2. Vegetative annual plants

1.2.1. Acentric repent long-shoot with simple – *V. filiformis* (7) and double – *V. beccabunga*-hydrophyton (2) intercalary racemes.

1.2.2. Polycentric long-shoot

1.2.2.1. **Radicibus fibrillosis praeditus** with anisotropic shoots and upper intercalary inflorescences – *V. beccabunga*-hydrophyton (2).

1.2.2.2. **Stolon-forming** with anisotropic monopodial shoots and upper intercalary racemes – *V. scutellata* (2).

1.2.2.3. Absconditus with anisotropic shoots and homoeothetical – *V. anagallis-aquatica*-hydrophyton (2).

2. Monocarpic annual plants

2.1. Vegetatively movable acentric plants with long plagiotropic shoots and a) intercalary inflorescences – *V. javanica* Blume (3); b) a terminal raceme – *V. persica* (7).

2.2. Vegetatively immovable monocentric plants

2.2.1. Long-shoot with orthotropic shoots and terminal inflorescences – *V. acinifolia* L. (6).

2.2.2. Upper rosette with orthotropic shoots and homoeothetical, heterothetical and terminal racemes – *V. cardiocarpa* (Kar. et Kir.) Walp.(6).

2.2.3. Semirosette with orthotropic shoots and homoeothetical, heterothetical and terminal racemes – *V. verna* (6).

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Structure and development of universal modules

One-axis Veronica shoots – monopodial and monocarpic (Fig. 1): Monopodial shoots – long oligocyclic oligocarpic plagiotropic (*V. officinalis*), dicyclic dimonocarpic cormus anisotropus procumbens (*V. umbrosa*) with the vegetative and vegetative-generative zones, and second vegetative growth zone, dicyclic or winter monocarpic (blooming once) cormus anisotropus procumbens (*V. chamaedrys*). The structure of the latter has an innovation zone, middle inhibition zone, an inflorescence and a second vegetative growth zone. The inflorescences of these shoots are intercalary frondosa double (*V. officinalis*, *V. umbrosa*, *V. chamaedrys*) or ordinary (*V. filiformis*) racemes. In *V. officinalis* and *V. filiformis* monopodial growth completes when the apical meristem stops functioning and the shoot stops growing, like as many arboreal plants (ANTONOVA & AZOVA 1999). The shoots of other species die off from the extremitas distalis with a living apical bud. In *V. anagallis-aquatica* – hydrophyte blooming lasts up to the end of the vegetative period. In late summer the shoot system is a multiplex frondose raceme.

Monocarpic shoots: Cormus anisotropus adscendens or orthotropic, oligocyclic (*V. incana*) and monocyclic (*V. pinnata*); long (*V. longifolia*, *V. teucrium*), semirosette (*V. gentianoides*, *V. spicata*), with a rosette orthotropic part (*V. bogosensis*, *V. schmidtiana*). Their division into structural-functional zones is far more visible than in monopodial shoots. They have different development in different species (Fig.1). The rosette part of a shoot performs a different

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function in different plants and is a part of several structural-functional zones. In *V. gentianoides* it is the innovation zone and a part of the middle inhibition zone, in *V. bogosensis* and *V. aphylla* an intercalary inflorescence and the second vegetative growth zone, in *V. schmidtiana* the middle inhibition and amplification zone, in the annual *V. arguteserrata* Regel et Schmalh. it is an inflorescence and a vegetative shoot part with a basal rosette in the annual *V. verna*.

The apical inflorescences of monocarpic shoots of perennial and vegetative annual plants are various: simple bracteose open terminal racemes (*V. linariifolia*), upper intercalary double frondose racemes (*V. teucrium*, *V. jacquinii*, *V. peduncularis*), double frondose homoeothetical racemes (*V. anagallis-aquatica*-hygrophyton), double and triple frondose-frondulose heterothetical racemes (*V. longifolia*), multiple frondose homoeothetical racemes (*V. anagallis-aquatica*-hygrophyton). Monopodial growth of one-axis shoots is sometimes replaced by an acrosympodial one. In that case false terminal inflorescences are formed and a homoeothetical raceme is transformed into a heterothetical one (*V. urticifolia*, *V. anagallis-aquatica*-hygrophyton). The complex inflorescences of acrobotryosous Veronicas are heterothetical, as a rule. Comparatively seldom partial racemes, but not flowers, are formed from axillary buds on apexes of terminal inflorescences of *V. incana* and *V. spicata*. *V. ciliata* sometimes does not develop a terminal inflorescence, and a double heterothetical raceme becomes homoeothetical.

