

# Comparative biomorphological study of the taxonomy and phylogeny of the genera *Consolida* (DC.) S.F. Gray and *Aconitella* Spach

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## Resum

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Les relacions filogenètiques a l'interior del gènere *Consolida* i entre els gèneres *Consolida* i *Aconitella* han estat posades de manifest com a resultat de la comparació de dades anatòmiques, cariològiques i morfològiques. Aquesta investigació ha confirmat la correcció de la divisió intragenèrica del gènere *Consolida*, proposada per E. HUTH (1895), per a tres de les cinc seccions que creixen al territori de la U.R.S.S. El rang taxonòmic ha estat especificat per al grup més modern i evolutivament avançat d'espècies del gènere *Aconitella*, que és considerat per molts autors a l'interior dels límits del gènere *Consolida*. La posició taxonòmica d'*Aconitella barbata* (Bunge) Soják, les característiques morfològiques de la qual són intermèdies entre els gèneres *Aconitella* i *Consolida*, ha estat precisada exactament. Les tendències evolutives principals de la tribu *Delphineae* han estat identificades: a partir del gènere mesofític completament perenne *Aconitum*, que és el més primitiu en els aspectes anatòmics, cariològics i morfològics, a través d'una sèrie de formes desconegudes, cap al gènere *Delphinium*; i també, a partir dels representants anuals de la secció *Delphinium* del subgènere *Delphinium*, cap als gèneres *Consolida* i *Aconitella*.

Mots clau: *Consolida*, *Aconitella*, *Delphinium*, *Aconitum*, Taxonomia, Anatomia, Morfologia, Evolució, Cariologia.

## Abstract

TRIFONOVA, V. I. (1990). Comparative biomorphological study of the taxonomy and phylogeny of the genera *Consolida* (D.C.) S.F. Gray and *Aconitella* Spach. *Collect. Bot.* (Barcelona) 19: 97-110

Phylogenetic connections within the genus *Consolida* and between the genera *Consolida* and *Aconitella* have been revealed as a result of the comparison of anatomical, karyological and morphological data. This study has confirmed the correctness of the intrageneric division of the genus *Consolida* proposed by E. HUTH (1895), for three out of the five sections growing on the territory of the USSR. Taxonomical rank has been specified for the youngest and most highly evolved group of species of the genus *Aconitella*, which is regarded by many botanists as being within the limits of the genus *Consolida*. The taxonomical position of *Aconitella barbata* (Bunge) Soják, whose morphological features are intermediate between the genera *Aconitella* and *Consolida*, has been stated exactly. The main trends in the evolution of the tribe *Delphineae* have been identified: beginning from the primarily perennial mesophytic genus *Aconitum*, which is the most primitive in its anatomical, karyological and morphological features, through a series of

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unknown forms to the genus *Delphinium*; and also from the representatives of the annual section *Delphinium* of the subgenus *Delphinium* to the genera *Consolida* and *Aconitella*.

Keywords: *Consolida*, *Aconitella*, *Delphinium*, *Aconitum*, Taxonomy, Anatomy, Morphology, Evolution, Karyology.

## INTRODUCTION

The objects of our study are the closely related genera *Consolida* and *Aconitella*, which were distinguished from the genus *Delphinium* L. in the last century. Another genus, *Chienia* W. T. Wang, described in 1964, was later classified by the author in 1979 as a synonym of *D. grandiflorum* L. We have attempted to trace the inter- and intrageneric connections of these two genera and to mark the main trends in the evolution of the tribe *Delphineae* Warming by comparing the results of the anatomical study of the seed coat and the petiole with data on karyotype research into the chromosome morphology and with the external morphological peculiarities.

**Genus *Consolida*** (DC.) S.F. Gray, 1821, Nat. Arr. Brit. Pl. 2:711.

*Delphinium* L. Sect. *Consolida* DC. 1818, Syst. 1:341.

In 1818 A. P. DE CANDOLLE distinguished a group of annual species with one nectary and one follicle from the genus *Delphinium* to form the independent section *Consolida* DC., equivalent to the group *unicapsularis* of Linnaeus. Three years later S. F. GRAY (1821) in a work on British flora promoted the section *Consolida* to the rank of a genus comprising only one species *C. regalis* (L.) S. F. Gray.

The genus *Consolida* consists of annual plants with a simple or branchy stem and multidissected leaves. The flower is zygomorphic with a double perianth, composed of five coloured sepals and one petal (nectary). The bottom of the upper unpaired (odd) sepal turns into a spur. The petal (nectary) is three-lobed, rarely subentire, extending into a nectariferous spur which is placed into the sepal spur. Staminodia are absent. The stamens are numerous and arranged into five spiral circles. There is only one carpel and a single follicle.

**Typus:** *C. regalis* (L.) S. F. Gray (*D. consolida* L.)

Today the genus *Consolida* numbers nearly 40 species, widely distributed in the temperate regions of the northern hemisphere: from the western coast of the Mediterranean Sea as far as Central Asia. The genus is characterized by a wide range of its ecological distribution. The species of the genus grow on low ground and on hills (up to 2 000 metres above sea level), on flat fields and on dry stony slopes, in steppes, semideserts and deserts. They are often found as weeds alongside *Centaurea cyanus* L. in grass crops and fallow fields.

