

Architectural units, axiality and their taxonomic implications in Alchemillinae

To my dear friend and colleague Tatyana V. Kusnetzova

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Summary: The article describes main architectural models and units of Alchemillinae and the main trends of architectural evolution in subtribe Alchemillinae are discussed. Two evolutionary lines are revealed, the first including monoaxial forms while the second deals with di- and triaxial forms. The structural and temporal alterations (deviation, acceleration etc.) of minor life cycles (life cycle of a shoot) prove to be the general and most widespread mechanisms of architecture evolution within this group. The most constant architectural traits are axiality and type of architectural units conjunction. The most labile traits are length of internodes and life span of monopodial shoots. The diversity of leaf base and bud structure within subtribe Alchemillinae is also described. Three series of leaf base forms relating to the kind of stipular fusion are revealed. Two bud types occur in the subtribe demonstrating different variants of primordia enveloping. The strong correlations between leaf base type, bud type and shoot structure characters of taxonomic significance are demonstrated. A partial revision of *Alchemilla* taxonomy based on the analysis of traditional and new characters is given.

Zusammenfassung: In diesem Artikel werden die wichtigsten Modelle und Einheiten der Architektur der Subtribus Alchemillinae beschrieben und die Haupttrends ihrer evolutionären Entwicklung besprochen. Zwei evolutionäre Linien werden aufgezeigt: die erste inkludiert monoaxiale, die zweite di- und triaxiale Formen. Strukturelle und zeitliche Änderungen (Abweichung, Beschleunigung etc.) des Lebenszyklus einzelner Sprosse erweisen sich als generelle und weit verbreitete Mechanismen der Evolution der Architektur in dieser Gruppe. Die konstantesten Merkmale sind Axialität und die Art der Verbindung architektonischer Einheiten. Als sehr instabil erwiesen sich Internodienlänge und Lebensdauer der Monopodial-Triebe.

Weiters werden Diversität der Blattbasen und Knospenstrukturen der Subtribus Alchemillinae beschrieben. Drei Serien von Blattbasen-Formen, verbunden mit Fusionen der Stipeln, können gezeigt werden; ebenso zwei Knospentypen, die unterschiedliche Varianten der Primordien-Umhüllung demonstrieren. Die starke Korrelation zwischen dem Typ der Blattbasis, dem Knospentyp und taxonomisch relevanter Sprossmerkmale wird aufgezeigt. Aufgrund unserer Ergebnisse, publizieren wir eine Teilrevision der *Alchemilla*-Taxonomie, welche sich auf die Analyse traditioneller und neuer Merkmale stützt.

Keywords: architectural models, architectural units, evolution, architecture, minor life cycle, deviation, acceleration, leaf base, bud, stipules, correlations, taxonomy

I. Theoretical implications and descriptions of architectural units

Architectural analysis of the plant body permits us to describe, compare and model the whole plant, and not only its parts as traditional morphology does. The description of the architectural model of a plant reveals a set of its growth rules i.e. essential qualitative characteristics of its construction (HALLÉ & OLDEMAN 1970; HALLÉ et al. 1978). However the problems and controversies appear rather similar in both: classical morphology and architectural analysis. One of the most important controversy is the problem of choice of an universal unit (or a set of units) for comparison. The most general and modern system of universal structural units of plant bodies is those proposed by GATSUK (1974, 1994). This system includes units of several

levels e.g.: **elementary metamer** (phytomer); **elementary shoot** (unit to some extent analogous to the “unit of morphogenesis” and “unit of elongation” sensu HALLÉ et al. (1978) and “growth unit” sensu BARTHELEMY (1991); **monopodial shoot (MS)** i.e. result of growth activity of a single meristem since its inception to death; it is almost synonymous to the “Sproßgeneration” traditionally used by German morphologists (e.g. TROLL 1964); **system of skeleton MS** i.e. the whole set of axes appearing on the MS with any persisting (skeleton) part; **partial shrub**, and so on. Similar systems of hierarchically arranged units of plant body have been proposed recently by HALLÉ (1986) and BARTHELEMY (1991); these systems coincide in general traits with each other and with the system of GATSUK but they are somewhat less detailed.

Theoretical implications – architectural units and axiality

The lower levels of these systems of units (up to the MS) are of high universality, these units being applicable to any plant description. On the higher levels of structural complexity (systems of MSs, the whole plant organisms) other kinds of units are required perhaps more closely connected with certain plant architecture. Such units cannot be universal: their number would be equal to the number of different architectural models within Angiospermae.

Considering data on different plant architectures some French morphologists (EDELIN 1990; BARTHELEMY 1991) come to the conclusion that in every case there exists a certain combination of structural units of lower level (i.e. MSs of various kinds) which repeats several to many times in overall plant architecture. This combination including, by definition, all the kinds of MS the plant can produce, is usually called the **architectural unit (AU)**. We define AU according to EDELIN and BARTHELEMY as a “specific elementary architecture” of a plant. To our opinion, AU represents a kind of “molecule” of plant architecture i.e. the minimal portion of plant bodies bearing all specific kinds of MSs in their specific arrangement.

Some Russian morphologists (ZAKHAROVA 1991, 1993; NOTOV 1993) introduced independently the term “basic structure” which sounds quite analogous to AU. This term is in fact a complete synonym for AU.

The kinds of MSs differ mainly in their relative position within AU i.e. order of branching, all other characters being in most cases correlated with it. The list of these characters may somewhat vary depending on the kind of architectural model, but in most cases this list includes:

- the number of elementary shoots within MS (i.e. **cyclicity** in the sense of WARMING 1884, SEREBRYAKOV 1952);
- orientation: plagiotropy vs. orthotropy (especially important for trees);
- position of reproductive structures;
- peculiarities of branching (syllepsis vs. prolepsis etc.), position of buds;
- length of internodes (especially important for herbs); etc.

It is evident that plants with different architecture differ in the AU's complexity i.e. the number of MSs variants within AU; so their architecture may be either **hierarchic** with many different kinds of MSs or **polyarchic** with few kinds of MSs (see EDELIN 1991) – or an intermediate between.

While the architectural model is proved to be a constant hereditary feature of a plant (HALLÉ et al. 1978) AUs may be different within the same individual because of the changes of shoot formation modes during the life history of a plant. ZAKHAROVA (1991, 1993) was the first who paid attention to this phenomenon when describing the changes during the life history of some *Gentiana* species. It is clear however that the most complete set of different MSs is represented only in AUs of a **plant in generative state** because only in this stage of life history one can observe the position of flowers on the certain kinds of MSs. These “generative” AUs are, as a rule, repeated many times in overall plant architecture forming its basic framework. So we consider them to be most important and valuable for morphological analysis.

The position of reproductive structures (flowers) within the AU is of special interest. It was shown long ago by SAINT-HILAIRE (1840) and BRAUN (1842) that each plant possesses an essential structural characteristic namely **a number of minimal branching order of innovation shoots which end in a flower**. Prominent Russian morphologists SEREBRYAKOV (1952) and SEREBRYAKOVA (SEREBRYAKOVA & BOGOMOLOVA 1984) also paid attention to this feature referred to **axiality**. Axiality is likely a stable characteristic of a taxon; it seems to be a quantitative character but in fact it is qualitative being always a small integer (1 to 4, rarely more). It is now quite clear for us that determining of axiality would be more correct within AU than within branching systems of innovation shoots because of vagueness of the latter notion. Axiality is obviously a necessary element of AU description; its high consistency permits its use in taxonomic treatment.

There is one more aspect of AU conception which should be emphasized. Clear AU description includes the characteristics of **all the shoots** of a plant – up to the pedicels of highest order. Such information on the plant body structure is more complete than the traditional characteristic of the architectural model (HALLÉ et al. 1978; SEREBRYAKOVA 1977) which gives only a general design of the shoot system of a whole plant and neglects various kinds of specialized, floriferous, ephemeral etc. shoots. Architectural characteristics obtained by the method of AUs may be called “architectural models” as well as HALLÉ's and SEREBRYAKOVA's models but it is clear that, compared with the latter, they are **submodels**; HALLÉ's model may embrace a number of such submodels. RAY (1988), studying architecture of Araceae in a very precise way similar to AUs method, revealed about ten such submodels within Chamberlain's model mentioned by HALLÉ for aroids. Nevertheless, we use only the term “architectural model” in the present paper because we do not need to compare our architectural variants obtained by AUs method with any conventional models sensu HALLÉ or SEREBRYAKOVA.

While traditional architectural analysis is quite appropriate for broad studies of architectural diversity on large ecosystems or taxa (Angiospermae as a whole; large families), the method of AU provides a tool for precise comparison of similar architectures of closely related plants. This comparison permits us, first, to state the similarity of general constructional design (in fact equivalent to the **Bauplan** of old German morphologists), then, second, to state one-to-one correspondence of all the elements within AUs under comparison (i.e. to state **homologies** between them) and, third, to seek for differences between any homologous (and hence comparable) elements in their structure, position etc. These differences may be treated as taxonomic characters of these taxa because of their stability and quality being the common

features of any architectural characteristic. Thus a new field of application of architectural data namely taxonomy can actively use the AU concept. There are only few works now dealing with both, architecture and taxonomy (RAY 1988; SANOJA 1992). We propose in our study one of some possible ways of such a synthesis. The first part includes theoretical considerations and characteristics of all AUs found in the subtribe Alchemillinae; in the second part we deduce evolutionary pathways of architecture transformation and also consider briefly leaf morphology in the subtribe Alchemillinae in the third part, and in the fourth part we shall deal with taxonomic treatment and critical revision of the subtribe using architectural data.

Materials & Methods

Subtribe Alchemillinae described by ROTHMALER (1937a) is included in the tribe Potentilleae, consisting of three genera, *Alchemilla* L. s.str., *Aphanes* L. and *Lachemilla* Rydb. These three genera differ clearly in their flower structure but within each genus, these traditional taxonomic characters are quite uniform. That is because some vegetative traits are used for sectional and subsectional subdividing of these genera; namely leaf characters and features of life form (ENGLER 1911; FRIES 1923a,b; FRÖHNER 1975, 1986; HAUMAN & BALLE 1934, 1936a,b; PERRY 1929; ROTHMALER, 1934, 1935, 1936, 1937a). The descriptions of the latter are often unclear and the similarity of life forms is often a result of convergence rather than common descent and/or taxonomic closeness. So architectural characteristics seem to be more reliable in this case.

The structure of the shoot system is examined in 45 species of *Alchemilla*, 69 species of *Lachemilla* and 16 species of *Aphanes* so that all the sections and subsections of the three genera are represented. [Here and below we do not take into consideration the numerous apogamous species within *Alchemilla vulgaris* L. s.l. and *A. alpina* L. s.l.]

We used herbarium specimens from MW, MHA, LE, KW, JE, MO, K, as well as living material cultivated at the Botanical Garden of Moscow State University (*Alchemilla alpina*) and from native habitats in Middle Russia (species of *A. vulgaris* complex).

For every species we show and describe the AU. There are two ways of presenting AU known to us: (1) architectural table and (2) schematic picture or diagram (EDELIN 1990). It is possible however to use both methods and we are doing so in the present work in order to make complete and precise descriptions.

The most important thing in describing the AU is the choice of characters (parameters). For our material it proves to be rational to use the following parameters:

1. The modus of conjunction of the successive AUs. There are two possible variants: first, new AU is produced by **terminal** bud on the first order MS of the previous AU (usually called **monopodial** growth) or, second, the new AU may be produced by a **lateral** bud (**sympodial** growth). The bud producing the new AU often corresponds (especially in herbs of temperate regions) to the conventional **innovation bud** resuming growth in the beginning of the vegetation period. But it should be mentioned that not all buds resuming growth in spring produce AUs because not all AUs develop completely in one vegetation period; some of them need two or more.

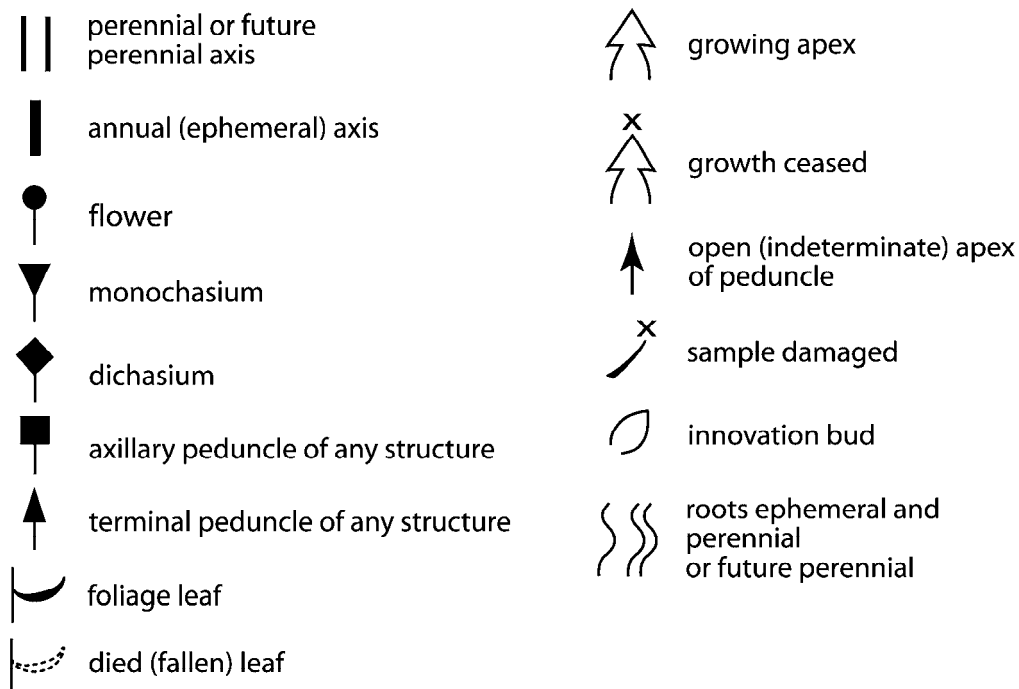
Architectural units, axiality and their taxonomical implications

We do not include this parameter in architecture tables because it attributes not to the single MS but to the whole model. So the type of AUs conjunction is included in the title of each model. All the other parameters listed below are included in tables.

2. The status of shoots concerning the position of flowers. A shoot may be either terminated by a flower (so it may be called **closed**) or may not (in this case it may be called **open**). This parameter is decisive for defining the axiality.
3. The MS type depending on the length of internodes. The MSs may be **rosette**, **semi-rosette** and **elongated**.
4. Contribution to **duration** (NUCHIMOVSKY 1969), i.e. occurrence of perennial parts in MS. The latter may be either almost completely perennial, or partly perennial (in both cases it may be called **skeleton shoot**) or completely ephemeral withering and falling down after a single growth period. The latter variant is represented mostly by specialized floriferous shoots.
5. The number of elementary shoots (ESs) within MS (cyclicity). If there is only one ES the MS may be called **monocyclic**; if there are more than one ES then MS is **polycyclic**.
6. The number of metamers per MS. It may be determinate and small (even 1) or indeterminate and perhaps rather large.

We arrange MSs in architectural tables in accordance with the relative order of branching within AU (the upper line in a table) and below, we give all the characteristics for the MS types. Exceptions are listed. The real branching order within AU may in fact exceed the number of MS kinds noted in a table; but it is implied that the characteristics of MSs of highest orders are quite similar to those of the last MS described in a table.