The inflorescences of annual Veronicas are various. Depending on ramification and the number of metameres on the prefloral part the inflorescences may be represented by:

1. A double or triple frondose heterothetical raceme, forming the whole epigeal part of a plant.
2. A double frondose-frondulose heterothetical or homoeothetical raceme on the apex of the main shoot.
3. A terminal or false terminal bracteoid raceme at the apex of the main shoot.

Double homoeothetical racemes are formed in some individuals of *V. biloba* and a number of other species of the *Alsinebe* section. In this case the terminal inflorescence is not formed, the shoot apex dies off. The fact that it was present some time ago is proved by a small undeveloped inflorescence or a scar between two laterate partial inflorescences. It is evident, that annual Veronicas have the same inflorescence types as those formed on apexes of monocarpic shoots of perennial herbs.

Partial inflorescences of all Veronicas are bracteoid open racemes. They vary with plants of different locations. Mesophytes have multi-flowered conic or ear-like racemes (*V. longifolia*, *V. teucrium*). In more shady and damp conditions internodes of partial inflorescences become longer and the racemes friable (*V. officinalis*, *V. chamaedrys*). Annual plants with orthotropic shoots (*V. bucharica* B. Fedtsch.) have cylindrical, cyme-shaped, umbellate inflorescences. It is interesting, that perennial plants of the upper forest and sub-alpine zones have the same raceme-forms (*V. ciliata*, *V. bogosensis*). When fruit and seeds become ripe, shoot internodes get longer, besides, pedicels of annual plants stretch (*V. ferganica* M. Pop.).

Steppe and meadow *Veronica* inflorescences (*V. teucrium*, *V. chamaedrys*, *V. prostrata*, *V. ciliata*) dart out into the upper tiers of herbage thanks to both, longer orthotropic shoots and hypopodia. The same is peculiar to forest and highland species with plagiotropic shoots (*V.*

officinalis, *V. pectinata*). Inflorescences of semi-rosette herbs reach the upper tier because the upper part of a monocarpic shoot becomes longer.

Thus, *Veronica* has several mechanisms that bring out flowers to the upper layers of herbage: by lengthening the inhibition zone of orthotropic monocarpic shoots, formation of the middle inhibition zone and undeveloped generative zone of semirosette shoots, lengthening hypopodia, stretching inflorescence internodes and pedicels.

Some forest and alpine plants have oliganthous partial racemes: they are umbellate in *V. bogosensis* and conic in *V. montana*. Partial inflorescences of upper intercalary inflorescences in *V. baumgartenii* Roem. et Schult. are sometimes reduced to one flower in terminal position. The series of partial inflorescences of this *Veronica* can build a comparative-morphological row, demonstrating transition of an open raceme into a relatively closed raceme, as the inflorescence axis becomes compound, and its reduction up to one flower.

Thus, the tendency to sympodialism and acrosympodial growth is observed in *Veronica* on the level of vegetative apices of oligocarpic oligocyclic monopodial shoots (*V. officinalis*), double homoeothetical racemes of monocarpic shoots (*V. urticifolia*), the main shoot of annual species (*V. anagallis-aquatica*-hygrophyton) and partial inflorescences (*V. baumgartenii*). These features are peculiar to the shoots of *Hebe*, which once again proves the hypothesis of genetically fixed monopodial growth of *Veronica* shoots.