In 1867 BOISSER, who attributed to the genus *Consolida* the rank of the section *Consolida* of the genus *Delphinium* L. s.l., made the first attempt to classify the system of the genus. He divided the section into 6 groups on the basis of the petal shape, but he did not attach any taxonomical rank to them and marked them with a special sign §. Three of them are here attributed to the genus *Consolida* and the rest to the genus *Aconitella*. In 1895 HUTH recognized the specificity of a number of annual species of the genus *Delphinium* and gave this genus the rank of a subgenus of the genus *Delphinium*. He divided this group into six tribes<sup>1</sup>

<sup>1</sup> The names of the tribes proposed by Huth (1895) are considered as nonvalidly published because he mistakenly applied this term to a category ranking lower than a section (International Code of Botanical Nomenclature, arts. 5 and 33.4, ex. 11, 1987 [GREUTER & AL., 1988]).



(differing from BOISSER's subdivision, 1867) on the basis of the spur and the pedicel size. Five of the tribes are related to the genus *Consolida* as currently defined and one to the genus *Aconitella*. These two works are the only attempts to create an intergeneric system of the genus *Consolida*. Most of the subsequent works present results on the regional floras processing different countries and geographical regions. The most complete list of the genus is presented in the articles of MUNZ (1967 a, b). In 1987 BLANCHE, MOLERO and SIMON studied karyotypes of some species of the genus *Consolida* and came to the conclusion that it was necessary to divide the *Consolida* section into two rows: Series *Consolida* and *Pubescentes* Blanché, Molero and Simon.

In this article we try to use the HUTH's system (1895), because it is correct for at least three out of the five sections growing in the territory of the USSR, and it was confirmed earlier by our biosystematic investigations (TRIFONOVA 1973; 1974 a; 1977; 1984 a,b). More detailed study is necessary to specify the taxonomical status and position of the sections *Parviflorae* and *Longibracteolatae* in the system of the genus.

**Sectio *Brevipedunculatae*** (Huth ex N. Busch) Kem.-Nath. Ranunc. Cauc.: 131, 1966.

*Delphinium* L., trib. *Brevipedunculatae* Huth. 1895, Bot. Jahrb. Syst. 20:338, 368 *non valide publ.*

*Pedunculi floribus multi breviores.*

TYPUS: *C. rugulosa* (Boiss.) Schröd.

DISTRIBUTION: from Asia Minor to Kazakhstan and India.

**Sectio *Consolida*.**

*Delphinium* L. trib. *Propria* Huth. Bot. Jahrb. Syst. 22:338, 383, 1895, *non valide publ.*

*Calcar sepala superans, 10-20 mm longius, pedunculi flores aequantes vel superantes.*

TYPUS: *C. regalis* (L.) S. F. Gray.

DISTRIBUTION: Europe, North Africa, Western and Central Asia.

**Series *Consolida*.**

TYPUS: *C. regalis* (L.) S. F. Gray.

**Series *Pubescentes*** Blanché, Molero & Simon, *Saussurea*. 18.(1):1-10. (1987).

TYPUS: *C. pubescens* (DC.) Soó.

**Sectio *Macrocarpae*** (Huth ex N. Busch) Kem. — Nath. Ranunc. Cauc. 130. (1966).

*Delphinium* L. trib. *Macrocarpae* Huth. Bot. Jahrb. Syst. 22:338, 374, (1895), *non valide publ.*

*Carpella cylindrica suprabasin latissima ad apicem paulum angustata, 12-27 mm longa.*

TYPUS: *C. orientalis* (J. Gay) Schröd.

DISTRIBUTION: Europe, North Africa, Asia Minor.

**Sectio *Longibracteolatae*** Huth ex Trif., Bot. Žurn. (Leningrad) 62(6):869. (1977).

*Delphinium* L. trib. *Longibracteolatae* Huth. Bot. Jahrb. Syst. 29:379. (1895), *non valide publ.*

*Pedunculi floribus aequilongi vel eos superantes.*

TYPUS: *C. tomentosa* (Auch. ex Boiss.) Schröd.

DISTRIBUTION: South-West Europe, Asia Minor, Syria, Iraq.

**Sectio *Parviflorae*** Huth ex Trif., Bot. Žurn. (Leningrad) 62(6):869 1977.

*Delphinium* L. trib. *Parviflorae* Huth. Bot. Jahrb. Syst. 29:389. (1895), *non valide publ.*  
*Flores parvi, calcar sepala aequans 5-7 mm longum.*

TYPUS: *C. flava* (DC.) Schröd.

DISTRIBUTION: Egypt, Asia Minor, Syria, Iran, Palestine, India.

**Genus *Aconitella*** Spach, 1839, Hist. Nat. Veg. 7:358; Soják, 1969, Fol. Geobot. Phytotax. 4(4):448.

*Aconitopsis* Kem.—Nath. 1939, Tr. Tbilssk. Bot. Dust. 7:127.

In 1839 SPACH separated the only known species of this group, *Delphinium aconitii* L. (*Aconitella aconitii* (L.) Soják) which has a helmet-shaped upper unpaired sepal, into the independent monotypic genus *Aconitella*, thus emphasizing the outward similarity of the new genus with the genus *Aconitum*. Later in 1867 BOISSER regarded the genus *Aconitella* as within the limits of the section *Consolida* of the genus *Delphinium* and divided it into three groups, differing in the petal shape. In 1895 HUTH combined these plants into one tribe: *Involuta*. He admitted the independence of only *A. barbata* and related it to the tribe *Parviflorae*. In 1939 KEMULARIA-NATHADZE, who knew nothing about SPACH's research (1839), again made this group into a separate genus under the name *Aconitopsis*, thus also emphasizing the resemblance of this genus to the genus *Aconitum*. It was not until 1969 that J. SOJÁK restored the priority name *Aconitella* for ten species of the genus. We