Legend to the figures



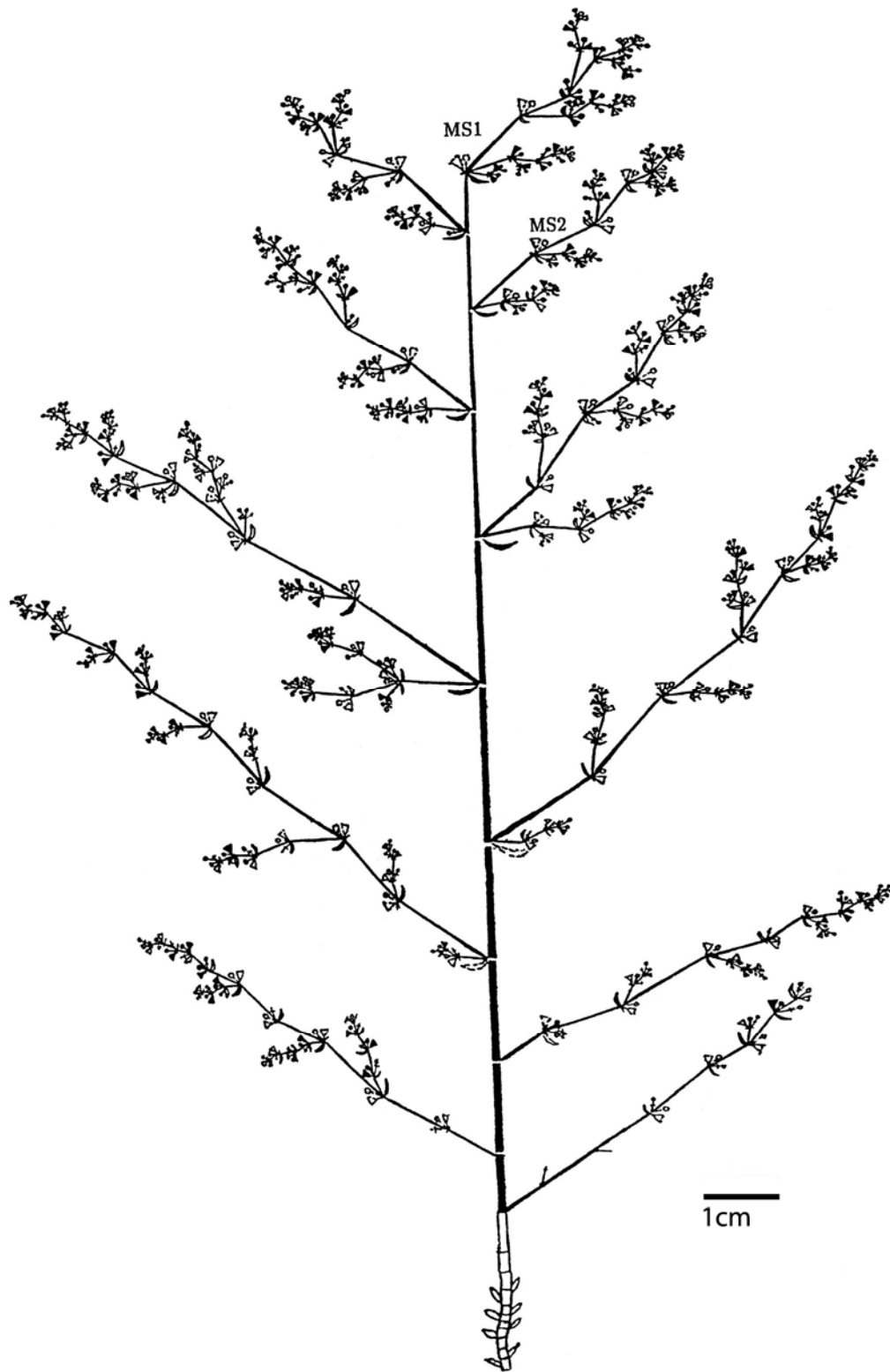


Figure 1: Monocarpic shoot of *Lachemilla velutina*.

Results

We show 10 “architectural models” (see above) within Alchemillinae according to their AU structure. Below we give their simple classification according to the three main characters: axiality, modus of AUs conjunction and length of internodes of skeleton MSs (and their architectural tables).

(1) Sympodial monoaxial model with elongated shoots

This model is found only in *Lachemilla*. It has two variants differing in the number of MSs types (see Table 1 and Table 2).

Variant A. Example: *L. velutina* (Wats.) Rydb. (Table 1; Fig. 1).

Table 1

	MS1	MS2
relation to the flower position	closed	closed
number of metamers	indeterminate	one to many (indeterminate)
length of internodes	elongated	elongated
contribution to duration	part of MS	no
cyclicity	monocyclic	monocyclic

Variant B. Example: *L. vulcanica* (Cham. et Schlechtend.) Rydb. (Fig. 2; Table 2).

Table 2

	MS1	MS2	MS3
relation to the flower position	closed	closed	closed
number of metamers	indeterminate	indeterminate	one to many (indeterminate)
length of internodes	elongated	elongated	elongated
contribution to duration	partly	partly	no
cyclicity	dicyclic	monocyclic	monocyclic

(2) Monoaxial temporary rosette model

Example: *Aphanes arvensis* L. (Fig. 3; Table 3)

Table 3

	MS1	MS2
relation to the flower position	closed	closed
number of metamers	indeterminate	one to few
length of internodes	temporary rosette or semi-rosette	elongate
contribution to duration	(undefined)	(undefined)
cyclicity	di- or monocyclic	monocyclic

This model is represented only in *Aphanes*: all species are annuals or biennials. In *Aphanes* MS of the first order shows the rosette part only at early developmental stages – at the time of

flowering all internodes elongate. This phenomenon is called **temporary rosette** by MARKOV (1990). In biennials however, one can observe the rare cases of persisting of the rosette part of the shoot.

As the life cycle of these plants is so short and simple there is only one single AU represented in the whole plant body. That is why we cannot define the way of conjunction of AUs.

(3) Monoaxial semi-rosette model

This model is observed only in *Lachemilla aphanoides* (L. fil.) Rothm. This plant is a biennial with a “mixed” type of shoot formation: it forms only lateral ephemeral flowering shoots during the first year of growth while the main axis elongates and flowers during the second year (Fig. 4, Fig. 5; Table 4).

Table 4:

	MS1	MS2
relation to the flower position	closed	closed
number of metamers	indeterminate	one to many (indeterminate)
length of internodes	semi-rosette	elongate
contribution to duration	partly (rosette part)	no
cyclicity	dicyclic	monocyclic

The type of AUs conjunction is undefined here like in the previous model.

(4) Diaxial monopodial model with all shoots elongated

Examples: *Alchemilla argyrophylla* Oliver, *A. johnstonii* Oliver, *Lachemilla polylepis* (Wedd.) Rothm.

Variant A. Example: *A. argyrophylla* (Fig. 6)

Variant B. Example: *A. johnstonii*

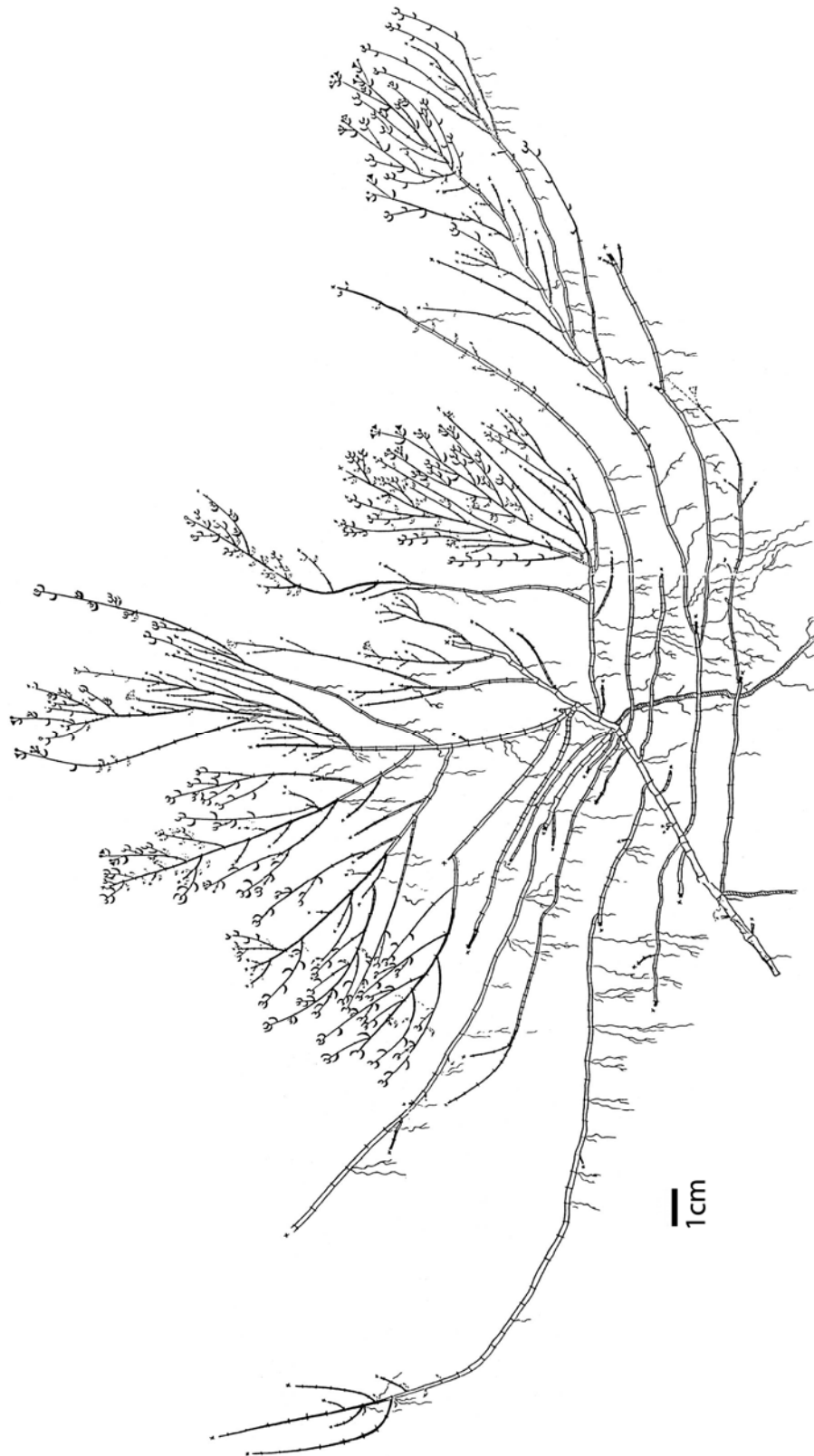
Table 5 is appropriate for both variants.

Table 5:

	MS1	MS2
relation to the flower position	open	closed
number of metamers	indeterminate	indeterminate (in var. A) or 1 (in var. B)
length of internodes	elongate	elongate
contribution into reside	completely	no
cyclicity	polycyclic	monocyclic

Figure 2: Partial shrub of *Lachemilla vulcanica*. >

Architectural units, axiality and their taxonomical implications



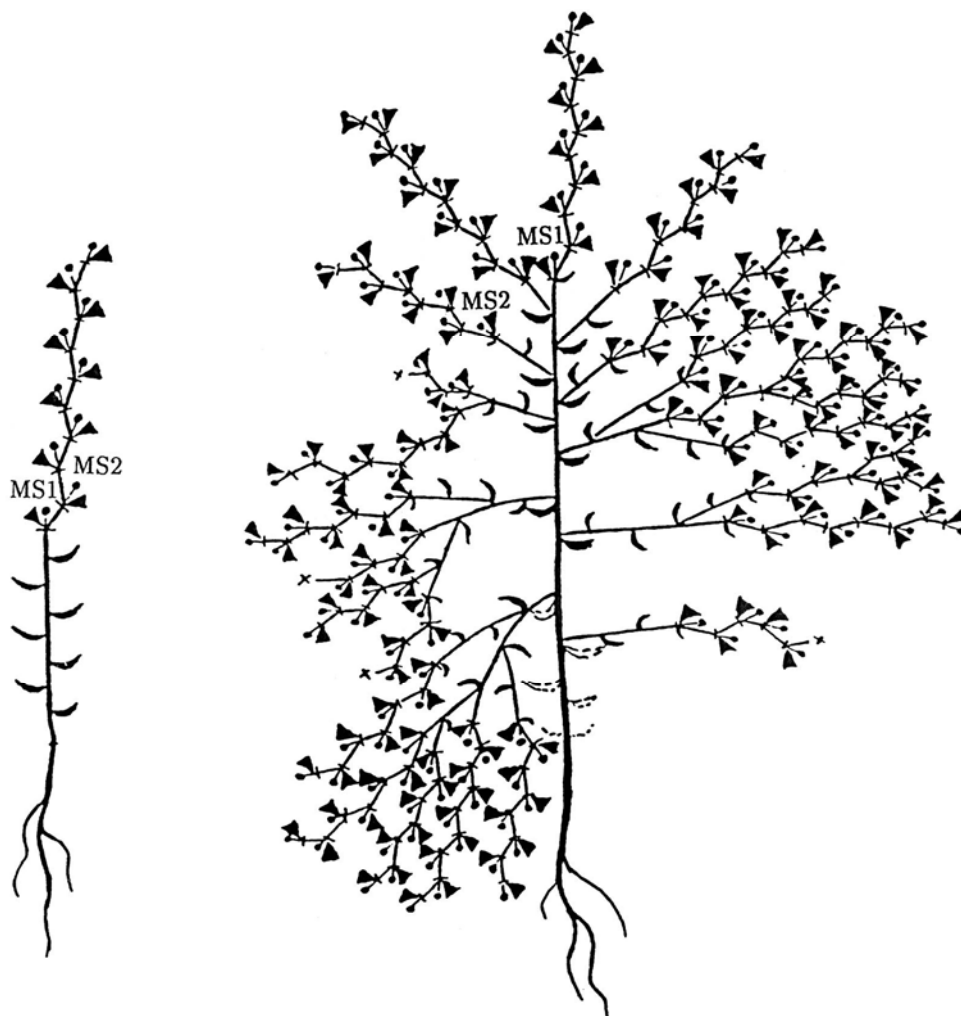


Figure 3: Shoot system of *Aphanes arvensis* (exemplars of different vigour).

(5) Sympodial diaxial model with elongated shoots

Examples: *Alchemilla elongata* Eckl. et Zeyh., *A. bifurcata* Hils et Boj. ex Baill. (Fig. 7; Table 6).

This model is represented only in *Alchemilla*.