Veronicas differ in rhythm of development of their shoots and in development degree in buds. According to SEREBRYAKOV's classification (1952), only a part of the vegetative sphere is formed in a bud of the chamaephyte *V. officinalis* in autumn, in geophytes the whole vegetative part is in an apical bud of the geophilous part of a shoot and in an innovation bud of the dwarf semishrub *V. pinnata*. *V. umbrosa* forms not only the whole vegetative shoot part but also inflorescences in autumn. At the end of summer *V. prostrata* and *V. serpillifolia* form plagiotropic autumn current twigs of monocarpic shoots, which will bloom next year. Analysis of development rhythm of model shoots and theoretical data shows that the fixed rest is not characteristic of the majority of Veronicas. They refer to non-periodical species. Non-periodicity is the primary sign of Veronicas, which conforms to the ideas of BELYANINA & KRYLOVA (1970). Evidently, the evolution of development rhythm of Veronicas proceeded in the following directions:

1. Reduction of monopodial growth of one-axis shoots up to one elementary shoots.
2. Monopodial growth of an elementary shoot completes with blooming and fruiting.
3. Synchronization of the development rhythm with seasonal climatic variations in the northern hemisphere; thermoperiodism.

One-axis *Veronica* shoots are formed according to the following shoot formation models (models 1-3 by SEREBRYAKOVA, 1977) and their variants:

1. Monopodial long-shoot model with plagiotropic shoots (species of *Veronica* subsection, *V. beccabunga*-hygrophyton).
2. Sympodial long-shoot model: a) with orthotropic shoots (*V. longifolia*, *V. teucrium*); b) with cormus anisotropus procumbens (*V. chamaedrys*), adscendens (*V. serpillifolia*) and absconditus (*V. anagallis-aquatica*-hygrophyton) shoots.
3. Sympodial semirosette (*V. incana*, *V. gentianoides*).

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4. Sympodial rosette: A. With an orthotropic rosette part of a shoot. Acrotonic ramification. Basisympodial growth. The rosette part dies off together with an inflorescence in autumn as distinct from model 2. The innovation zone is a hypogeogenous rhizome (*V. aphylla*, *V. schmidtiana*). B. With plagiotropic shoots; scattered ramification; meso-acrosympodial growth (*V. bombycina*, *V. telephifolia*).

Veronica caespitosa Boiss. forms rosette shoots in a specific way. This Veronica has long plagiotropic shoots of N-order, with a rosette part on the apex. Normally they do not bloom. As the result of their acrotonic ramification vegetative-generative or vegetative rosette orthotropic, later procumbent, shoots are formed during the second year. Renewal of long shoots is mesosympodial. The resulting shoot system is analogous to a ramification shoot system of dwarf shrubs in terminology by MAZOURENKO & KHOKHRYAKOV (1977). Universal modules of *Hebe* are formed according to the same models.

When shoot formation models of annual plants are defined, the most significant signs are the following: direction of shoot growth, internode length, position of rosette parts. So, the following shoot formation models of annual Veronicas can be mentioned:

1. The long-shoot model: a) with orthotropic shoots (*V. acinifolia* L.); b) with plagiotropic shoots (*V. persica*).
2. The semirosette model: a) with a basal rosette part of a shoot (*V. verna*); b) upper rosette: hypocotyls and epicotyls are long (*V. cardiocarpa*). Annual plants may be non-ramifying, weakly or strongly ramifying. This does not depend on a shoot formation model.

Shoot formation models are genetically constant. Genetical conservatism of module organisms goes with variability of forms and body size (MARFENIN 1999). This is mainly observed on the level of organ systems – in the structure of long-living one-axis shoot complexes (Fig. 2). The structure of these shoot systems depends on the growth length and the way one-axis shoots die off. In perennial herbs with cormus anisotropus adscendens and orthotropic monocarpic shoots the structure of those complexes depends on the inflorescence complicity and the time when innovation shoots appear. A disjunctive system of a monocarpic shoot (MAMEDOVA 1985) is formed on the basis of a one-axis shoot when complex inflorescences are formed and innovation shoots appear during blooming (*V. teucrium*, *V. jacquinii*, *V. longifolia*). Lateral shoots (partial inflorescences and innovation shoots) are separated by a middle inhibition zone. Those systems live for several months: from the time when innovation shoots are formed till the time when distal parts of monocarpic shoots die off. When a simple terminal inflorescence is located on shoot apices, the structure of this complex depends on the ramification type of a monocarpic shoot. It may be a monocarpic shoot system with basitonic (*V. longifolia*), mesotonic (*V. serpyllifolia*) and acrotonic (*V. telephifolia*) ramification. In the last two cases plagiotropic basal shoot parts are included into the lower inhibition zone. They are summer-autumn current twigs of monocarpic shoots. Obviously, blooming of a cormus amplificandi of initial forms takes place next year. As a result they will be transformed into innovation shoots. All the transformations of a cormus amplificandi into an innovation shoot may be observed in the ontogeny of various species. The same is typical of some *Gesneriaceae* species (MAMEDOVA 1985). Evidently, a strong seasonal character of climate is the main factor, leading to the situation when epigeal orthotropic parts of monocarpic shoots of perennial herbs with their living apices die off completely and relatively early.