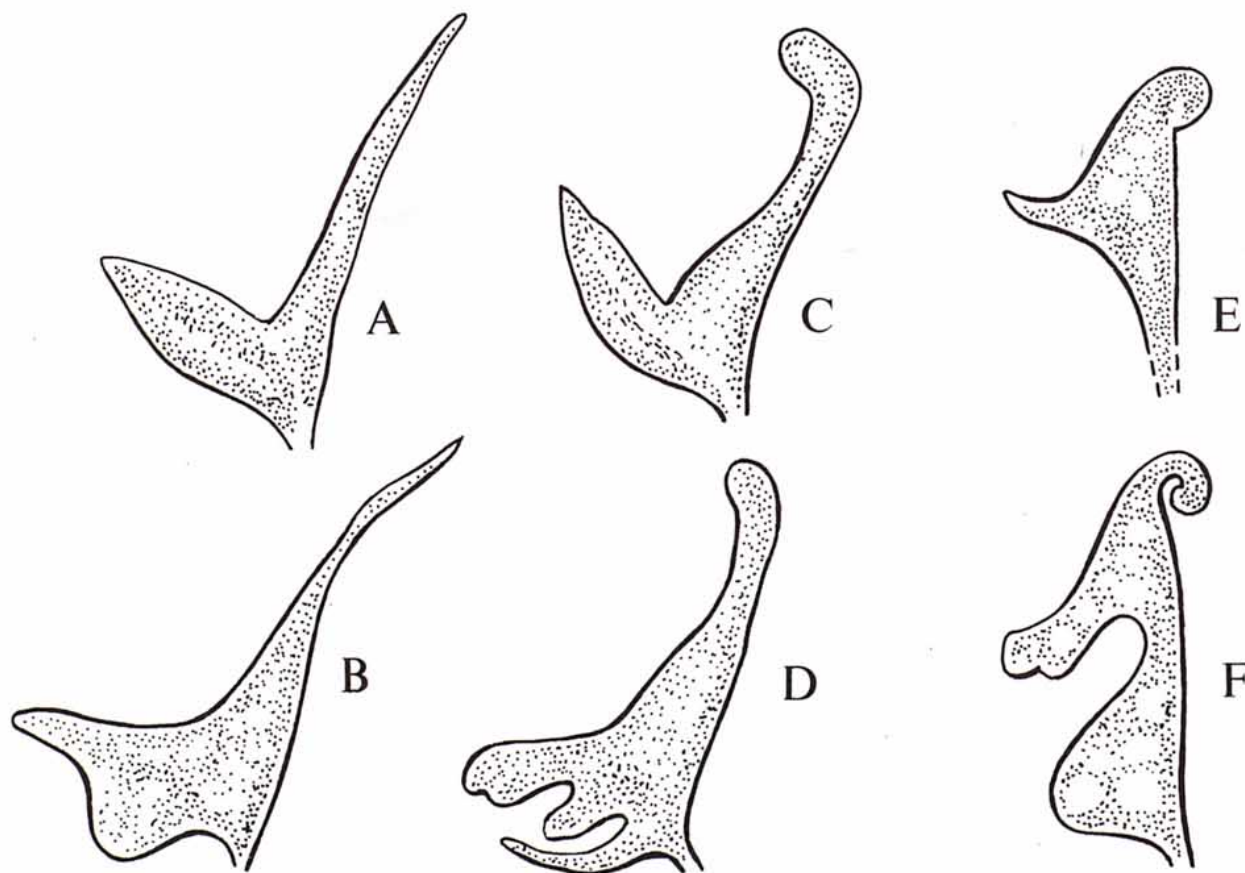


Fig. 1.— The shape of the unpaired sepal and petal in some representatives of the genera *Consolida* (DC.) S. F. Gray, and *Aconitella* Spach.

A, B- *Consolida divaricata* (Ledeb.) Schröd.: A- sepal, B- petal; C, D — *Aconitella barbata* (Bunge) Soják: C- sepal, D-petal; E, F — *A. hohenackeri* (Boiss.) Soják: E- sepal, F- petal.



consider the attribution of one of the species — *A. desertii syriaca* (Zohary) Soják — to the genus *Consolida* to be correct on the account of its three-lobed petal and pubescent follicle. But unfortunately the position of this species is still not definite, because the only herbarium specimen was lost before the publication of M. ZOHARY'S article (1941). On the basis of Zohary's description and the single existing slide with flower parts spread out, MUNZ (1967 b) also places this species in his synopsis among the genus *Consolida*.

The genus *Aconitella* comprises nine species spread mainly over Western Asia: from the European parts of Turkey in the west as far as the Northern regions of Iran and the Trans-Caucasian area in the east. The Middle Asian endemic *A. barbata* (Bunge) Soják, attributed to the Turkestan floristic province, also belongs to this genus.

The representatives of the genus are annual xerophytes growing mainly in steppes and semideserts (on stony and chalky hillsides, 500-2000 m), rarely in fallow fields.

The genus *Aconitella* is entirely different from the genus *Consolida* on account of the shape of the upper unpaired sepal and the petal. Most of the plants of the genus possess a helmet-shaped upper unpaired sepal and a snail-like twisted petal spur. The petal is five-lobed (while in the genus *Consolida* it is three-lobed) with broad oblique or ovate lower lobes. Two species — *A. saccata* (Huth) Soják and *A. barbata* — possess a different spur and petal shape. The spur in *A. saccata* is hook-shaped and saccate, is bent back and has a little nodule on the top. The petal has triangular acuminate sharp lower lobes, while in *A. barbata* the spur is slightly curved and blunt and the petal is characterized by sharply-pointed long lower lobes.