Table 6:

	MS1	MS2	MS3
relation to the flower position	open	open	closed
number of metamers	indeterminate	few	one
length of internodes	elongate	elongate	elongate
contribution to duration	partly	no	no
cyclicity	monocyclic	monocyclic	monocyclic

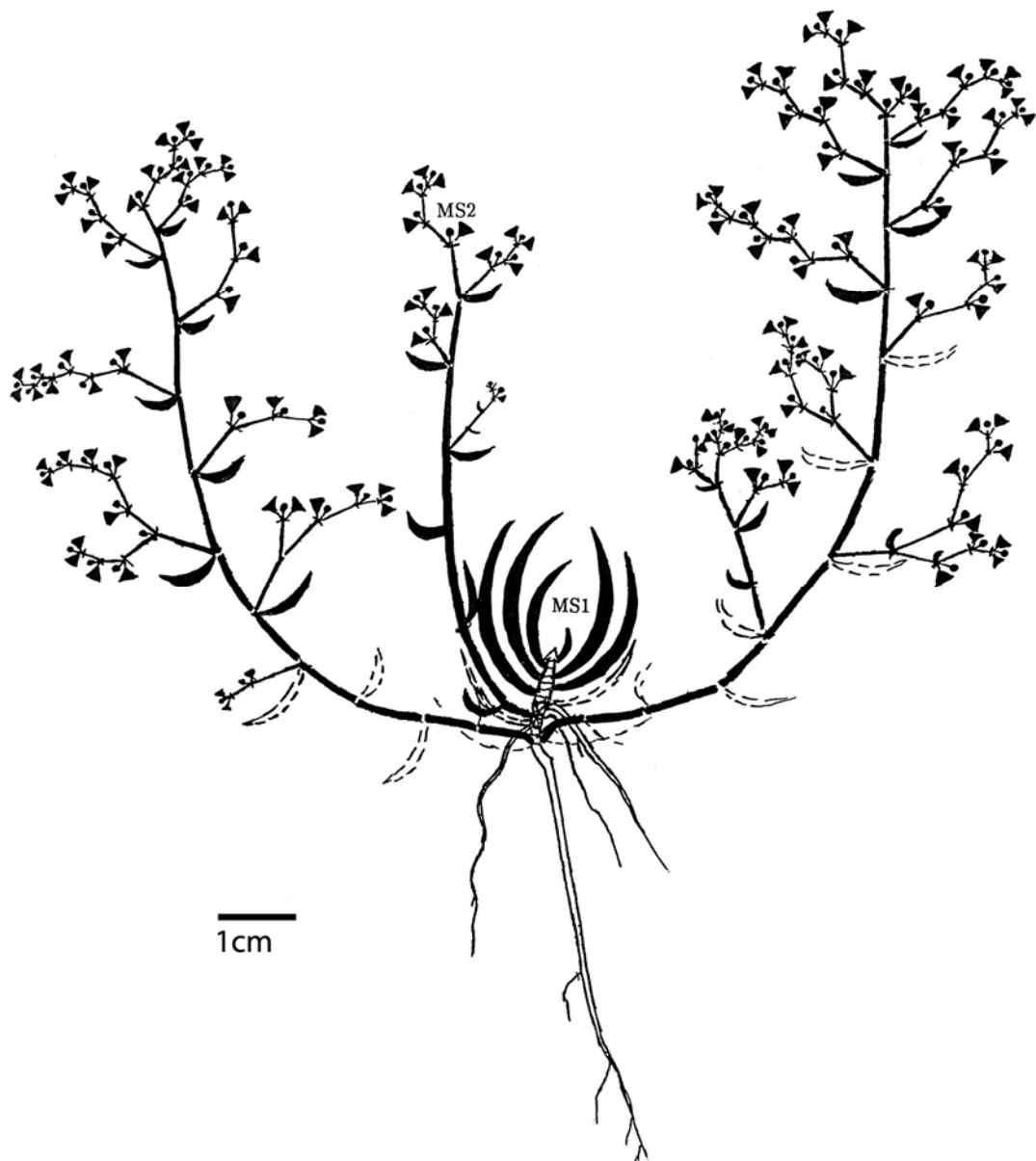


Figure 4: Shoot system of *Lachemilla aphanoides* on the rosette stage (first year).

The MSs in Table 6 are not arranged in complete accordance with their order of branching. Two kinds of shoots possess the same order of branching (Fig. 7) e.g. order 2: first, long open shoots and second, short closed shoots, because of the rather complicated structure of the synflorescence in these species they possess **paracladia** (long open shoots) and elements of **floral unit** (short closed shoots) with different structure (KUSNETZOVA 1992).

A. A. NOTOV & T. V KUSNETZOVA

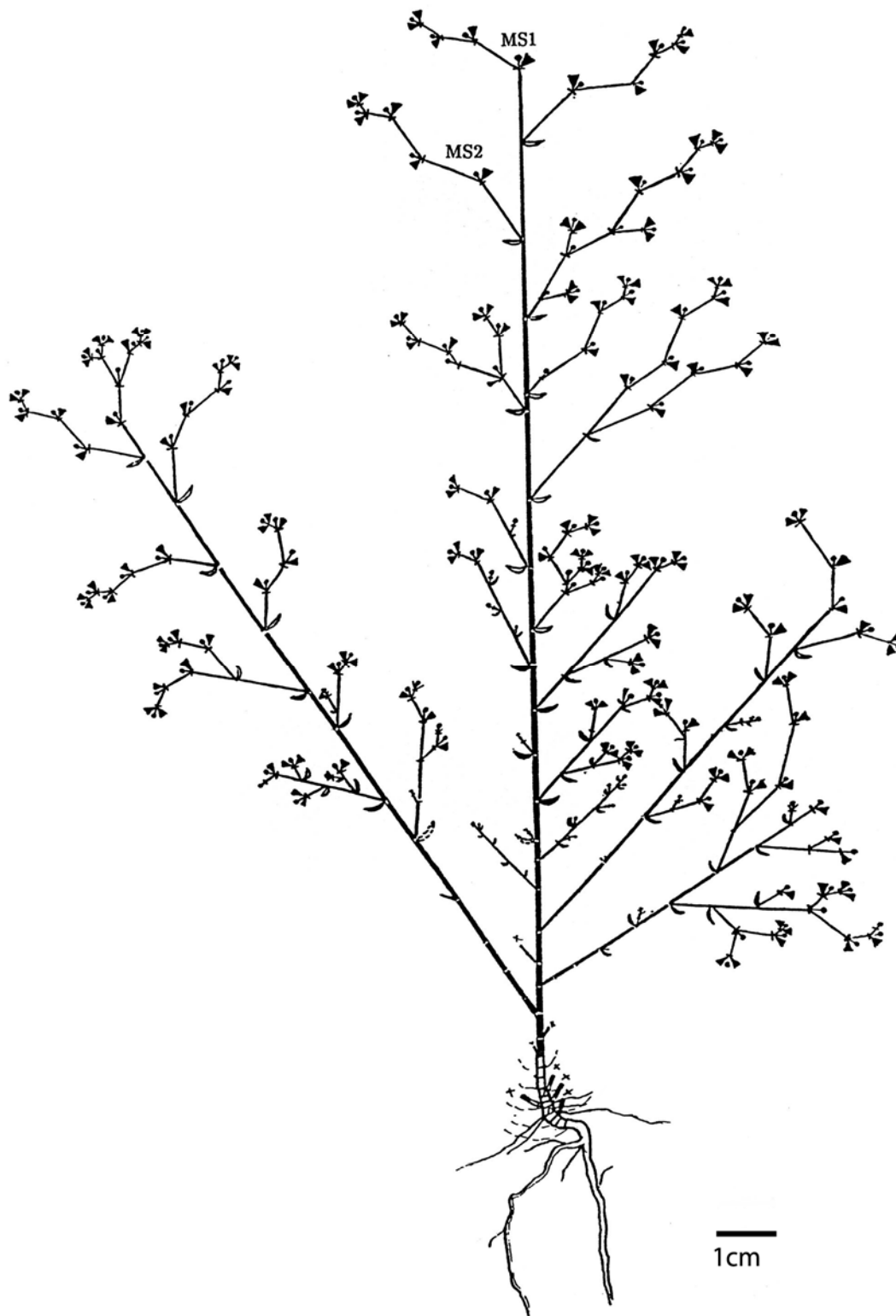


Figure 5: Shoot system of *Lachemilla aphanoides* with terminal inflorescence (second year).

Architectural units, axiality and their taxonomical implications

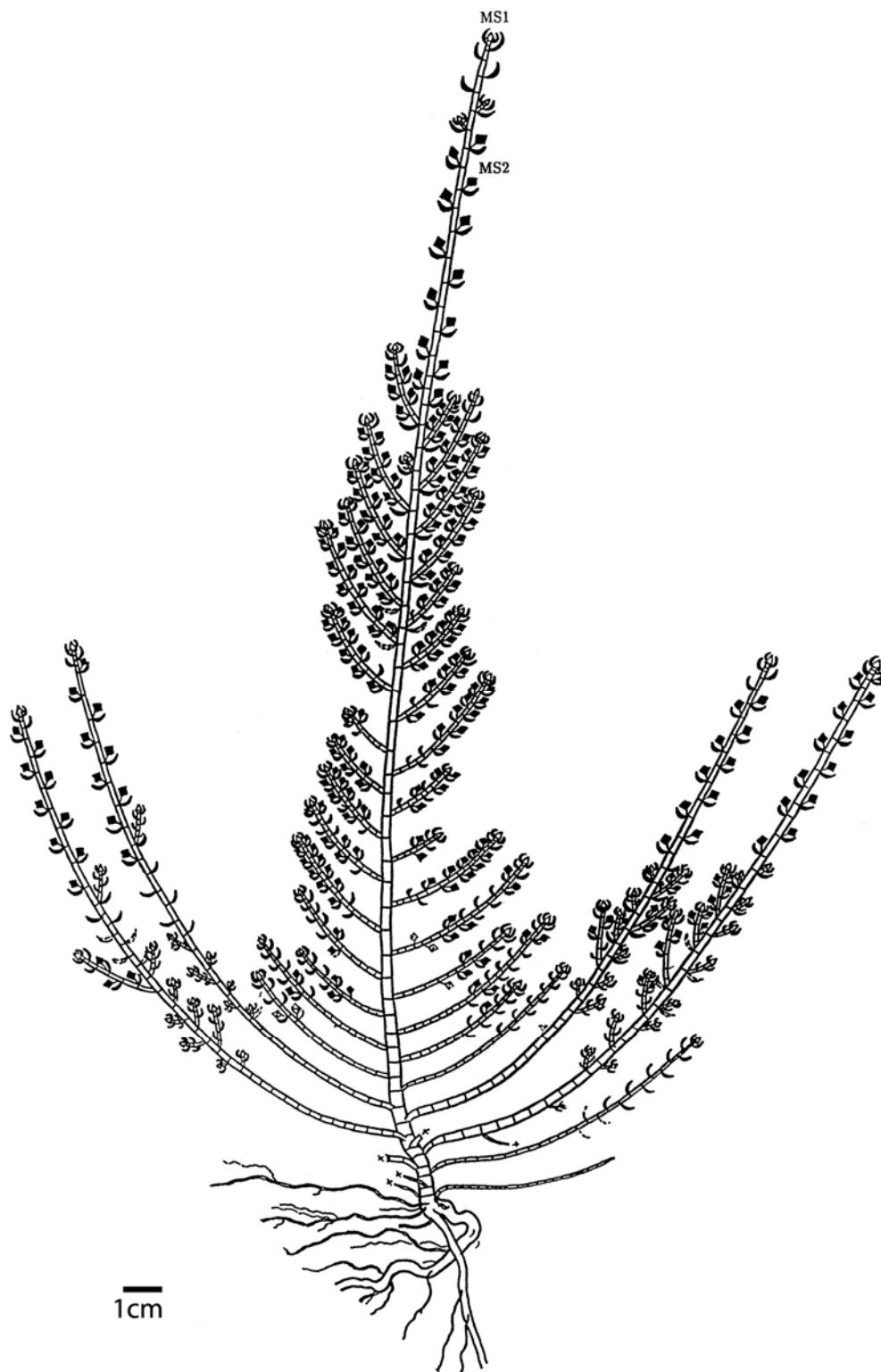


Figure 6: Shoot system of young generative plant of *Alchemilla argyrophylla*.

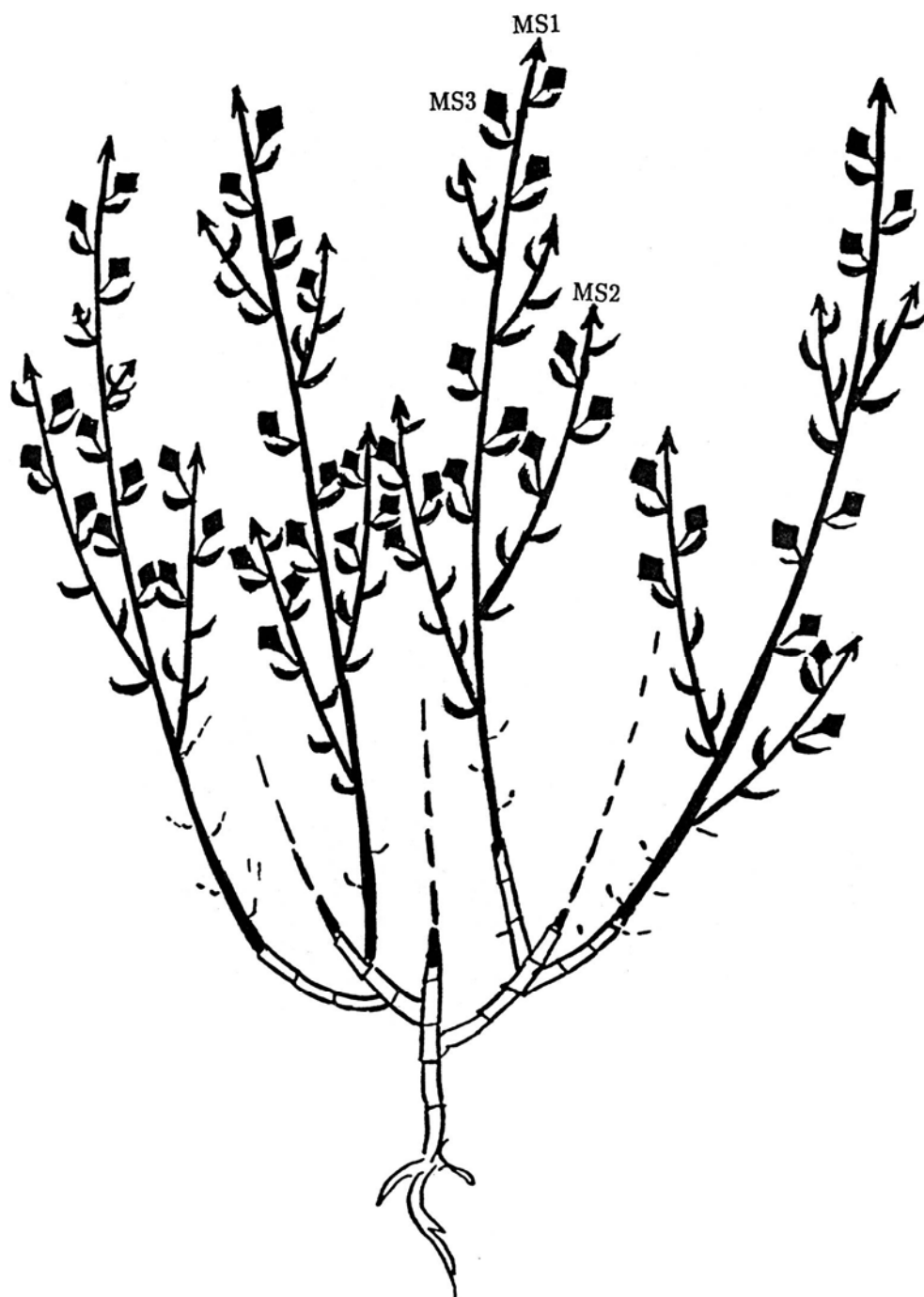


Figure 7: Sympodial diaxial model with elongated shoots (scheme).