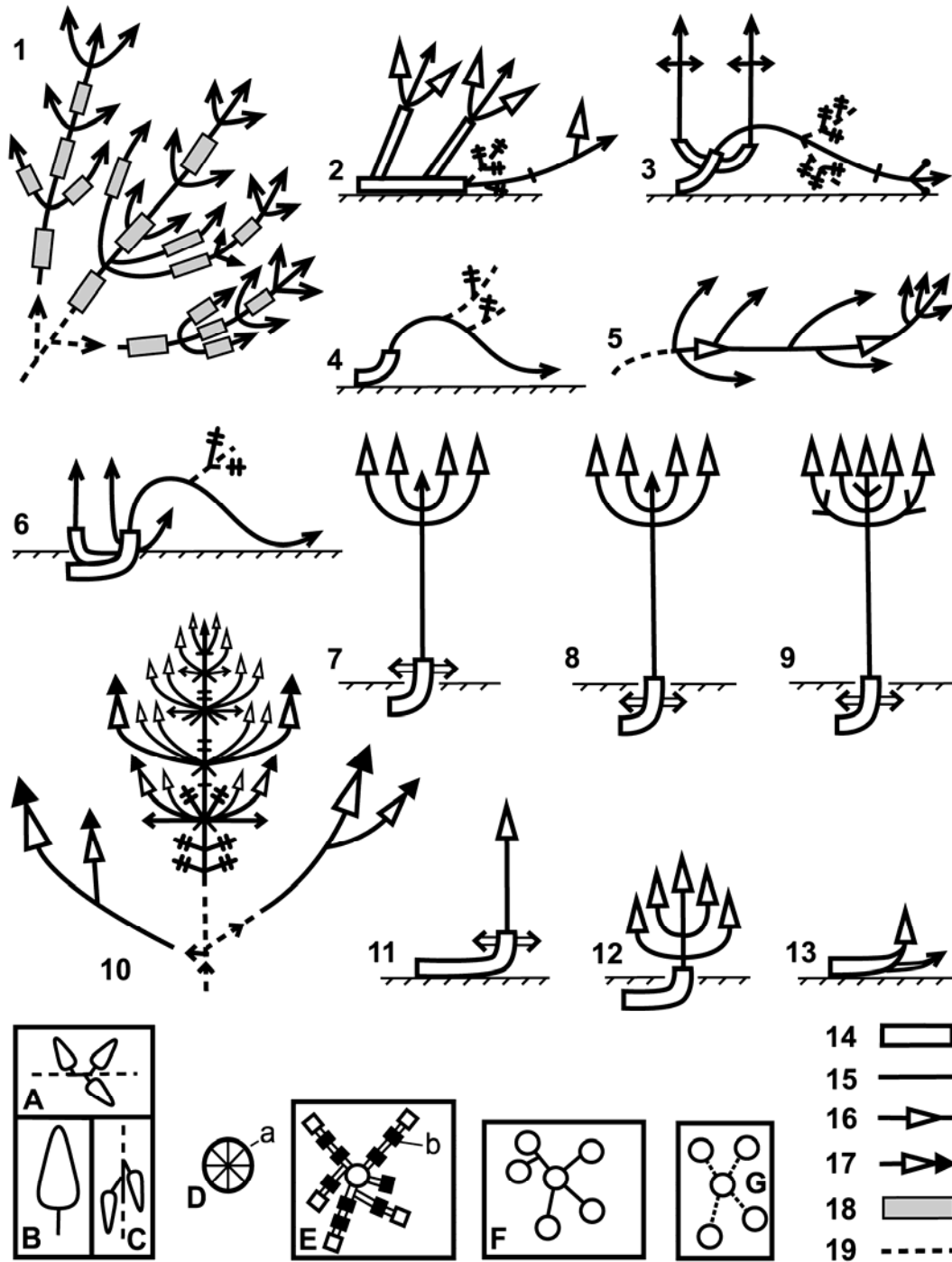


Figure 2. Structure of shoot systems and *Veronica* individuals: 1 – *V. officinalis*, *V. beccabunga*, 2 – *V. umbrosa*, 3 – *V. multifida*, 4 – *V. prostrata*, 5 – *V. filiformis*, 6 – *V. chamaedrys*, 7 – *V. jacquinii*, 8 – *V. teucrium*, 9 – *V. longifolia*, 10 – *V. anagallis-aquatica*-hydrophyte, 11 – *V. serpyllifolia*, 12 – *V. macrostemon*, 13 – *V. telephifolia*; 14 – perennial shoot parts, 15 – annual shoot parts, 16 – simple intercalary racemes, 17 – paracladia, 18 – intercalary inflorescences, 19 – dead shoot parts. A–G: upper view; a – initial shrub, b – shoots of previous years.

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Conditionally all monocarpic shoot systems described above may be treated as universal modules of perennial herbs and vegetative annual plants. Functionally they correspond to monocarpic shoots of herbs. They are elementary biomorphological units of more complex structural-biological systems – **principle modules** (Fig. 2). In laxe frutescens herbs this is a sympodium-monochasium rhizome consisting of monocarpic shoot residues of previous years. In long-rhizome herbs this is a partial shrub (SEREBRYAKOV 1962), which is a modification of a dwarf shrub ramification shoot system on a new level of biomorph organization. With aeroxyl dwarf shrubs and radice verticali praedita herbs, having long procumbent di- and monocarpic monopodial shoots (*V. multijida*), the long-living one-axis shoot complex is a system of shoots of 2nd–3rd ramification order, living for almost a year. The initial shoot dies off from the distal end up to the nearest lateral shoot while the latter is blooming. This is the same as the central shrub axis dying off when lateral shoots appear (KAZARYAN 1959, 1965) and is likely to be connected with inner correlations in an organism. These complexes are naturally repeated in the structure of individuals of those biomorphs, being their principle modules.