In terms of its external morphological features the genus *Aconitella* is an integrate group united by a common areal. The only exception is *A. barbata*, the only representative of the genus in Middle Asia: the form of its upper unpaired sepal spur and of the petal is intermediate between the genera *Consolida* and *Aconitella* (fig. 1). And the anatomical study of the petiole structure (TRIFONOVA, 1977) showed that this species is identical to the representatives of the genus *Aconitella* and should definitely be regarded as within the limits of the genus.

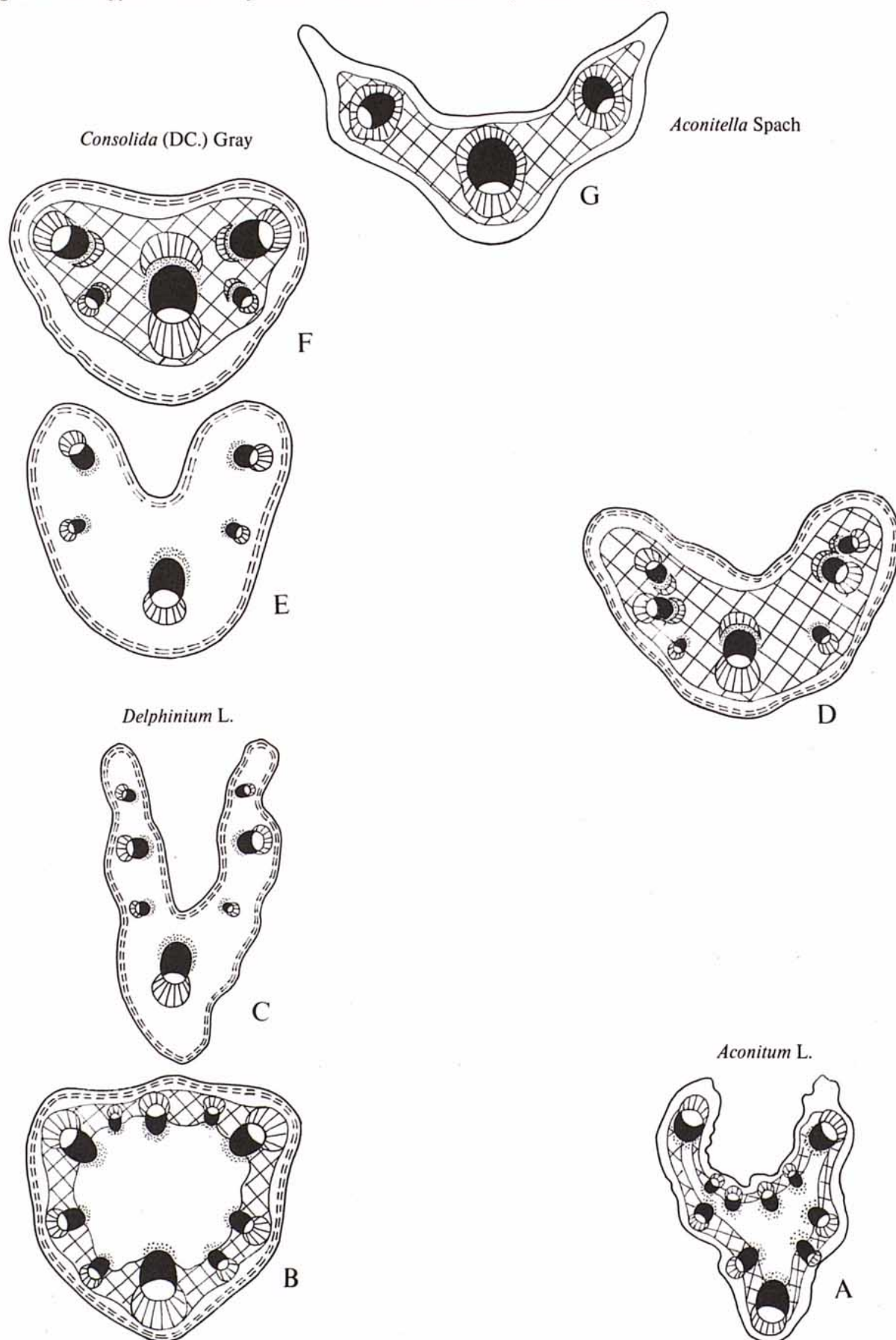
### Petiole (anatomical-morphological characteristics)