Architectural units, axiality and their taxonomical implications

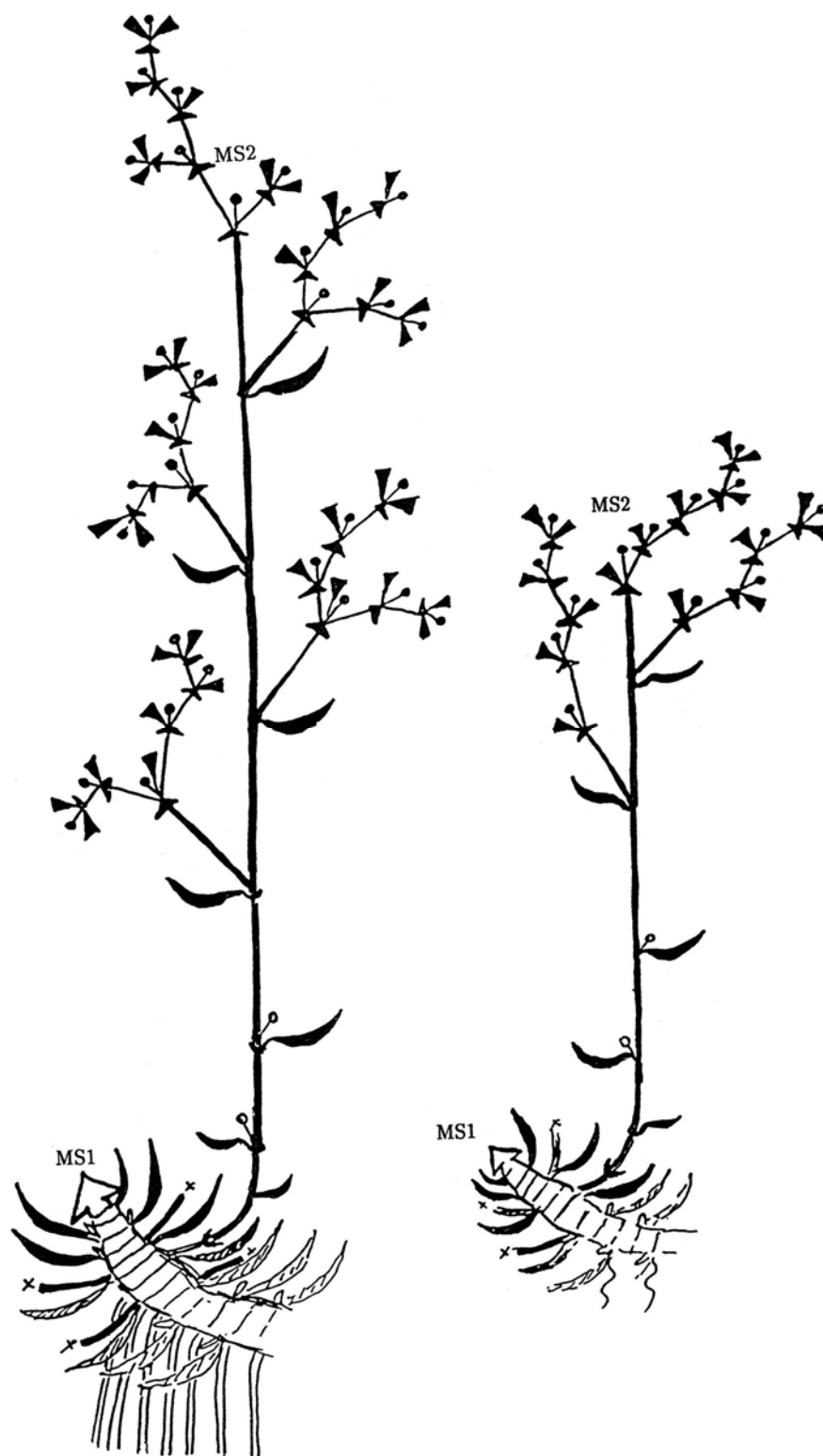


Figure 8: Shoot systems of *Alchemilla vulgaris* (left) and *Alchemilla alpina* (right).

(6) Monopodial rosette diaxial model

Examples: *Alchemilla vulgaris* L. s.l., *A. alpina* L. s.l., *Lachemilla nivalis* (H.B.&K.) Rothm.

Variant A. Example: *A. vulgaris* (Fig. 8)

Variant B. Example: *L. nivalis*

Table 7 is appropriate for both variants.

Table 7:

	MS1	MS2
relation to the flower position	open	closed
number of metamers	indeterminate	one to many (var. A) or one (var. B)
length of internodes	rosette	elongate
contribution to duration	completely	no
cyclicity	polycyclic	monocyclic

Variant of *A. pentaphyllea*. This rather strange variant of model 6 is found only in *A. pentaphyllea* L. Their **innovation buds** on the MS2s bear ephemeral lateral floriferous shoots (Fig. 9). These shoots may lie flat after flowering thus spreading the innovation buds around and serving as a mean of vegetative propagation. The buds give rise to the MS1s, they form new AUs.

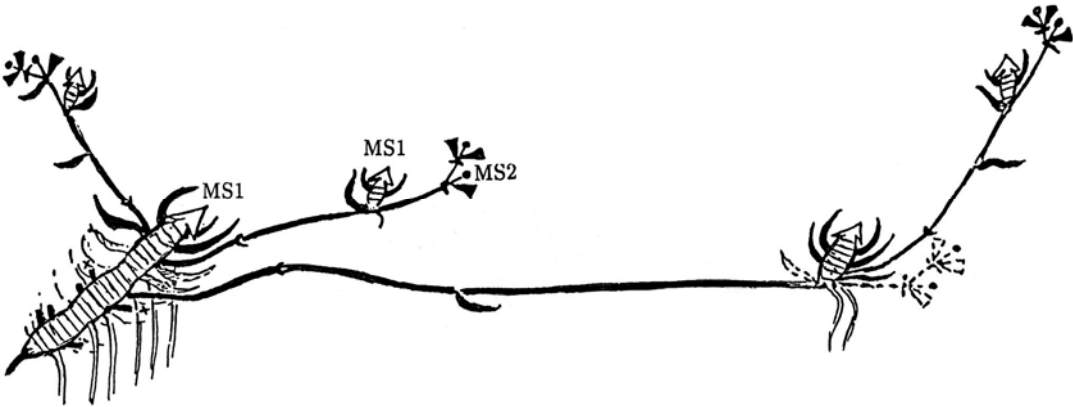


Figure 9: Shoot system of *Alchemilla pentaphyllea*.

(7) Monopodial diaxial model with both, rosette and semi-rosette skeleton shoots

Examples: *Alchemilla volkensis* Engl., *Lachemilla orbiculata* (Ruiz et Pav.) Rydb.,

L. pectinata (H.B. et K.) Rothm.

Variant A. Example: *L. orbiculata* (Fig. 10)

Variant B. Example: *L. diplophylla* (Dils) Rothm.

Table 8 is appropriate for both variants.

Figure 10: Fragments of shoot system of *Lachemilla orbiculata*. >

Architectural units, axiality and their taxonomical implications



Table 8:

	MS1	MS2	MS3
relation to the flower position	open	open	closed
number of metamers	indeterminate	indeterminate	one to many (var. A) or one (var. B)
length of internodes	rosette	semi-rosette (proximal part elongated)	elongate
contribution to duration	completely	completely	no
cyclicity	polycyclic	polycyclic	monocyclic

In Table 8 the correlation between branching order and MS number does not hold (compare model (5) and Table 6) because ephemeral floriferous shoots (MS3) may be formed both, on rosette shoots thus possessing branching order 2 and on semi-rosette shoots possessing branching order 3. Our material also shows that this model is rather variable in relation to the position of floriferous shoots on semi-rosette skeleton shoots, the former being positioned either on elongated (proximal) or on the rosette (distal) part of MS2.

The rosette skeleton shoot (MS1) is **the only one** in the plant body: it is the genuine main axis, the axis of first (absolute) order. This shoot is in most cases rather long-living and produces MS2 several times.

(8) Monopodial diaxial semi-rosette model

Variante A. Example: *L. rupestris* (H.B. et K.) Rothm. (Fig. 11)

Variante B. Example: *L. pinnata* (Ruiz et Pav.) Rothm. (Fig. 12)

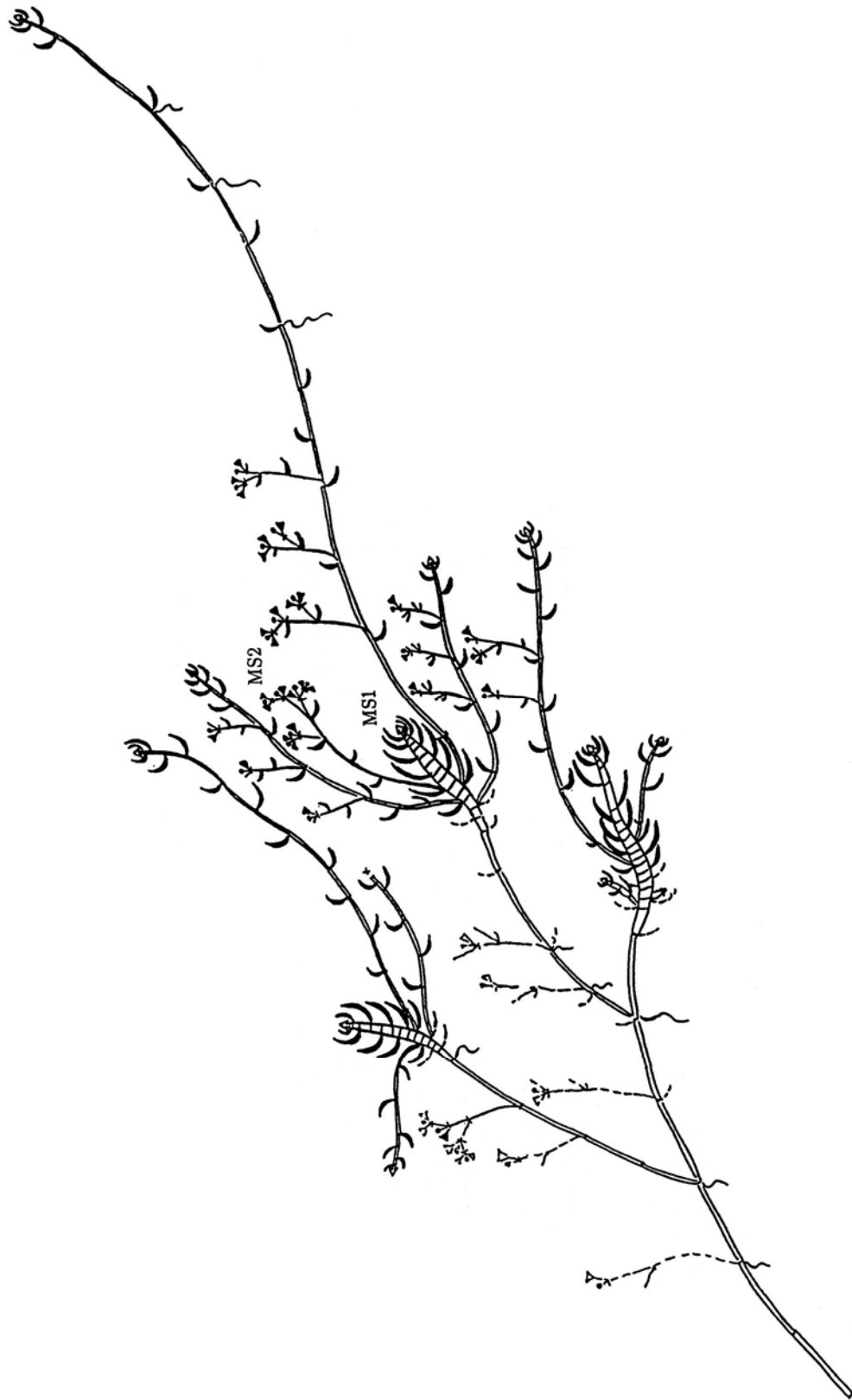
Table 9:

	MS1	MS2
relation to the flower position	open	closed
number of metamers	indeterminate	one to many (var.A) or one (var. B)
length of internodes	semi-rosette (proximal part elongated)	elongated
contribution to duration	completely	no
cyclicity	polycyclic	monocyclic

This model differs from the previous one only in one point: the main (rosette) axis is rather short-lived and dies off completely before a plant reaches a flowering stage. This axis does not bear lateral floriferous shoots and must not be taken into consideration when defining the AU structure (see theoretical implication). So Table 9 describing both variants A and B is rather simple. However some species possess the architecture intermediate between models (7) and (8) in relation to the life-span of the main axis.

Figure 11: Fragment of shoot system of *Lachemilla rupestris*. >

Architectural units, axiality and their taxonomical implications



(9) Monopodial diaxial model with elongated shoots and with rosette main shootExample: *Alchemilla fischeri* Engl. (Fig. 13; Table 10).

Table 10:

	MS1	MS2
relation to the flower position	open	closed
number of metamers	indeterminate	one
length of internodes	elongate	elongate
contribution to duration	completely	no
cyclicity	polycyclic	monocyclic

This plant also has a short-lived rosette main axis which does not persist until flowering; so we do not take it into consideration.

(10) Monopodial rosette triaxial modelExample: *Alchemilla villosa* Jungh. (Fig. 14; Table 11)

Table 11:

	MS1	MS2	MS3
relation to the flower position	open	open	closed
number of metamers	indeterminate	indeterminate	1
length of internodes	rosette	elongate	elongate
contribution to duration	completely	no	no
cyclicity	polycyclic	monocyclic	monocyclic

Conclusion

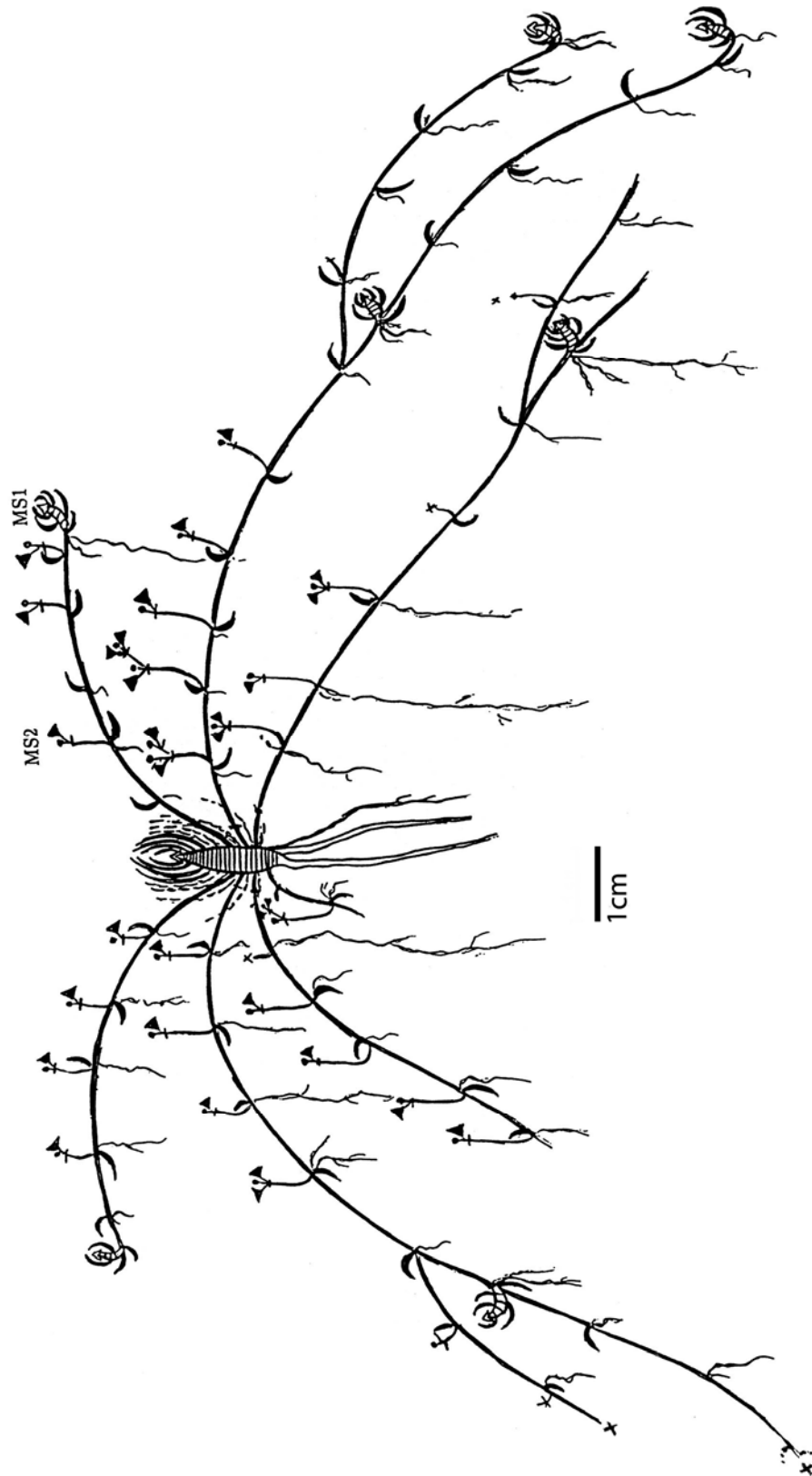
We have found ten architectural models in the subtribe Alchemillinae, five of them possessing different architectural variants. We use both architectural tables and schemes to characterize AUs inherent to each model. Three main kinds of AUs are found dependent on axiality i.e. monoaxial (1–3), diaxial (4–9) and triaxial (10).