The principle module of the shrub *H. andersonii* is a cormus formativus or ramification shoot system (MAZOURENKO & KHOKHRYAKOV 1977). It is formed by shoots of the 3rd–4th ramification order. A similar shoot system is the long-living one-axis shoot complex of *V. officinalis*. The vegetative annual *V. beccabunga*-hygrophyton forms the same shoot system within one vegetative period, but not for 4–5 years. The shoots of these biomorphs are monopodial, similar to spreading (humistrarus) forms of arboreal plants (MAZOURENKO & KHOKHRYAKOV 1977) before their apical meristems die off from proximal ends. Those systems are principle modules of the *Hebe* shrubs, perennial Veronicas with spreading and repent oligocyclic oligocarpic monopodial shoots, and vegetative annual plants with annual shoots similar in structure. The principle module of *V. anagallis-aquatica*-hygrophyton is a multiple frondose homoeothetical raceme, formed on the basis of an initial shoot because of continuous flowering, formation of serial complexes and inclusion of an inflorescence zone into an amplification zone towards the end of the vegetative period.

The principle module of dense frutescent herbs and monocentric semishrubs is reduced: amplification shoots and complex inflorescences do not develop. At the same time the bud became bigger in size, bud scales (squamae) appeared, a great part of a shoot is formed at the inter-bud phase of its development. As a result the universal module of such plants is a monocyclic monocarpic shoot and the whole plant is similar to unitary (one-module) organisms consisting of one principle module – the initial shrub.

The body of vegetative annual plants and annual plants is formed by one principle module. It is similar to the principle module of perennial herbs, but, unlike them, it develops during one vegetative period.