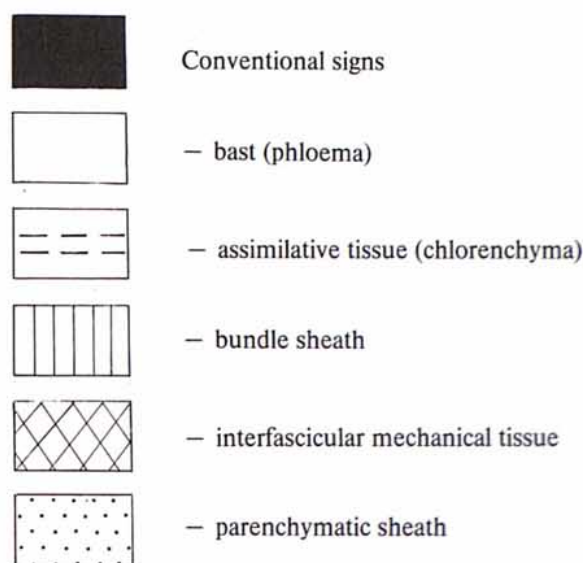
The representatives of the tribe *Delphineae* are characterized by grooved petioles, with a horseshoe-, saddle- or crescent-like transverse section. There are 3-15 vascular bundles arranged in a circle (radial type) or along an arc (dorsiventral type) with mechanical tissue of A- or R-type. In accordance with TAMURA'S classification (1962) we use the term radial type to refer to petioles with a ventral bundle and with vascular bundles arranged in a circle, while those without a ventral bundle and with vascular bundles arranged along an arc we refer to as the dorsiventral type. In accordance with KUMAZAWA (1930) we recognize two types of bundle sheaths: mechanical A- or *Anemone*-type, in which lignified cells are located outside the vascular bundle, and R- or *Ranunculus*-type, in which they are located outside and inside of the vascular bundle or surrounding bundles.

Petiole evolution in the tribe *Delphineae* took the form of reduction of the number of vascular bundles and of the ventral bundle and strengthening of the mechanical tissue (fig. 2). The perennial genus *Aconitum* and the most primitive representatives of the genus *Delphinium* (perennial subgenera *Delphinastrum* (DC.) W. T. Wang and *Oligophyllum* Dimitrova) are characterized by a radial type of petiole with a great number of vascular bundles (up to 15) and A-type bundle sheath. The group of annual species of the genus *Delphinium* — the section *Delphinium* of the subgenus *Delphinium* — with a dorsiventral type V-like petiole and a smaller number of vascular bundles (only up to 7) appeared as a result of the reduction of ventral and additional bundles. In some Chinese members of this subgenus — the section *Anthriscifolium* W. T. Wang — the petiole is still of radial type, but already with a small number of vascular bundles (6-8). Petioles of a similar shape and structure (BLANCHÉ & AL., 1988) are also observed in the subgenus *Staphisagria* (DC.) Peterm., which is characterized by its



Fig. 2.— The supposed trends of petiolar evolution in the tribe *Delphineae* Warming





A- *Aconitum ranunculoides* Turc. ex Ledeb.; B- *Delphinium ternatum* Huth, subgenus *Olygophyllum* Dimitrova; C- *Delphinium peregrinum* L., subgenus *Delphinium*; D- *Consolida camptocarpa* (Fisch. & Mey ex Ledeb.) Nevsky, section *Brevipedunculatae* (Huth ex N. Busch) Kem.-Nath., E - *C. ajacis* (L.) Schur, section *Macrocarpae* (Huth ex N. Busch) Kem.-Nath.; F - *C. glandulosa* (Boiss. et Huet) Bornm., section *Consolida*; G- *Aconitella anthoroidea* (Boiss.) Soják.

unique position in the genus *Delphinium* owing to its blend of advanced and primitive features.

The entirely annual genus *Consolida*, which has a more specialized reproductive structure, arose from the section *Delphinium* of the subgenus *Delphinium* through a number of unknown forms. We can trace two lines of development within this genus. On the one hand, there appeared a group of xerophytic plants (the section *Brevipedunculatae*), characterized by the petioles in which the number and order of arrangement of the vascular bundles is the same as in the section *Delphinium*. They differ from each other by the shape of the transverse section, the presence of fully developed interfascicular mechanical tissue and the more advanced bundle sheath, which is intermediate between A- and R-types. On the other hand, in the course of a further reduction of the number of vascular bundles (up to 5), another group was formed, represented by the section *Macrocarpae* and associated with the section *Delphinium* by a common areal. The section *Longibracteolatae* with a minimum number of vascular bundles for the tribe (3-4) and a V-shaped transverse section is the most closely related to the section *Macrocarpae* in petiole structure.

The section *Macrocarpae* with horseshoe-shaped, deeply grooved petioles probably gave rise to the section *Consolida* in which most species have similar shaped but not so deeply grooved petioles. The strengthening of the mechanical tissue is typical of this section: it takes the form of the appearance of interfascicular mechanical tissue, the penetration of mechanical cells into the pith of the petiole and the presence of a transitional-type bundle sheath (between A and R). Petiole structure in *C. rigida* (DC.) Bornm. (the only species from the section *Parviflorae* we have studied) was discovered to have identical petiole structure to the section *Consolida*.

The youngest and most evolved group of species—the genus *Aconitella*— was formed in the course of further specialization: the number of vascular bundles decreased to up to three,



the assimilation function was lost and simultaneously the mechanical function was strengthened (the R-type bundle sheath surrounds the vascular bundle).

The data gathered by us confirm the correctness of WORSDELL's hypothesis (1908) that in the family *Ranunculaceae* radial-type petioles with a ventral bundle are more primitive than dorsiventral ones. This point of view is also supported by TAMURA (1964) and R. SHRÖDINGER (1914), who indicated that the dorsiventral type of petiole structure occurs in the more advanced groups.

Concerning the further development of the radial-type petioles, we can add to TAMURA's data (1964) on the two main trends in the evolution of the *Ranunculaceae* family: 1) the ventral bundle reduction and 2) the increase in the number of vascular bundles. The evolution of the radial type petiole may take place in a complex manner by a decrease in the number of vascular bundles and a simultaneous reduction of the ventral bundle. This was proved by our research. The mechanical tissue evolution developed from the A-type to the R-type bundle sheath of KUMAZAWA (1930) and from interfascicular mechanical tissue to the lignification of the petiole heartwood (TAMURA, 1962).