II. Evolutionary pathways of architectural models in Alchemillinae

Above, we gave the descriptions of 10 architectural models occurring in Alchemillinae treating their AUs. Now we try to state the frequency of occurrence of these models in different taxa within the subtribe. We can mention (see Fig. 15) that the general spectrum of architectural diversity in Alchemillinae is almost the same as in other closely related groups within Rosaceae, e.g. *Potentilla* (ZHITKOV 1972; PAVLOVA 1987), but the frequencies of occurrence of various models are quite different. Numerical data in Fig. 15 are of course of relative value because there are numerous differences in taxonomic treatments of species boundaries by different authors. These controversies are partly due to the presence of regular apomixis in some groups within *Alchemilla*.

Figure 12: *Lachemilla pinnata*: the whole plant. >

Architectural units, axiality and their taxonomical implications



Di axial models are the most widespread in the subtribe. They are represented in all three genera being the most polymorphic. Monoaxial forms are rare and triaxial ones are represented only in *Alchemilla* subsection *Villosae*.

The sympodial semi-rosette model which is so customary in temperate herbs (SEREBRYAKOVA 1977) including Rosaceae (e.g. *Potentilla*, *Agrimonia*) is almost absent in Alchemillinae. We mention this model only arbitrary in one species possessing a short life history (*Lachemilla aphanoides*). Architectural spectra within each of the three genera constituting the subtribe are also quite different. *Alchemilla* has rather polymorphic architecture (see Fig. 15); only in *Alchemilla* we can observe triaxial as well as di axial models (the latter being sympodial or monopodial) with elongated shoots. Monoaxial models however are completely absent in *Alchemilla*. These forms occur only in *Lachemilla* and *Aphanes* (Fig. 15).

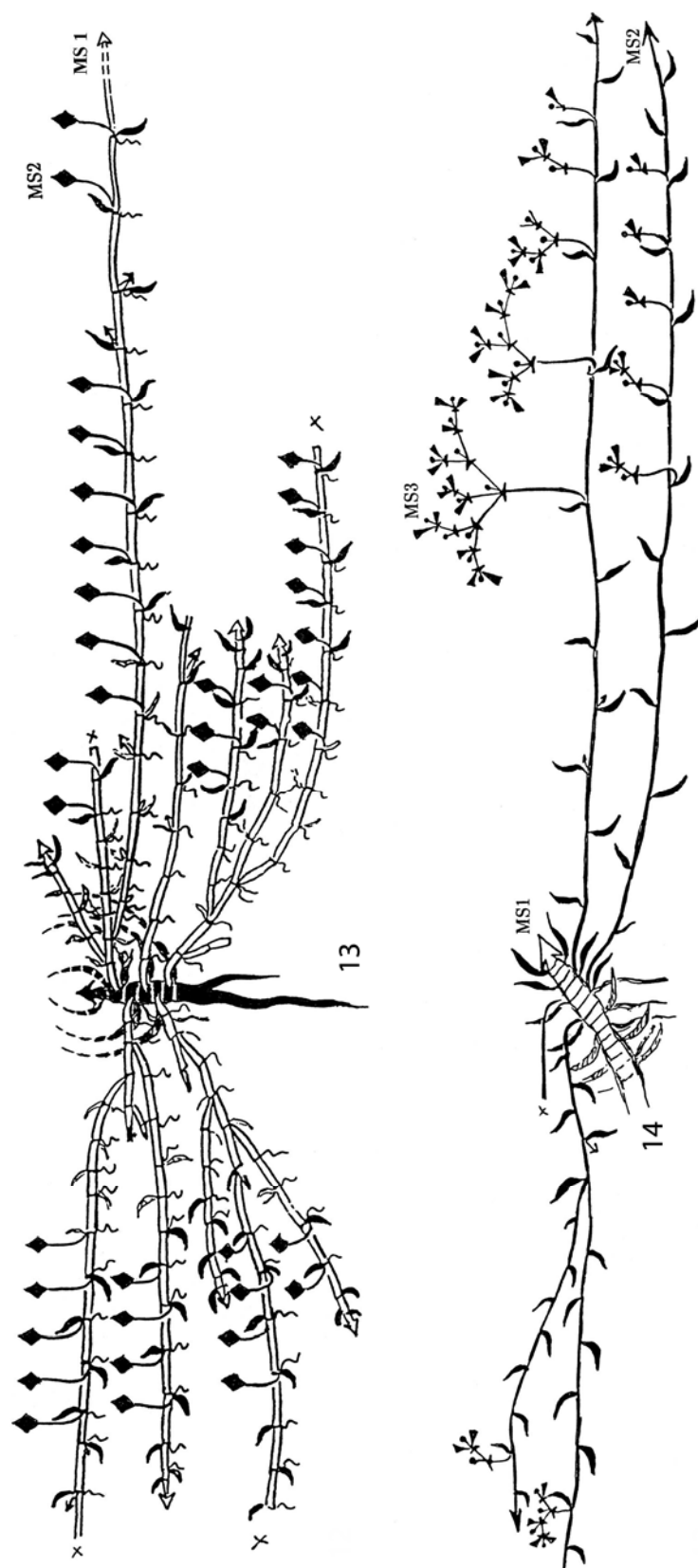
Comparative analysis of architectural diversity produces a general scheme (Fig. 16) with two main series of forms each with several “branches”. These series are purely structural but may be considered from the evolutionary point of view.

The left series includes mostly monoaxial forms the right one di axial and tri axial models. The linkage between the two series is problematic. We could only consider the architecture of *L. aphanoides* to be intermediate between mono- and di axial plants (Fig. 17, IIb). This biennial produces lateral peduncles during the first year thus behaving as di axial but next year it produces terminal floriferous shoots thus becoming monoaxial. Similar intermediate types of shoot development are found in some closely related genera in *Potentilla* (ZHITKOV 1972, 1973): these forms are also pauciannual. We can conclude that a kind of correlation exists between the unstable (intermediate) type of shoot development and shortened life history. This unstable model (that of *L. aphanoides*) may be regarded as ancestral for temporary rosette monoaxial forms (Fig. 17, IIa) and some peculiar pauciannual di axial forms in *Aphanes pumila* (Fig. 17, Va'; Fig. 16, A). This evolutionary hypothesis may be corroborated by studying the life histories of taxa under consideration. The earliest stage of main shoot development, namely rosette stage, is quite identical for all the models under consideration; the subsequent stages being different. Besides that in forming lateral peduncles *L. aphanoides* is similar to *Aphanes pumila*, but it is also similar to temporary rosette species in forming a terminal peduncle. So we can draw the reconstruction of an evolutionary pathway from an intermediate type of shoot development (*L. aphanoides*) to di axial forms (like *Aphanes pumila*) by elimination of the latest stage of main shoot growth, i.e. the stage of terminal peduncle formation. This process may be regarded as **terminal abbreviation** in the minor life cycle, i.e. the life cycle of the main shoot (SEREBRYAKOVA 1977, 1983); the result is the change of axiality (compare Tables 4 and 7 in Part I of our work and note the differences in the string relation to the flower position for MS1). The origin of monoaxial semi-rosette and temporary rosette forms from the intermediate one (*A. aphanoides*) may be explained in the analogous way, i.e. as a **median deviation** in the life cycle of the main axis (MS1s in Tables 3 and 4 in Part I), the latter being expressed in the reduction of lateral peduncles and elongation of internodes in rosette region.

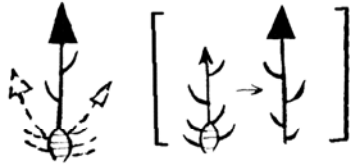
Figure 13: *Alchemilla fischeri*. the whole plant. >

Figure 14: Fragments of shoot system of *Alchemilla villosa*. >>

Architectural units, axiality and their taxonomical implications



A. A. NOTOV & T. V. KUSNETZOVA

			Alchemilla	Lachemilla	Aphanes	
MONOAXIAL	sympodial with elongated		—	19	—	
	semi-rosette and temporary rosette		—	1	15	
DIAxIAL	with elongated shoots	monopodial		63	2	—
		sympodial		7	—	—
	Monopodial with rosette, semi-rosette and elongated shoots		300 agamosp.	22	1	
			21	39	—	
		 variant of <i>A. pentaphyllea</i>	3	—	—	
			1	—	—	
TRIAXIAL		5	—	—		

This hypothetical evolutionary scheme is in accordance with our considerations on *Aphanes* phylogeny namely its origin from *Lachemilla* subsection *Glomerulatae*; the latter including *L. aphanoides*. The arguments will be given below (Part IV).

Considering the right series of forms in Fig. 17 also as evolutionary, we suppose the forms with elongated shoots to be the most primitive in this group (Fig. 17, III). The sympodial diaxial model with elongated shoots (Fig. 17, IV) may be considered as derivative from the monopodial one (Fig. 16, B, upper part). These two models may be linked together by the series of architectural types differing in the life span of a monopodial shoot (MS1s in Tables 5 and 6 in Part I). The beginning of the series is represented by *A. argyrophylla* and *A. elgonensis* with long-lived polycyclic monopodial shoots consisting of numerous architectural units (AUs see Part I). These species produce new MS1s from basal dormant buds rather occasionally. The middle part of the series is built of various forms within *A. johnstonii*. There may be the plants with rare and irregular substitution of MS1 by a new one together with the growth cessation of the former, all MS1s being oligocyclic. One can also observe other forms within the same species namely possessing regular substitution of MS1s together with a rather short life span (4–5 years), i.e. with few AUs. These MS1s may be also treated as oligocyclic. The end of this series is *A. bifurcata* with a monopodial shoot developing in only one vegetation period. It is worth mentioning that this monopodial shoot is monocyclic, however, it consists of several zones similar to the elementary shoots of forms possessing perennial oligocyclic MSs. So, this shoot is homologous to the perennial polycyclic shoots (MS1s) of the species listed above. The distal part of this shoot is ephemeral so it may be called a peduncle. The evolutionary derivation of such a shoot from the perennial one may be regarded as a result of **acceleration** in minor life cycle (life cycle of MS1). This acceleration is the cause of the change of shoot system growth modus from monopodial to sympodial (Fig. 16, B). This change produces a considerable alteration of the major life cycle, i.e. life cycle of the whole plant (SEREBRYAKOVA 1983). The acceleration of shoot system development is often considered as one of the main trends of the evolution of the plant body (KHOKHRJAKOV 1975; SEREBRYAKOVA 1983) so our hypothesis seems to be true.

Monopodial models with rosette shoots (Fig. 17, Va) seem to us to be derivatives of monopodial models with all shoots elongated (Fig. 16, lower part). The arguments are follows:

- we never find rosette shoots in the life history of long-shoot species even in its earliest stages; so it is not likely for rosette-shoot species to be ancestral for long-shoot ones;
- in rosette-shoot species we often observe several proximal internodes on the shoots of any order to be elongated. This phenomenon may be regarded as serial recapitulation of an ancestral trait e.g. elongated internodes.

Considering the evolutionary relations between different models of the monopodial rosette diaxial group (Models 6–8 in Part I), the most primitive is those with all the skeleton shoots being completely rosette and the innovation bud on the peduncle lacking (Fig. 17, Va; Table 7 in Part I). Appearance of the innovation bud on the peduncle (Fig. 17, Vb: variant of *A. pentaphyllea*) is probably a result of homoeosis (SATTTLER 1988). This peculiar structural trait

is regularly observed in *Alchemilla pentaphyllea*, but may be occasionally found as teratological variant in *A. vulgaris* s.l. and in some species of section *Brevicaulon* subsection *Chirophyllum* (Fig. 16, C). Similar phenomena (probably due also to homoeosis) are described in some *Potentilla* species (SEREBRYAKOVA & PAVLOVA 1986; PAVLOVA 1987). Numerous architectural variants with elongated proximal internodes on all the skeleton shoots except the main axis (MS1 in Table 8, Part I) may be arranged in a series (Fig. 17, Vc, Vd; Fig. 16, D) demonstrating gradual loss of the rosette together with the increase of an elongated region. This series also gives a picture of some other modes of evolutionary transformation of shoot system namely shifting of the floral zone from rosette region to the elongated zone on MSs of the second and higher orders together with the complete reduction of the floral zone on the main axis. Parts of this series can be found within some sections or subsections (sections and subsections are treated according to ROTHMALER (1934, 1935, 1936, 1937); see Fig. 16, D). This series is terminated by forms with all the skeleton shoots completely elongated with the exception of the main shoot. The formation of an elongated proximal region on monopodial shoots of second and higher orders may be regarded as a basal deviation in their life cycles. This deviation is followed by acceleration in some cases: shortening of the life cycle of semi-rosette skeleton MSs. In some species (some forms of *L. pinnata*) one may observe regular (several times in a vegetation period) replacing of semi-rosette shoots by new ones (sympodisation). These shoots are short-lived (monocyclic) (Fig. 16, D, 8).

One more modus which can be demonstrated in the same series is shortening of the life span of the main axis. This modus may be treated as terminal abbreviation in minor life cycles of this axis (Fig. 16, D, 6, 7, 8). So in some species (Models 8 and 9 in Part I) the axis of the first order is not included in the main AU of an adult plant. However, it is noteworthy to take this axis into consideration to link together models 6, 7, 8, and 9 (see Part I) forming essentially a gradual morphogenetic (and probably evolutionary) series.