Vegetative mobility and morphological integrity of individuals

From the view point of vegetative mobility and morphological integrity of individuals Veronicas have the following biomorphs: vegetative immobile, vegetative mobile with non-specialized morphological disintegration, vegetative mobile with a rhizoma epigeogenum, vegetative mobile with specialized morphological disintegration. Analysis shows, that the vegetative mobility in the genus *Veronica* is caused by the following peculiar features:

1. Long-term monopodial growth of plagiotropic shoots, accompanied by striking root and dying off of some parts (*V. officinalis*).
2. Formation of a rhizoma epigeogenum owing to autumn current twigs (*V. jacquini*) and a longer assimilating shoot phase with semirosette herbs.
3. Formation of shoots of an incomplete development cycle.
4. Formation of a cormus anisotropus ascendens, whose basal part performs a function of settling. As distinct from p. 2, this part grows within the greater part and sometimes the whole vegetative period (*V. serpyllifolia*).
5. Formation of a cormus anisotropus with ascending inflorescences. Buds of the last metamere in the inhibition zone form innovation shoots, so the whole vegetative part of a shoot performs a function of vegetative settling (*V. telephifolia*).
6. Formation of transitional long ramifying shoots (*V. chamaedrys*), geophilous shoot parts (*V. spuria*), hypogeogenous rhizomes (*V. longifolia*), stolons (*V. scutellata*).
7. Early dying off of shoot parts resulting in formation of creeping, stolon-forming, septupled vegetative polycarpic annual plants.

Intraspecific variety of *Veronica*

Intraspecific variety of *Veronicas* is caused by ontogenetic and morphological polyvariety (ZHOUKOVA 1995). The ontogenetic polyvariety arises as a result of acceleration of perennial and vegetative annual plants in the vegetative and generative spheres, when all the morphological potencies of an individual are realised within the first year of its development (*V. serpyllifolia*, *V. anagallis-aquatica*) and annual plants are formed. The morphological polyvariety is observed in different structure of individuals and may be caused by several modi. Change of a shoot growth way causes changes of inflorescences from homoeothetical double racemes to heterothetical (*V. urticifolia*) and vice versa (*V. biloba*, *V. arguteserrata*). Change of structure of elementary metameres and their parts – leaves, internode length, number of axillary buds – considerably changes the look of a plant and gives grounds to define new species and subspecies as *V. chamaedrys* (SENNIKOV 1995) and *V. anagallis-aquatica* subsp. *anagalloides* (Guss) A. Jelen (KLINKOVA 1993). Change in number of form-building breeding ground leads to a different degree of inflorescence ramification of mesophytes (*V. longifolia*), to formation of serial buds and shoot complexes, made of them, with hygrophytes and hydrophytes (*V. anagallis-aquatica*) and to a greater ramification in annual plants. Reduction of elementary metameres or their structural elements leads to lessening of the primary shoot vegetative part of annual plants (*V. syriaca* Roem. et Schult.), simplification of complex inflorescences with perennial plants (*V. longifolia*, *V. incana*, *V. spicata*), transformation of foliage leaves into bracteae (*V. gentianoides*, *V. incana*, *V. spicata*), formation of pauciflorous partial inflorescences in perennial plants (*V. montana*, *V. baumgartena*) and pauciflorous terminal racemes in annual plants (*V. acinifolia*). Undoubtedly, polyvariety displays modificational variability, that may be regarded as pre-adaptation, which made it possible for species to expand their natural habitat, to leave the areas, where those peculiar features had been formed, and to be initial forms for new taxons and biomorphs.

The facts of analysis and theoretical data let us characterize **the initial life form** as an aeroxylous shrub, whose cormus formativus system (the principle module) used to look like a perennial frondose multiple raceme. The shoot apex might have been a double frondose homoeothetical raceme. The universal module of this plant was an oligocyclic oligocarpic shoot with axillary multiflowered open bracteoideous racemes. The shoot formation model

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was monopodial with long shoots. Towards the end of monopodial growth of one-axis shoots both terminal and false terminal inflorescences, especially with high ramification shoots, might have been formed.

Basic tendencies and modi of biomorphological evolution of Veronicas

1. Terminal raceme formation. Terminal racemes of initial biomorphs of *Pseudo-Lysimachium* and *Veronicastrum* sections had appeared before monocarpic shoots as universal modules as a result of terminal derivation (TAKHTADZHIAN 1964) of a cormus formativus and ramification shoot. In those cases the floral zone shifted to the distal shoot end (PARKIN 1914) and lateral pedunculi were reduced (CROISZAT 1943).