### The seed (anatomical-morphological characteristics)

The tribe *Delphineae* is characterized by inverse-pyramidal seeds (rarely globular ones) winged or without wings. The seed surface is smooth, wrinkled or covered with scaly-laminated excrescences. The transverse section of a seed is triangular or oval with a thin seed coat. The latter is formed (TRIFONOVA 1973, 1974, 1984 a, b) by two integuments and is characterized by a number of common features, which, on the one hand, prove its primitive structure (the presence of a multilayer testa with comparatively well-preserved, slightly differentiated parenchymatic layers) and, on the other hand, demonstrate a certain advance (the presence of epidermal excrescences of various shapes, sizes and origins and of hydrophilous contents). The genera differ sharply from each other. Evolution within the tribe took the form of a reduction and decrease in thickness of the seed coat layers and a differentiation between their two main functions—absorption and protection—while at the same time the protective function was reinforced. Thus the seed protection function was assumed by the thick external epidermis of the testa. This resulted in a change in cell shape and size: large, tangentially-stretched cells with relatively thin outer walls (*Aconitum*) evolved into smaller, radially-stretched cells with much thicker outer walls and in the decrease and dislocation of hydrophilous contents into inner layers. The change from smooth wrinkled seeds to winged scaly ones in turn enabled the seeds to be more widely scattered and increased their vitality. These changes correlate with changes in the exomorphic features. In the first stage the xerophytic perennials separated from the mesophytic tall stemmed perennials, and then the annual species with a more advanced flower structure appeared. Thus, the perennial species of *Aconitum* with wrinkled or already winged seeds possesses tangentially stretched cells of the outer epidermis of the testa with relatively thin walls. Hydrophilous contents are located both in the internal and external layers. So this genus is close to the representatives of the most primitive subgenera of the genus *Delphinium* (*Delphinastrum* and *Oligophyllon*) which already possess seeds of various shapes.

In *Delphinium peregrinum* L., which is the representative of the young annual group of the section *Delphinium* of this genus, already only scaly seeds are found. The cells of the external epidermis of the testa are still tangentially stretched, but their external walls are already much thicker.

The evolution of the genus *Consolida*, which is closely related to the annual members of the genus *Delphinium* consisted of two trends. One gave rise to the section *Brevipedunculatae*, which occupies an unique position in terms of seed coat structure.

Unlike the representatives of other sections, it is characterized by the smaller cells of the



external epidermis of the testa with very convex and thin external walls. The distribution and quantity of hydrophilous contents in the species of this section closely resemble those of the section *Consolida*. The other trend gave rise to the section *Macrocarpae*, which grows on the territory of the ancient Mediterranean area like the members of the section *Delphinium* of the genus *Delphinium*. The *Macrocarpae* section is characterized by a seed coat with rather large tangentially (rather than radially) stretched testa cells with very thick external walls. All the layers of the spermoderm perform the functions of water absorption and transfer.

Further specilization has led to the *Consolida* section which has a wider areal and an advanced seed coat structure. The external epidermis cells of the testa are stretched radially rather than tangentially. A small quantity of hydrophilous material is located mainly in the inner layers of the spermoderm.

The external epidermis cells of the testa with their very thick outside walls fulfil a protective function in the genus *Aconitella*. These cells are similar in shape to the cells of the species of the genus *Consolida*. The inner layers of the spermoderm which contain a small amount of hydrophilous material, perform the function of water absorption and transfer.

### Karyotype

Until quite recently the only basic chromosome number known for the tribe *Delphineae* was  $x=8$ . In 1977 GAGNIDZE and ZAKHARYEVA reported for the first time on a new chromosome number for *Aconitella hohenackeri* (Boiss.) Soják. Later in 1983 BLANCHÉ and MOLERO presented  $2n=18$  for *D. bolosii* Blanché & Molero, and HONG DE-YUAN in 1986 reported  $2n=18$  for *Aconitella scleroclada* (Boiss.) Soják var. *rigida* (Frein et Sint.) Trifonova under the name *Consolida scleroclada* (Boiss.) Schröd. var. *rigida* (Frein et Sint.) Davis and  $2n=14$  for *C. persica* (Boiss.) Schröd. Our study, carried out in 1972-1974 (unpublished), fully confirm the somatic chromosome number  $2n=14$  for *C. persica* from the territory of Armenia and  $2n=12$  for *A. hohenackeri* from Georgia (USSR).

Table 1.

Chromosome numbers in the representatives of the tribe <i>Delphineae</i> Warming		
Genus	x	2n
<i>Aconitum</i>	8	16,32,48,64
<i>Delphinium</i>	8,9	16,18,32,48
<i>Consolida</i>	7,8,12*	14,16
<i>Aconitella</i>	6,8,9	12,16,18

\* Chromosome number  $x=12$  reported by L. BÖNICKLE (1911) for *C. ajacis* (L.) Schur under the name *D. ajacis* L. was not confirmed by any other authors. These data can not be used for systematics purposes, for there were no pictures or references to the specimen studied.

The basic chromosome number  $x=8$  is common to all four genera (Table 1). The comparison of idiograms in diploid members of the genera with  $2n=16$ , reported in the articles of LEWITSKY (1931), LEWIS & AL. (1951), KURITA (1955, 1957, 1958, 1965), TRIFONOVA (1973, 1974), TRIFONOVA & ZEMSKOVA (1986), KOEVA-TODOROVSKAYA & NENOVA (1976-1977) and HONG DE-YUAN (1986) revealed considerable similarity in their chromosome morphology.