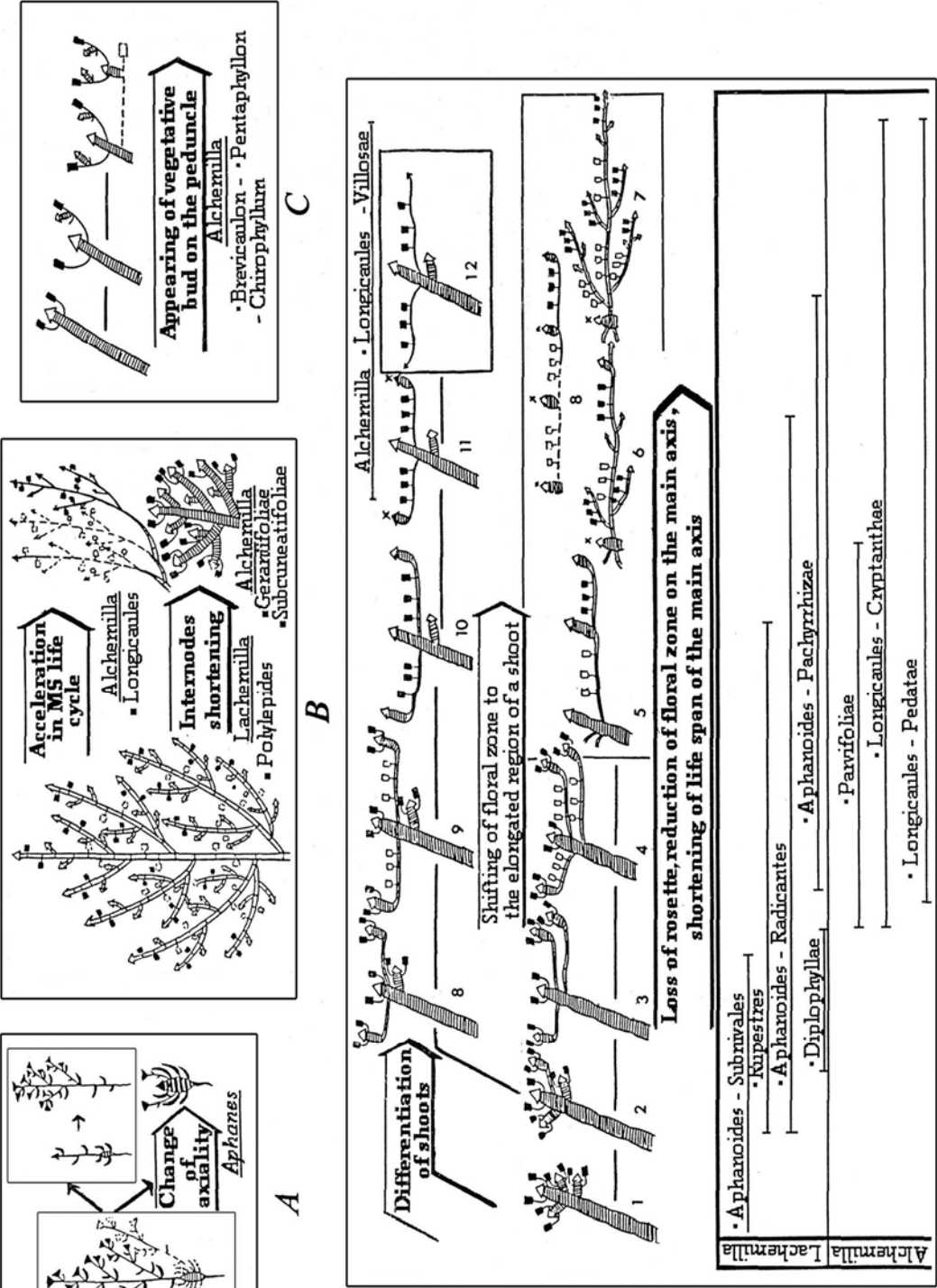
It is worth mentioning that there are probably two independent branches within the group of monopodial diaxial models discussed above (Fig. 17). The first branch includes the forms with uninodal peduncles (with only one node on the main axis of the peduncle) while the second one is formed by models with multinodal peduncles.

Our data show that the number of peduncle nodes is a rather constant feature within sections and subsections so we can suppose the two independent evolutionary pathways from monopodial diaxial forms with elongated shoots (Fig. 17, III) to the semi-rosette diaxial and then to the secondary long-shoot diaxial forms (Fig. 17, V) in uninodal and in multinodal branches.

Triaxial forms (Fig. 17, VI) are probably the derivatives of monopodial rosette diaxial ones. This evolutionary transformation is a result of differentiation of skeleton MSs of diaxial forms (MS1 in Table 7 in Part I) in life span, internodium length and flowering capacity (Fig. 16, D). The first steps of such a differentiation may be observed in *L. pectinata* (Fig. 16, D, 9, 10). Each MS1 may give rise to skeleton lateral shoots of two kinds: first, the rosette MS1s are completely

Figure 16: Modes of evolutionary transformation of architectural models within Alchemillinae. Lines on D (lower part) mean the spectra of architectural diversity within sections and subsections. Names of sections are marked with quadrangle while the names of subsections are marked with hyphen. Further explanations in text. >

Architectural units, axiality and their taxonomical implications



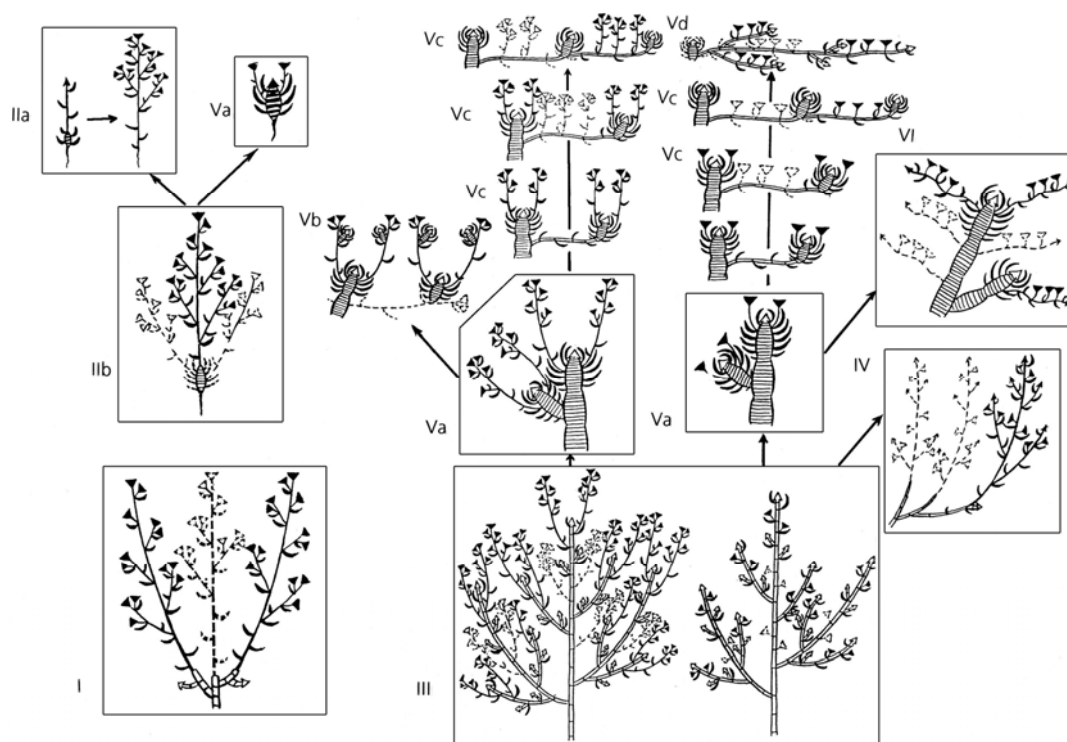


Figure 17: Evolutionary pathways of architectural models in Alchemillinae. For explanations see text.

similar to their mother shoot, and second, shoots with elongated proximal region (Model 7 and Table 8 in Part I). The shoots of the latter kind may involve further losing the rosette region and diminishing their life span up to one single vegetation period. These shoots become the true peduncles: One may observe the change of axiality as a result of abbreviation and acceleration in the life cycle of MS2 (Table 11, Part I). Skeleton rosette axes of such forms (Fig. 16, D, 11, 12, 13) don't bear peduncles.

Summing up all the data considered above we can state that most of the hypothetical evolutionary transformations of architectural models in Alchemillinae are probably due to the alteration of the minor life cycles of MSs (deviation, acceleration and so on). These alterations may be either structural (e.g. transformation of internodes length) or temporal (e.g. shortening of the life span – Fig. 16, B). It has to be mentioned however that in all these cases the life cycle of only **one type of MS** is altered. The result is obviously **differentiation** of MSs within the whole shoot system i.e. alteration in AUs composition and structure. All these phenomena lead to alterations of the major life cycle. It should be mentioned that even temporal alterations in minor life cycles may result in architectural transformations of a whole plant body.

Our study proves the usefulness of architectural analysis of the whole life history of a plant including the juvenile stages. These stages help us to reveal the interrelations within (a) a group of paucianual forms including *L. aphanoides*, *Aphanes pumila* and the temporary rosette model; (b) a group of monopodial diaxial models with rosette and semi-rosette shoots. In both cases the architecture of juvenile plants permits us to draw evolutionary hypotheses.

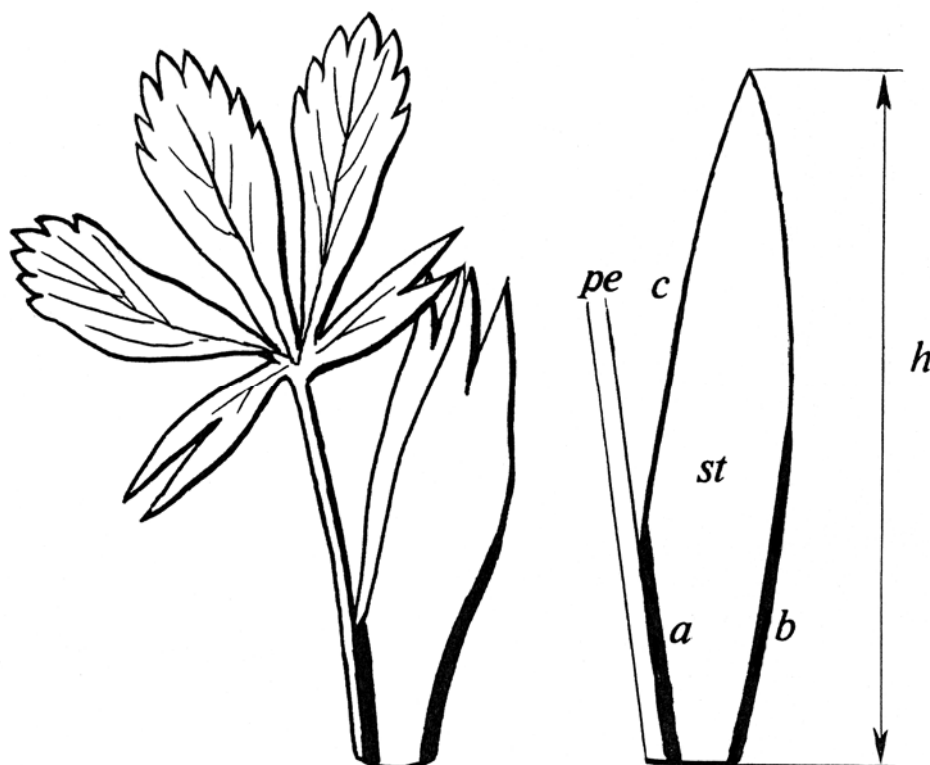


Figure 18. The general scheme of structural elements of leaf base. st – stipules, pe – petiole. Thick lines: areas of potential fusion. a – fusion with petiole, b – abpetiolare fusion, c – free distal parts of stipules.

According to our data the most constant architectural features in Alchemillinae are (1) axiality and (2) the type of AUs conjunction (sympodial or monopodial). Both characteristics are used in the names of the models. Within the group of monopodial models we can state a rather high stability of the nodes number on the peduncle (see above) so two evolutionarily independent branches of monopodial forms are revealed.

The most labile architectural features are : (1) length of internodes and (2) life span of MSs. Changing of these parameters probably causes architecture evolution.

III. Leaf and bud structure in Alchemillinae

While estimating hypotheses on the taxonomic significance of architectural features in Alchemillinae we have searched for the correlations between them and any other feature characterizing the vegetative region of a plant. So we suppose the occurrence of distinct and clean-cut characters connected with leaf base, stipules, and also bud structure. Taxonomists studying Alchemillinae, usually pay attention to the consistency of stipules as well as to the leaf blade segmentation, but few researchers have studied either sheath structure or the way of stipules fusion (ENGLER 1911; DE WILDEMAN 1921 a, b; FRIES 1923 a, b; FRÖHNER 1986). FRIES is known to be the first who found correlations between leaf base structure and shoot type.

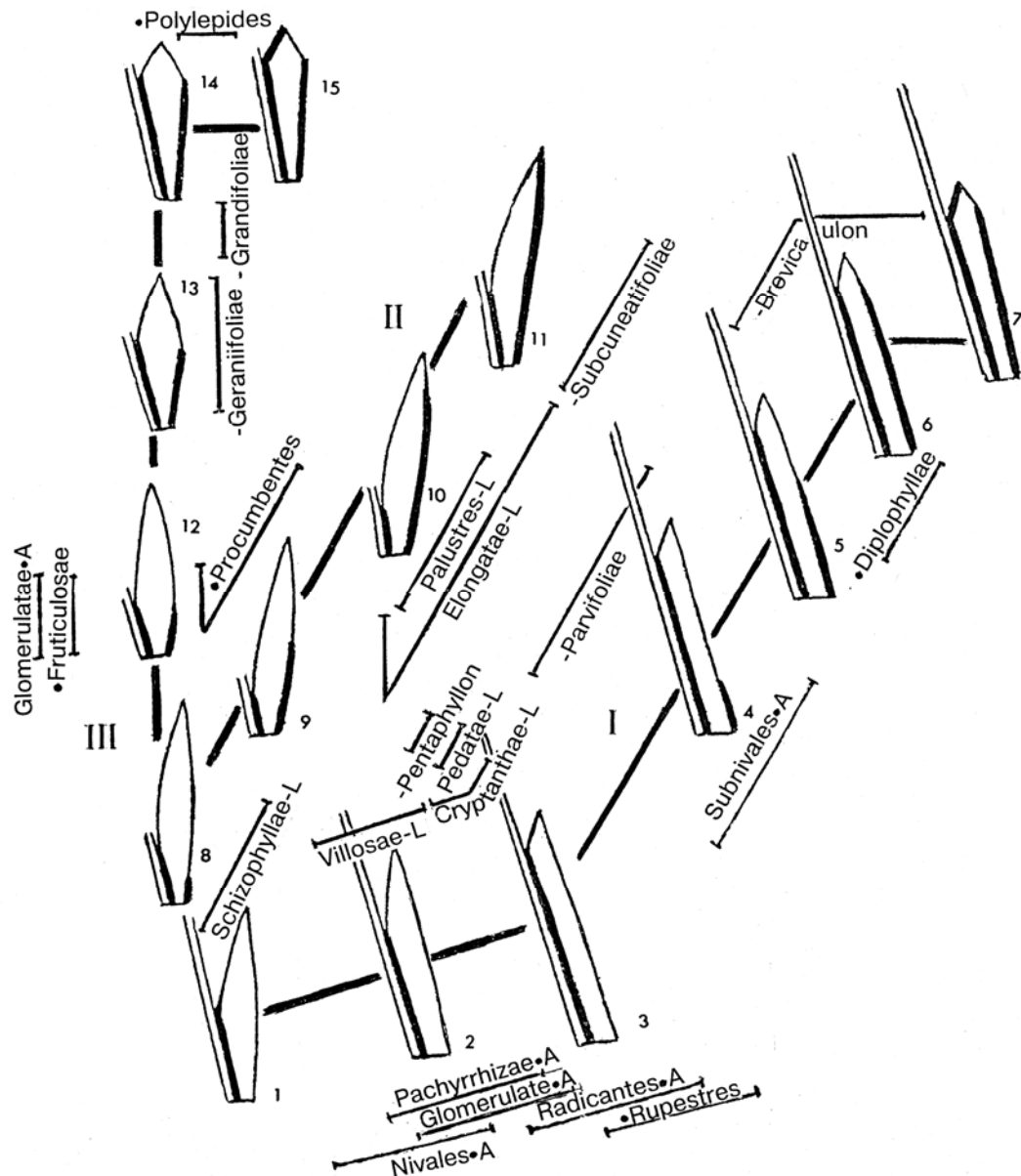


Figure 19. Types of leaf base structure in Alchemillinae. Spectra of leaf base diversity within sections and subsections are marked by lines. Sections of *Alchemilla* are marked with hyphens, sections of *Lachemilla* are marked with black circles. *L* – section *Longicaules*. *A* – section *Aphanoides*. Subsections are not marked. Further explanations in text.