In the *Veronica* section apical racemes were formed when the universal module (a monocarpic shoot with an upper intercalary inflorescence) was transformed as a result of terminal abbreviation (TAKHTADZHIAN 1964), the carrying axis ceased growing after an inflorescence had been formed (PARKIN 1914), inflorescences were rejuvenated owing buds, formed by younger meristems (NECHAYEVA 1957; NECHAYEVA et al. 1973) and the way of shoot system growth (SAVINYKH 1981). Evidently, the same transformations took place when annual plants *V. anagallis-aquatica* subsp. *anagalloides* of *Peregrinae* A. Jelen subsection of *Alsinebe* section arose.

Annual plants in *Alsinoidea* and *Diplophyllum* sections were formed as a result of ontogeny abbreviation (TAKHTADZHIAN 1964) and acceleration in the generative sphere (GOULD 1977). Ontogeny of a creeping vegetative annual plant with simple intercalary racemes ended in a formation of the first raceme, the carrying axis ceased growing and an annual plant with terminal inflorescences was formed. Thus, terminal racemes of Veronicas are analogous organs.

2. Monocarpic shoot formation. In *Pseudo-Lysimachium* section changes of the universal module because of geophily and basal derivation resulted in formation of hypogeogenous rhizomes, geophilous shoot parts, and later on – a new principle module – a partial shrub. Intensification of a shoot development cycle and basal abbreviation (shortening of their basal parts) lead to formation of winter and monocyclic shoots.

In *Veronicastrum* section monocarpic shoots might have been formed by reduction of partial racemes of a synflorescence and transformation of basal paraclades into innovation shoots.

Monocarpic shoots in *Veronica* section arose when the principle module of initial forms was simplified by terminal abbreviation during the ontogeny of the universal module. Growing was restricted by the first flowering, the second vegetative growth zone was reduced. Intensification of the development cycle lead to annual innovation of shoot systems. Basal deviation and geophily lead to formation of transitional shoots, hypogeogenous rhizomes, prostrate epigeal shoots of autumn generation and epigeogenous rhizomes.

3. Formation of rosette shoot parts was caused by deviation of various parts of the universal module and geophily.

4. Formation of annual plants was possible in three layers of biomorph evolution – mesophilous, hygrophilous and xerophilous as a result of acceleration in the generative sphere.

The tendencies mentioned above caused specialization in a form of differentiation of both principle and universal modules.

The second way of specialization was change in “behaviour” of plants, expressed in peculiar features of their spreading. When shoots lay flat and struck roots they became epigeal creeping herbs. The structure of the principal and universal modules was preserved. Specialization was caused by prolongation of ontogeny of individuals by means of morphological disintegration, vegetative reproduction and formation of clones.

Transformations of shoot systems (mainly primary shoot systems) of annual plants of *Alsinebe* section were caused by the same modi as transformations of universal modules of perennial herbs. As a result of terminal abbreviation monopodial growth was restricted and false terminal inflorescences were formed, i.e. inflorescences changed by way of the first pseudocycle (MARESQUELL & SELL 1965; SELL 1969). Basal abbreviation, ephemerisation and embryonisation (KHOKHRYAKOV 1978) lead to formation of plants with a short vegetative part (subsection *Syriacae*).

Basal deviation, that looked like unstretched internodes of the first metameres, caused formation of semirosette annual plants with a basal rosette part. Terminal deviation of the same type caused formation of semirosette annual plants with an upper rosette part. Inflorescence internode inability to stretch lead to formation of frondose cymose inflorescences of annual plants: heterothetical (*V. campylopoda* Boiss.) and homoeothetical (*V. rubrifolia* Boiss.), panicles, double (*V. praecox* All., *V. ferganica* M Pop.) and ordinary (certain individuals of *V. ferganica*) racemes.

Extreme cases of terminal and basal abbreviations might have lead to the formation of very tiny plants, consisting in their epigeal parts of one vegetative metamere and false terminal 1–2-flower raceme (certain individuals of *V. rubrifolia*, *V. acinifolia*). Changes of shoot systems of annual plants also prove parallel and convergent development of life forms of Veronicas. Parallel changes of life forms in different *Veronica* sections and certain analogies in shoot system formation of *Hebe* species demonstrate action of the law of homological rows in hereditary mutability by VAVILOV (1968) in formation of plant shoots.

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