Karyotypes are characterized by two pairs of large submeta- or metacentric chromosomes and by six pairs of smaller subtelocentric or telocentric chromosomes.

The karyotype evolution of the tribe *Delphineae* took the form of an increase in the asymmetry of the chromosome set and changes in the basic chromosome number. However, while the degree of asymmetry increased in pairs III-VIII, the second pair of large chromosomes became more symmetrical. So the centrometric index<sup>1</sup> in this pair of chromosomes in the representatives of the genera *Aconitum* and *Delphinium* is 2,4-1,9 while in *Consolida* and *Aconitella* it is 1,3-1,0.

The karyotype of the genus *Aconitum* is characterized by the basic chromosome number  $x=8$  and by a great number of polyploids. Most of the species of the genus *Delphinium* which have been studied are also characterized by the basic chromosome number  $x=8$ , but unlike the karyotype of the genus *Aconitum*, different morphological types of chromosomes are revealed. Another somatic chromosome number  $2n=18$  has been found in one species, *D. bolosii* (BLANCHÉ & MOLERO, 1983). It was LEWITSKY (1931), who indicated the resemblance of the karyotypes in these two genera, noting that the karyotype of the genus *Aconitum* represents "a more primitive, less differentiated state of" the karyotype of the genus *Delphinium*. Karyotypes of representatives of the most primitive subgenera *Delphinastrum* and *Oligophyllon* are similar in morphology to those of the genus *Aconitum* and differ from the latter only by a greater degree of the asymmetry in pairs III-VIII of the chromosome set. The representatives of the subgenus *Staphisagria* occupy a unique position in the genus *Delphinium* and are characterized by a less asymmetrical set of chromosomes with three pairs of large metacentric chromosomes.

The entirely annual members of the genus *Delphinium*—the section *Delphinium*—possess the most asymmetric karyotype, in which the second pair of large chromosomes of the set develops from submetacentric to telocentric.

Most of the *Consolida* species are characterized by the basic chromosome number of  $x=8$ . A new chromosome number  $x=7$  is found in *C. persica* from the section *Brevipedunculatae*, which is also characterized by the peculiar structure of its seed coat and petiole. In *C. camptocarpa* (Fisch. & Mey ex Ledeb.) Nevsky from this section, the chromosome number is  $x=8$  (TRIFONOVA, unpublished). In the opinion of HONG DE-YUAN (1986)  $x=7$  may have derived from  $x=8$  by "successive unequal changes". The karyotype is typical for the representatives of the tribe with  $x=8$  and differs only by the absence of the last, smallest pair of the chromosome set and by the degree of asymmetry of one chromosome from the second or third pair of the set. Our own investigations (TRIFONOVA, 1973) have shown that the karyotypes of the sections *Macrocarpae* and *Consolida* are clearly distinguished by the relative size of the long arms of the first two pairs of chromosomes and also by the degree of asymmetry of the five smallest pairs of chromosomes in the set, and also by the location of the satellite chromosomes in the set. BLANCHÉ & AL. (1987) reported that the series can differ in the degree of asymmetry of one chromosome from the set.

The species formation process is most active in the most recent and highly evolved group—the genus *Aconitella*—in which three main chromosome numbers  $x=6, 8, 9$  are found in the

<sup>1</sup>  $IC = 1/s$ , where  $l$  = the length of a long arm  
 $s$  = the length of a short arm

*Editor's comment:* TRIFONOVA named her index as "Centromeric index", this concept being in contradiction with the same denomination appearing in the pages of BLANCHÉ (pp.: 82-83, this volume).

The actual names and definitions accepted in the current literature are:

$R = l/c$ , defined by LEVAN, FEDGA & SANDBERG, 1964, *Hereditas* 52: 201-220. TRIFONOVA'S concept.

$F\% - CI = \frac{100 S}{1+S}$ , defined by SHINDO & KAMEMOTO, 1963. *Amer. J. Bot.* 50: 73-79. BLANCHÉ'S concept.

Where  $l$  = long arm length and  $s$  = short arm length.



of the satellite chromosomes in the set. BLANCHÉ & AL. (1987) reported that the series can differ in the degree of asymmetry of one chromosome from the set.

The species formation process is most active in the most recent and highly evolved group—the genus *Aconitella*—in which three main chromosome numbers  $x = 6, 8, 9$  are found in the four species studied. It is interesting that different morphological types with equal chromosome numbers  $x = 8$  are found in two species. Among the species with basic chromosome numbers other than  $x = 8$  the most dissimilar in morphology is *A. hoherackeri* with  $x = 6$ . Its karyotype is characterized by four pairs of large metacentric chromosomes gradually diminishing in length, and by two pairs of smaller telocentric and submetacentric chromosomes. The first pair of the chromosomes with their satellites is identical to the first pair in the *A. barbata* karyotype, and a certain resemblance is observed between the second and the sixth pairs of chromosomes. All that testifies to the fact that there is a certain relation between these species in spite of the different numbers of chromosomes. GAGNIDZE & ZAKHARYEVA (1977) consider that the main chromosome number  $x = 6$  in *A. hoherackeri* originated from  $x = 8$  as the result of chromosome reorganisation. So both the number of centromeres and the basic chromosome number decreased, leading eventually to changes of their morphology in the direction of greater symmetry. The genus *Aconitella* is represented by another basic chromosome number,  $x = 9$ . HONG DE-YUAN (1986) regards this number as derived from that of  $x = 8$  as the result of centric fusion. Instead of the second pair of large metacentric chromosomes, another pair of clearly defined telocentric chromosomes was formed.