We have studied leaf base and stipules in 36 *Alchemilla* species, 30 *Lachemilla* species, and 4 *Aphanes* species, so that all sections and subsections within the three genera are proportionally represented in the sample. The results of the study corroborate our supposition.

Leaf base

The leaf base in Alchemillinae species is generally regarded as a sheath formed by lateral stipules partly fused with the petiole (Fig. 18a). There may be some other fusions in this

region e.g. the fusion of two stipules on the side of a stem opposite to the leaf blade (abpetiolare side – Fig. 18b). The free distal parts of stipules (not fused with the petiole) may be however fused together on the adaxial side of the petiole (adpetiolare fusion – Fig. 18c).

These characters may be combined with each other in different ways within Alchemillinae. The whole diversity of leaf base structures may be arranged into three series (Fig. 19). The leaves within the first series (Fig. 19, I) demonstrate the noticeable fusion between stipules and petiole ($a/h > 0.5$ where h is stipule length – see Fig. 18). The beginning of the series is constituted by leaves with open sheath, i.e. without abpetiolare stipules fusion (rosette leaves of *A. villosa*, *A. nivalis*, where $a/h = 0.6–0.7$; see Fig. 19, 1–2). The series is continued by leaves with higher values of a/h (rosette leaves of *A. pedata*, *A. cryptantha*, *L. pinnata* show $a/h = 0.8–0.9$; see Fig. 19, 3). The next part of a series is formed by the leaves with rather high value of a/h (it is more than 0.8) and also with closed sheath i.e. with any extent of abpetiolare stipules fusion. For rosette leaves of *A. microbetula*, *L. holosericea* $b/h = 0.2–0.4$ (Fig. 19, 4) while for the same leaves of *A. sericea*, *A. hirsuticaulis* $b/h = 0.9$ (Fig. 19, 6). The first series is terminated by leaves possessing a completely closed sheath (the rosette leaves of *A. alpina* (Fig. 19, 7) demonstrate also adpetiolar fusion).

The second series (Fig. 19, II) is built of leaves with constantly low a/h (it is less than 0.5); stipules are slightly fused with the petiole. However one can notice that abpetiolar fusion of stipules increases through this series (Fig. 19, 8–11). While for *A. bifurcata* leaves $b/h = 0.2–0.3$, (Fig. 19, 8), in *A. elongata*, *A. ellenbeckii* this index reaches 0.5–0.7 (Fig. 19, 9–10). The end of the series is constituted by leaves with complete abpetiolare fusion of stipules ($b/h = 1.0$; Fig. 19, 11). Examples are: *A. stuhlmannii*, *A. argyrophylla*, *A. elgonensis*, *L. subnivalis*.

In the third series (Fig. 19, III) the indices a/h and b/h increase simultaneously. For *L. velutina* and *L. vulcanica* leaves on skeleton shoots $a/h = b/h = 0.3$. The same indices are revealed for leaves on elongated flower-bearing shoots of numerous monopodial rosette species e.g. *A. alpina*, *A. vulgapis*, *A. pentaphyllea*, *L. nivalis*, *L. subsericea* as well as on elongated regions of skeleton shoots of *A. cryptantha*, *A. microbetula*, *L. rupestris*, *L. mandoniana*, *L. pinnata* and other species with the same architecture (Fig. 19, 12). For the leaves on skeleton shoots of *A. johnstonii*, *A. hagenia*, and *L. polylepis* $a/h = b/h = 0.6–0.8$ (Fig. 19, 13–14). Leaves of *L. polylepis* demonstrate adpetiolare fusion of distal parts of stipules (Fig. 19, 15).

Our data show that the degree of stipular fusion of any kind is rather constant within species (even so polymorphic ones like *A. alpina*) as well as within sections and subsections (ROTHMALER 1934, 1935, 1936, 1937; see Fig. 19).

Bud

Studying early stages of leaf development in Alchemillinae we reveal two bud types according to the kind of protection of young primordia:

1. Every leaf primordium is covered by sheath and stipules of the previous leaf; leaf blade primordium is always outside the sheath of its own leaf (type A — Fig. 20A);
2. Leaf blade primordium is covered by a collar made of sheath and stipules of the same leaf (type B — Fig. 20B).

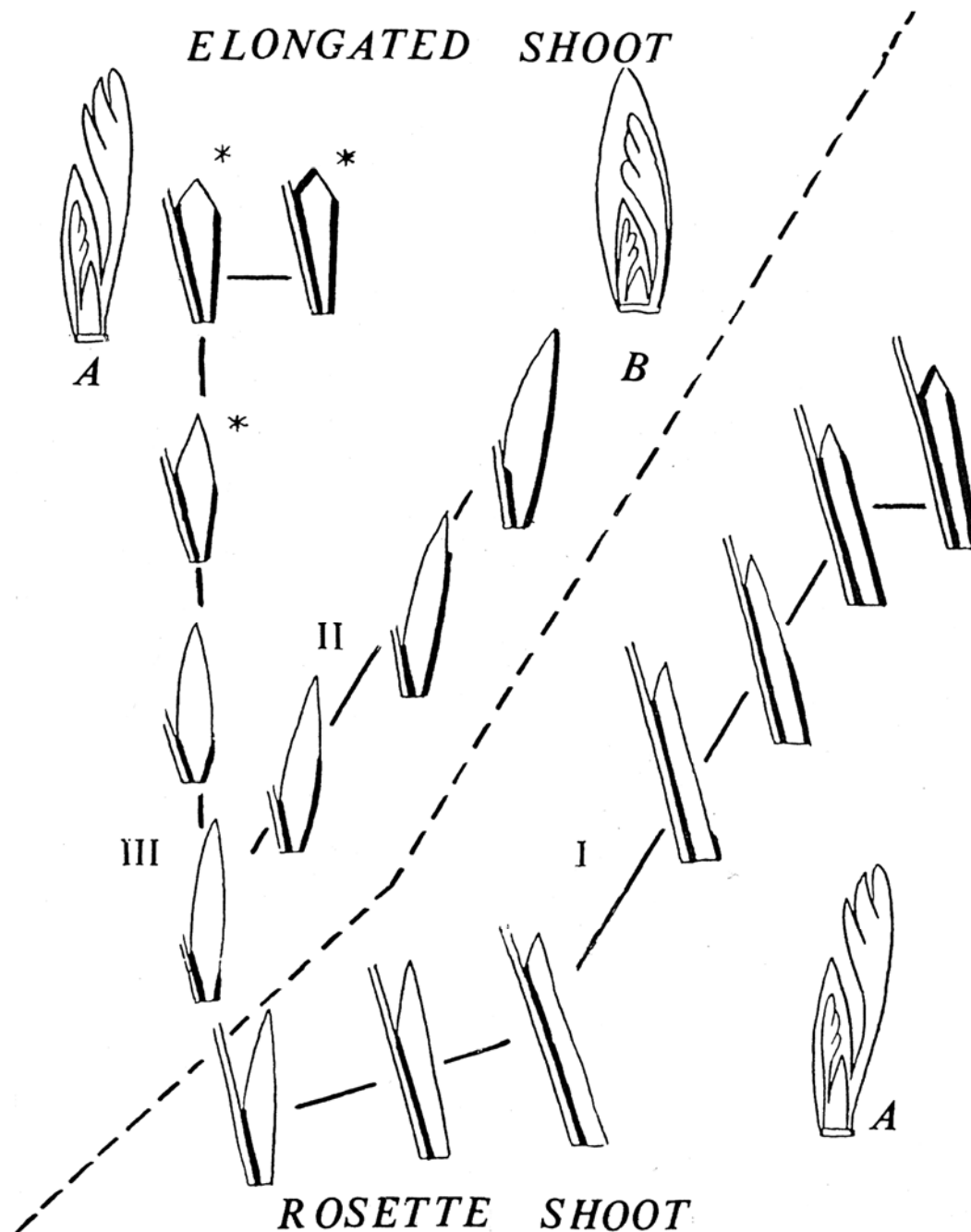


Figure 20. Correlations between leaf base, shoot and bud structure. A, B – bud types. Further explanations in text.

These differences in primordia protection and enveloping are due to the differences in their ontogenetic pathways. The bud of type A appears when the leaf blade primordium grows faster than primordial sheath and stipules (Fig. 20A). As a result the leaf blade is outside its own sheath since the earliest stages of leaf development. The bud of type B is a result of fast growth of primordial sheath and stipules while leaf blade growth is delayed (Fig. 20B) so the primordial leaf blade appears to be covered by its own sheath.

Correlations between shoot, leaf base and bud structural peculiarities

Our data shows that rosette shoots of Alchemillinae species usually bear leaves with $a/h > 0.5$. These shoots arise from the buds of type A (Fig. 20). On the contrary, elongated shoots bear as a rule leaves with $a/h < 0.5$ developing in most cases from the buds of type B (Fig. 20).

These correlations do not hold only in three of 68 species investigated: *A. johnstonii*, *A. hagenia*, and *L. polylepis*. These plants possess elongated shoots together with $a/h > 0.5$ and buds of type A (on Fig. 20 these variants are marked with an asterisk). All these species are taxonomically isolated: e.g. *A. hageniae* is the only species within the monotypic section Grandifoliae; *L. polylepis* and *A. johnstonii* s.l. belong to the oligotypic sections namely Polylepides and Geraniifoliae containing two species each. So we can suppose that for most other Alchemillinae species the revealed correlation of characters hold true. Therefore it seems reasonable to use leaf and bud features together with architectural ones for a taxonomic revision of Alchemillinae.

IV. Partial revision of Alchemillinae taxonomy

The subtribe Alchemillinae described by ROTHMALER (1937c) proves to be the natural taxonomic group. This subtribe embraces three genera namely *Alchemilla* L. s.str., *Aphanes* L. and *Lachemilla* Rydb.

LINNAEUS (1753) was the first who distinguished two genera within this group, namely *Alchemilla* and *Aphanes*, based on differences in flower structure. Plants from South America closely related to European *Alchemilla* were discovered by European botanists only at the beginning of XIXth century. PERSOON (1805) treated them as *Aphanes*. However, he noted that these species should belong to a separate genus because of their peculiar floral structure (two stamens and numerous pistils). At the end of XIXth century, data on South-American Alchemillinae became rich enough to describe the subgenus *Lachemilla* within *Alchemilla* (LAGERHEIM 1894).

The generic rank of the three groups discussed above namely *Alchemilla*, *Lachemilla* and *Aphanes* was stated by ROTHMALER (1937c). Since that time the generic limits are quite stable in Alchemillinae. However the situation concerning infrageneric groups is quite dissimilar. There is a number of artificial sections and subsections within Alchemillinae described by different authors (see below), so their taxonomy has to be improved.

One of the most important problems connected with Alchemillinae taxonomy on the infrageneric level is “character choice”. As it was already mentioned several floral characters (e.g. number of stamens and their arrangement) are constant within the genera. That’s why they are used for genera delimitation and diagnosis. Some other floral characters may vary even within a species (e.g. number of carpels are varying in some species of *Lachemilla* and in several taxa of *Alchemilla* subsection *Longicaules*). In both cases it is clear that these characters are inappropriate for sections and subsections delimitation. So other characters have to be used for this purpose.

The structure of vegetative parts of a plant is usually applied for infrageneric subdividing in Alchemillinae. E.g. FRIES (1923a,b) treated African Alchemillas using the characters of shoot

type (length of internodes) and leaf sheath (open or closed). In his opinion, these characters were correlated with each other: rosette shoots always occurred together with open sheaths and elongated shoots with closed sheaths. These characters became the basis for description of several taxa; many of them being rather natural.

An original system of *Alchemilla* s.str. was built by HAUMAN & BALLE (1934, 1936). These authors used the peculiarities of life forms, shoot type and leaf blade dissection; however their descriptions of life forms were not precise so convergencies were not distinguished from essential similarities. That was the reason why many taxa described by these authors proved to be artificial.

FRÖHNER (1975, 1986) revised taxonomic characters used for Alchemillinae treatment and revealed a set of new characters some of them connected with vegetative organs (seedling structure, leaf blade dissection in juvenile plants etc.). However he studied only European taxa, but not the whole subtribe.

The system of Alchemillinae drawn by ROTHMALER (1934, 1935, 1936, 1937c) is the most elaborated and well-known – it needs special consideration. Recognition of sections and subsections is based mostly on vegetative characters (life form, shoot type, shape and dissection of the leaf blade, leaf sheath closeness – see Fig. 21, Fig. 22 and Fig. 23). Unfortunately there is no standard plan of taxon diagnosis in this system so some of the diagnoses look rather incomplete. For example, species belonging to the section *Longicaules* of the genus *Alchemilla* are characterized as “herbaceous plants with creeping stems or stoloniferous; internodes elongated; leaves are sparse or condensed into rosettes; pistils one to many” (ROTHMALER 1935). It is not surprising that the group of species embraced by such a diagnosis proves to be heterogeneous (Fig. 24).

There are also some morphological fallacies and controversies in ROTHMALER's descriptions of several taxa; often connected with inadequate homologisation of plant parts. For example, ROTHMALER states that all the species belonging to the section *Aphanoides* (genus *Lachemilla*) possess “dense inflorescences”, however these inflorescences are situated on the peduncles developing in non-homologous positions, i.e. terminal or lateral: these dense inflorescences cannot be compared with each other. Another example is section *Longicaules* which is characterized by “elongated internodes” (see above). As we have shown in Part 1 of our work, these elongated internodes may occur in different and, hence non-homologous shoots (skeleton shoots, peduncles etc.). This character does not express the essential similarities of the species belonging to this section.

As we have shown, the system of ROTHMALER is not perfect, but it is the most modern and also the most carefully elaborated system of the whole subtribe Alchemillinae. That is why we shall use this system as a background for our treatment of this taxon.

Figure 21. Main morphological traits and areas of infrageneric taxa within the genus *Alchemilla*. First line: names of sections. Second line: names of subsections. Third line: life forms. Fourth line: structure of leaf blade and sheath. Fifth line: relative length of sepals and epicalyx leaflets. Sixth line: shape of hypanthium. Seventh line: number of pistils. Eighth line: shape of stigma. Ninth line: areas of distribution. Tenth line: architectural model. Eleventh line: peduncle structure. Twelfth line: bud structure. >

Architectural units, axiality and their taxonomical implications

BREVICaulON			PENTA- PHYLLON			LONGICAULES						PARVI- FOLIAE	SUBCUNEATH- FOLIAE	GRANDI- FOLIAE	GERNII- FOLIAE
Chirophyllum	Heliosium	Calycanthum	Palustres	Elongatae	Villosae	Pedatae	Cyparitiaae	Schizophylae							
η'	4	4	4	$\eta', 4$ semi	4	4	4	η' semi	4	4	4	4	η, η'	η	η, η'
1	1 (2)	1	1 (3)	1-2	1	1-2	3-8 (12)	1	1-4	1-2	1	1-4	1-2	1	1-2 (4)

In order to partially correct the subtribe taxonomy, we have to analyze all characters ever used in Alchemillinae taxonomy as well as the new characters revealed in the present study i.e. architectural model and leaf/bud peculiarities. The purpose is to evaluate the relative taxonomic significance of various characters.

We worked out the following criteria for evaluation of taxonomical significance of characters:

- stability within species and maybe within taxa of higher rank;
- appropriate level of their diversity i.e. presence of two or more distinct character states within a taxon under consideration.
- appropriate value of differences between various character states; this value is presumably connected with a certain level of evolutionary conservatism of these character states (PESSENKO 1989)

Examined characters:

- epidermal structure;
- nodal anatomy;
- root anatomy;
- pericarp anatomy;
- pollen structure;
- anatomy of axial organs;
- leaf and bud structure;
- floral structure;
- architectural model.

We studied the diversity of all these characters examining a sample of various Alchemillinae species belonging to different genera and sections (NOTOV 1993). Most of these characters do not agree with criteria listed above. Some of them are quite stable within genera (or even subtribe), so they are not appropriate for infrageneric taxa treatment. These characters are: epidermal structure, nodal anatomy, pericarp anatomy, pollen structure. All these characters may obviously be used for the whole subtribe description.

Other characters need special consideration.

Anatomy of axial organs

The species investigated differ in the degree of cambial activity in skeleton shoots. This activity obviously correlates with life form. Woody species (shrubs and dwarfish shrubs, e.g. *A. argyrophylla*, *A. johnstonii*) usually perform prolonged cambial functioning during the whole life span of a shoot. On the contrary, herbaceous species (*A. pentaphyllea*, *A. vulgaris*) have low cambial activity usually ceasing at the end of the first year.

The prolonged cambial activity may be rhythmic or continuous. This peculiarity is likely not correlated with climate (seasonal or non-seasonal) since the causes of rhythmic growth and cambial functioning are endogenous. For example, *Lachemilla polylepis* growing in non-seasonal climate has shoots with a kind of annual rings in the xylem. On the contrary, *A. argyrophylla*, *A. johnstonii*, and *L. subnivalis* growing in the similar climatic conditions demonstrate no annual rings in the stems.

Figure 22. Main morphological traits and areas of infrageneric taxa within the genus *Lachemilla*. Further explanations see Fig. 21.

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Architectural units, axiality and their taxonomical implications

POLYLEPIDES	RUPESTRES	PROCUMBENTES	A P H A N O I D E S				FRUTICULO-SAE	DIPLO-PHYLLAE
			Nivales	Subnivales	Glomerulatae	Radicantes		
h	4	semi h	4	4	semi h	4	semi h	4

The phellogen functioning is correlated with cambial activity. An active cambium usually occurs together with high phellogen productivity. In such cases the cortex is falling off soon and a thick periderm appears. Periderm later renews several times, the old periderms consequently being removed. On the contrary, in species possessing low cambial activity stems may bear cortex through the whole life.

Some peculiarities of stem anatomy are correlated with shoot type. In rosette shoots we observe, as a rule, distinct vascular bundles while in elongated shoots the ring of vascular tissue is complete.

As we have shown, some traits of stem anatomy are correlated with life form. The latter may serve as auxiliary character for taxonomic treatment of Alchemillinae. The same is thus true for some anatomical features. Several other anatomical traits however may correlate with shoot type and hence, with architectural model so they may be more significant for taxonomy (see below).

Floral structure

As we have mentioned above, several floral characters are constant within the genera. However some other characters are rather variable. We studied this variability in the sample of Alchemillinae species representing different genera. (NOTOV 1993).

The variable floral characters are: shape of hypanthium, presence/absence of epicalyx, relative lengths of sepals and epicalyx leaflets, their spatial orientation, number of pistils, shape of stigma (Fig. 21, Fig. 22 and Fig. 23). The number of pistils varies considerably within species possessing typically more than one pistil per flower. In such species the pistils number may vary even within an individual. Examples may be found within subsection *Cryptanthae* (genus *Alchemilla*) and subsection *Subnivales* (genus *Lachemilla*). Even species typically possessing a single pistil (*A. pentaphyllea*, *A. bifurcata*, *L. polylepis*, some species of *A. vulgaris* complex, and some *Aphanes* species) may occasionally possess two or more pistils per flower (NOTOV & GLASUNOVA 1994; TIKHOMIROV et al. 1995).

The relative length of epicalyx leaflets is also rather variable within sections. This character may also vary within a species (examples are *A. elongata*, *A. pedata*, *A. microbetula*, *L. subnivales*, and species of subsection *Glomerulatae*). There are however some taxa where this character is constant. E.g. most species belonging to subsection *Calycanthum* (section *Brevicaulon* genus *Alchemilla*) demonstrate the equal length of both, sepals and epicalyx leaflets. There are several species within this subsection namely *A. hirtipedicellata*, *A. catochnoa*, *A. viridiflora* which possess epicalyx leaflets noticeably shorter than sepals. Besides that, long epicalyx leaflets (as long as sepals) may occur in some species of section *Heliodrosium*. It is clear that the taxonomic value of this character is not very high.

The complete absence of epicalyx is also a rather labile character. However this is not true for *L. diplophylla* and *Aphanes bachiti*, where an epicalyx is always absent. ROTHMALER stated the absence of an epicalyx for *L. fruticulosa*; this feature became the background for the description of the monotypic section *Fruticulosae* (ROTHMALER 1935, 1937c). Investigating the type specimen of *L. fruticulosa* we found some flowers with a small epicalyx! Some species of subsection *Glomerulatae* also demonstrate the same state of this character. Precise comparison of herbarium specimen of *L. fruticulosa* and *L. velutina* – the latter belonging to the subsection *Glomerulatae* – proves their complete identity.

Architectural units, axially and their taxonomical implications

QUADRI- DENTATAE	INAEQUI- DENTATAE	AEQUI- DENTATAE
1	1	1

Figure 23. Main morphological traits and areas of infrageneric taxa within the genus *Aphanes*. Further explanations see Fig. 21. The last two lines are absent (data uncertain).

Some floral characteristics traditionally used in Alchemillinae taxonomy namely hypanthium shape, orientation of sepals and epicalyx leaflets, relative length of pedicels, shape of stigma and so on are very labile not only within species but even during the life history of one single

flower. These features in most cases express the different stages of flower development and are of course not appropriate for taxonomy.

So, we may conclude that flower characters are of low taxonomic value on sectional and subsectional level.

Leaf and bud structure

As we demonstrated in Part III of our work, structure of leaf sheath is a constant feature within sections and subsections within Alchemillinae. These features are correlated with shoot type and bud structure (see above). The consistence of stipules (leafy or glumaceous) also proves to be significant for description of several infrageneric taxa (ROTHMALER 1935, 1937a, 1937b, 1937c).

Architectural model

The results of the comparative morphological studies presented in the three previous parts show that architectural characteristics of Alchemillinae species are qualitative and discrete. The spectrum of different architectural models is rather wide within each of three genera (Fig. 21, Fig. 22, Fig. 23). So, we may suppose them to be of any taxonomic significance on sectional and subsectional level. This is not only true for architectural characteristics in strict sense but also for peduncle structure. As it was shown in Part II of our work the number of nodes on the peduncle is rather stable in evolutionary sense and may be inherent to a natural taxonomic group. To verify these suppositions we have to check the stability (or polymorphism) of all these characteristics within species or several taxa of higher rank.

Figures 21, 22, and 23 clearly show the results of such checking. Most of sections described by ROTHMALER (1934, 1935, 1936, 1937c) include species possessing only one architectural model. These sections are: *Brevicaulon*, *Pentaphyllon*, *Geraniifoliae*, *Subcuneatifoliae*, *Grandifoliae*, *Parvifoliae* (genus *Alchemilla*); *Polylepides*, *Rupestres*, *Procumbentes*, *Fruticulosae*, *Diplophyllae* (genus *Lachemilla*); *Quadridentatae*, *Aequidentatae* (genus *Aphanes*).

However there are some sections where almost all the models known in the subtribe are represented. These sections are: *Longicaules* (genus *Alchemilla*) and *Aphanoides* (genus *Lachemilla*). These sections seem to be artificial (see above). The diagnose of section *Longicaules* given by ROTHMALER includes only one feature common for all the species belonging to this section namely “elongated internodes”. Section *Longicaules* is also heterogeneous in relation to many characters such as stipules consistence, structure of leaf sheath and bud (Fig. 24).

The taxonomic integrity of section *Aphanoides* is also doubtful. This section may be distinguished from closely related section *Procumbentes* only by the flowers gathered in “laxe fascicles” while *Procumbentes* possess “dense fascicles”. This difference seems to us to be rather ambiguous. Other characters delimiting these sections are even more unclear e.g. leaf blade dissection, shape of stigma, pedicels length, carpels number (ROTHMALER 1935).

Summing up all results of character analysis we decided to make a partial revision of Alchemillinae system. Our taxonomic innovations are:

1. Diagnosis of genera and infrageneric taxa made by ROTHMALER (1935, 1936, 1937c, 1962) are improved using new characters (NOTOV 1993).

2. Section *Longicaules* of the genus *Alchemilla* described by ROTHMALER is subdivided into four sections.

Further revisions are in preparation.

Below we give the description of sections and subsections using both traditional and new taxonomic characters.

ALCHEMILLA L., s. str.

Section ***Longicaules*** Rothm. emend. Notov

Alchemilla L. – sect. *Longicaules* Rothm., p.p., 1935, Feddes Repert. 38: 34–35.

Plants monopodial or sympodial possessing elongated shoots (Fig. 24). Two shoot types are present namely vegetative and generative. Vegetative shoots are elongated and open (without terminal flower). They bear floral and vegetative zones interchanged. Floral zone bear axillary dichasia (=generative shoots) while vegetative zones bear axillary vegetative shoots of the next order. Monopodial species possess vegetative shoots all of them being perennial. Sympodial species demonstrate only basal part of seasonal growth increment to be perennial. All the plants are diaxial. Leaves are palmate-lobate with 5–7 lobes. Stipules leafy, their parts fused with the petiole being one third of their length. Stipules fusion on abpetiolare side takes 1/2–3/4 of their length. Free upper parts of stipules are dentate. Stipules primordia when in bud envelop the primordial blade of the same leaf. Pistils 1–3.

Neotypus: *A. elongata* Eckl. et Zeyh.

Tropical East and South Africa.

Subsect. 1. *Palustres* Rothm. emend. Notov

Alchemilla L. – Sect. *Longicaules* Rothm., subsect. *Palustres* Rothm., 1936, Feddes Repert., 40: 210.

Plants monopodial with elongated shoots. Abpetiolare fusion of stipules takes 3/4 of their length. Pedicels in almost all cases glabrous. Pistil 1.

Lectotypus: *A. palustris* Th. Fr.

East tropical Africa.

Subsect. 2. *Elongatae* Rothm. emend. Notov

Subsect. *Elongatae* Rothm., 1936, Feddes Repert., 40: 210.

Plants sympodial with elongated shoots. Abpetiolare stipules fusion taking 1/2 of their length. Pedicels pubescent. Pistils 1–3.

Lectotypus: *A. elongata* Eckl. et Zeyh.

South Africa.

Section ***Schizophyllae*** (Rothm.) Notov

Alchemilla L. – Sect. *Longicaules* Rothm. subsect. *Schizophyllae* Rothm., 1936, Feddes Repert., 40: 211.

Plants sympodial with elongated shoots. Two shoot types are represented namely vegetative and generative. Vegetative shoots are open, with vegetative and generative zones interchanged. Generative zones bear axillary dichasia (=generative shoots) while vegetative zones bear axillary vegetative shoots. Only basal parts of annual growth increments are perennial. Plants diaxial. Leaves palmate-lobate with 5 lobes. Stipules leafy, their fusion with petiole taking one-third of their length. Abpetiolare stipules fusion absent or taking 1/10 of their length. Free upper parts

sect. L O N G I C A U L E S Rothm.					
subject. Villosae Rothm.	subject. Pedatae Rothm.	subject. Cryptanthae Rothm.	subject. Schizophyllae Rothm.	subject. Palustres Rothm.	subject. Elongatae Rothm.
sect. VILLOSAE (Rothm.) Notov	sect. PEDATAE (Rothm.) Notov		sect. SCHIZO- PHYLLAE (Rothm.) Notov	sect. LONGICAULES Rothm. emend. Notov	

Figure 24. Main morphological traits and areas of sections and subsections within section *Longicaules* (genus *Alchemilla*) and their comparison with taxa described by ROTHMALER. First and second lines: names of sections and subsections described by ROTHMALER. Third line: leaf structure. Fourth line: leaf sheath structure. Fifth line: architectural model. Sixth line: bud structure. Seventh line: areas of distribution. Eighth line: names of sections described by NOTOV (1993).

of stipules bifid. Stipules primordia when in bud cover the primordial leaf blade of the same leaf. Pistil 1.

Lectotypus: *A. bifurcata* Hils et Boj. ex Baill.

Madagascar.

Section ***Pedatae*** (Rothm.) Notov

Alchemilla L. – Sect. *Longicaules* Rothm. p.p. (subsect. *Pedatae* Rothm.), 1936, Feddes Repert., 40: 211.

Plants monopodial-rosette. Two shoot types are represented namely vegetative and generative. The main vegetative shoot (shoot of 1st order) is rosette while vegetative shoots of higher orders possessing proximal elongated plagiotropic region and distal rosette one, rarely these shoots being completely elongated. Vegetative shoots open, generative shoots closed. Plants diaxial. Generative shoots multiflorous, dichasia (or monochasia) rather large bearing leafy bracteoles. Rosette leaves palmate-lobate with 7-13 lobes, their stipules glumaceous, almost completely fused with the petiole. Abpetiolare stipules fusion absent. Stipules primordia when in bud do not envelop primordial leaf blade of the same leaf. Pistils one to many.

Typus: *A. kiwuensis* Engler.

East tropical Africa, West Africa, Madagascar.

Section ***Villosae*** (Rothm.) Notov

Alchemilla L. – Sect. *Longicaules* Rothm. subsect. *Villosae* Rothm., 1936, Feddes Repert., 40: 210.

Plants monopodial-rosette. Two shoot types are represented namely vegetative and generative. The former are perennial, rosette and open while the latter being ephemeral, elongated and open. Plants triaxial. Generative shoots possessing several nodes with foliage leaves, prostrate. Rosette leaves palmate-lobate with 7–9 lobes, their stipules glumaceous, almost completely fused with petiole. Abpetiolare stipules fusion absent. Stipules primordia when in bud not enveloping primordial leaf blade of the same leaf. Pistil 1.

Lectotypus: *A. villosa* Jungh.

Madagascar, Ceylon, South India, Java.

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A. A. NOTOV & T. V. KUSNETZOVA

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