## Conclusion

The tribe *Delphineae* consists of herbaceous annual and perennial plants with zygomorphic flowers and a certain number of perianth pieces (except stamens).

Two genera, *Aconitum* and *Delphinium*, are represented mainly by perennial mesophytes, growing in forests and on the edges of forests in moderate regions of the Northern hemisphere. The percentage of xerophilous species among them is rather low. Close relations between these two genera are also revealed in their common areals, the similarity of the seed coat and petiole structure, the similarity of the karyotype and a number of other features. This may lead to the supposition that they originated from one common ancestor, a hypothesis which is also confirmed by the great morphological resemblance of the representatives of these genera growing in Eastern Asia, where they are believed to have originated. On the other hand, we cannot exclude the possibility that the more highly evolved genus *Delphinium* derived from one of the branches of the genus *Aconitum*, because it certainly contains the most primitive plants of the tribe. Western and South-Western China—the regions with the greatest number of primitive and endemic species—is one of the centres of the genus *Delphinium*. The youngest and most highly evolved group of species—the Mediterranean section *Delphinium*, belonging to the annual subgenus *Delphinium*—could have originated, according to WANG (1962), from representatives of the *Antriscifolium* section of the same subgenus during its expansion from South-Western China westwards as far as Middle Asia and the Mediterranean area. North America could have been another centre of the formation of the genus.

The habitus of the species forming the section *Delphinium* is similar to that of the species of the genus *Consolida*. The greatest resemblance is between the flowers with two nectaries, which represent the only nectary of *Consolida* as if with two nectaries of *Delphinium*, nectary of *Consolida* apparently represent the fused nectary of *Delphinium* divided into two parts. The formation of the genus *Consolida* was accompanied by the reduction of the number of reproductive organs: the number of follicles was reduced to one, the concrescence of the petals into one is also observed, the staminodia disappear and the number of stamens decreases, the latter being arranged in five spiral circles, instead of eight, as in *Delphinium*.



The absence of polyploids shows that the genus is comparatively young, while in *Delphinium* and *Aconitum* polyploidy played an important role in the formation of the species.

The section *Macrocarpae* is the closest to the section *Delphinium*: they both grow on the territory of the ancient Mediterranean area and their seed coat structures are very similar. Further specialization led to the appearance of the section *Consolida* with an advanced seed coat and petiole structure and a broader areal. On the other hand, a group of xerophytic species also appeared (the section *Brevipedunculatae*) possessing a unique seed coat and petiole structure and a basic chromosome number which was new for the genus.

We cannot agree with the point of view expressed by MALYUTIN (1973) that the genus *Consolida* originated from the Chinese endemic section *Anthriscifolium* of the subgenus *Delphinium*, since they are not connected by a common areal. The section *Anthriscifolium* is distinctly characterized by some primitive features and possesses, in particular, the most primitive petiole structure in the genus *Delphinium*.

The next stage of evolution was the appearance of the genus *Aconitella* which is characterized by a reproductive organ structure similar to that of the genus *Consolida*. This is undoubtedly the most specialized and youngest group of species, with a limited areal and advanced karyotype, petiole and seed coat structure. The appearance of three main chromosome numbers  $x = 6, 8, 9$  facilitated the isolation of the genus *Aconitella* from its ancestor and other genera.

The point of view of SPACH (1839) and KEMULARIA-NATHADZE (1939) on the supposed origin of the genus *Aconitella* (*Aconitopsis* Kem.-Nath.) from "the species closely related to the representatives of the section *Lycotomum* of the genus *Aconitum*" seems to us not fully substantiated. They have nothing in common except outward resemblance which can reflect only a parallel development of shapes forms. At the same time there are more distinct differences, not only in exomorphic features, but in more profound structures too. The genus *Aconitum* is characterized by its perennial cycle of development, its great number of reproductive organs (2 petals with pockets, 3-8 staminodia, 3-7 follicles) and by the most primitive structure of the seed coat, the petiole and the karyotype for the tribe *Delphineae*.

At the same time the genus *Aconitella* is very close to the genus *Consolida*. They both possess one petal, one follicle and no staminodia and *Aconitella* differs from the genus *Consolida* only in petal shape and the upper unpaired sepal.

We agree with SOJÁK (1969), who proposed the parallel development of *Aconitella* and *Consolida* from one common ancestor.

On the other hand it is quite possible that the genus *Aconitella* originated from the section *Consolida*, the most advanced section of the genus *Consolida*. They are close to each other in petiole and the seed coat structure. Both genera are connected with xerophilous flora of the ancient Mediterranean area. Their similarity is confirmed by the existence of the transitional form *Aconitella barbata*, which still possesses a spur (which however is already blunt) and has a five-lobed petal whose general outward appearance is similar to the three-lobed petal in the representatives of the genus *Consolida* (fig. 1). This species is identical in petiole structure to the representatives of the genus *Aconitella*. (fig. 2).

Thus evolution started from plants possessing radial-type petioles with a large number of vascular bundles and an A-type bundle sheath, a seed coat in which the division of the spermodermis functions is still not clearly defined and a single basic chromosome number  $x = 8$  (the genus *Aconitum* and the perennial representatives of the genus *Delphinium*), through certain transitional forms to the appearance of the entirely annual genera *Consolida* and *Aconitella*. The latter is characterized by a three-bundled dorsiventral petiole with well developed mechanical tissue, a differentiated seed coat and by a karyotype with three main chromosome numbers  $x = 6, 8, 9$ .



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