On the position of the tribe *Eritrichieae* in the Boraginaceae system

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ABSTRACT: A system of the tribe *Eritrichieae* for the first time developed from evolutionary-morphological and floristic-genetic approaches, contains 6 subtribes and 22 genera. A comparative analysis of all characters and chorology of species allowed to find the position of the tribe *Eritrichieae* in the Boraginaceae system and proposed an assumed paths of its evolution.

KEY WORDS: Boraginaceae, tribe *Eritrichieae*, phylogenetic system, evolution, primary sculpture of nutlets.

INTRODUCTION

The tribe *Eritrichieae* Benth. et Hook. f. the largest one in the family *Boraginaceae* Juss. contains 449 species mainly distributed in the mountains in Eurasia, from the Arctic to the Himalayas, and in the west of North America. The tribe was described in 1876 by G. Bentham and J.D. Hooker in “Genera Plantarum”. They separated it from the tribe *Cynoglosseae* DC. by fruit characters. Eremes of the *Eritrichieae* genera are attached to pyramidal or columnlike carpobasis by the medial or lower part of the ventral side. Therefore, in postfloral growing their free tops rise above the carpobasis leaving free an ascending style. Composition of the tribe significantly changed in different systems of the borage family (Brand 1931; Zakirov 1941; Popov 1953; Riedl 1967; Wang et al. 1980; Al-Shehbaz 1991). In recent years independence of the tribe *Echiochileae* Langstrom et M.W. Chase has been proved by morphological and molecular research (Lonn 1999; Langstrom & Chase 2002; Langstrom & Oxelman 2003). Morphological and palynomorphological study (Ovchinnikova 2000, 2001, 2006b) has confirmed independence of the tribe *Craniospermeae* M. Pop. with one genus *Craniospermum* Lehm.

Complete scientific study of systematics and evolution of *Eritrichieae* is an important constituent for the development of a phylogenetic system of *Boraginaceae* as a whole.

MATERIALS AND METHODS

Material for analysis was obtained in Herbaria from LE, MHA, MW, TK, NS, NSK, SSBG, ALTB, AA, TASH. The characters of pollen grains of 25 species from 14 genera were examined by SM and SEM (Ovchinnikova 2000, 2001, 2006b). Twelve pollen types were identified for description of pollen grains in the tribe *Eritrichieae* (Diez & Valdes 1991; Ning et al. 1993; Popova & Zemskova 1995; Retief & Van Wyk 1999; Hargrove & Simpson 2003; Ovchinnikova 2006b). Pollen grains are dumb-bell-shaped, 3-colporate apertures alternate with three pseudocolpi, very small, 2.0–7.0 x 4.74–12.6 μm. Two independent lines of pollen grain evolution with different locations of apertures were exposed in the tribe. The line of pollen types with an equatorial ora in the subtribes *Cryptanthinae*, *Allocaryinae*, *Anoplocaryinae*, *Amsinckiinae* was related to the more ancient types in the tribe and underlined relationship with the line *Ehretioideae* – *Heliotropioideae* Guerke. The line of pollen types with dorate oras in the subtribes *Eritrichiinae* and *Echinosperminae* was related to the line *Ehretioideae* – *Heliotropioideae* Guerke. The line of pollen types with dorate oras in the subtribes *Eritrichiinae* and *Echinosperminae* was formed as a result of hybridization of several later lines of evolution.

Comparative-morphological SM study of nutlets in 243 species from 17 genera of the tribe *Eritrichieae* and 9 tribes of *Boraginaceae* are subjected by the analysis. It was concluded that characters of fruit morphology are
sufficiently effective for purposes of taxonomy. Eight types of the cell arrangement (nutlet surface) and 11 types of the primary sculpture (pericarp ultrasculpture) by terminology of W. Barthlott (1981) are distinguished as a result of detailed SEM Multiscan 200 GS, LEO 420 study of nutlets in 122 species (including 20 species with heterocarpia). Features of primary sculpture (see Fig. 1) have important significance for revealing evolutionary pathways and inferring relationships among taxa in the tribe Eritrichieae and family Boraginaceae (Ovchinnikova 2006a, 2007a, b; 2008).

RESULTS

A system of the tribe Eritrichieae for the first time developed from evolutionary-morphological and floristic-genetic approaches, contains 6 subtribes and 22 genera. Critical analysis of data on morphology, palynomorphology and chemotaxonomy, as well as comparative morphological SM and SEM study of fruit characters in the Eritrichieae representatives made it possible to describe two new subtribes: Allocaryinae and Anoplocaryinae, to confirm independence of the tribes Asperugeae, Heterocaryae and Rochelieae, to exclude the subtribe Pseudomertensiinae and the genera Myosotidium Hook. and Selkirkia Hemsl. from the tribe Eritrichieae composition (Ovchinnikova 2007c).

Below is given information on nomenclature of 6 subtribes of the tribe Eritrichieae, as well as of other tribes, earlier included in this tribe, with a list of genera, indication of the number of species and regions of distribution.


Areal: Eurasia, North America; Boreal and Tethyan subkingdoms.


Genera: 1. Lappula (70 species); 2. Lepechiniella Popov (16).

Areal: Eurasia, North America, Africa, Australia; Boreal, Tethyan and Madrean subkingdoms.


Genera: 1. Cryptantha (incl. Johnstontella Brand) (60 species); 2. Oreocarya Greene (incl. Hemisphaerocarya Brand) (45); 3. Eremocarya Greene (1); 4. Greeneocharis Guerke et Harms (1); 5. Nesocaryum Johnst. (1).

Areal: North and South America; Madrean subkingdom, Andean Region of Neotropis.


Areal: Kamchatka, North America, Mexico, Chile, Australia; Boreal and Madrean subkingdoms, Andean Region of Neotropis, Australis.


Genus: Anoplocaryum Ledeb. (4 species).

Areal: North Asia, Boreal subkingdom.


Genus: Amsinckia (20 species).

Areal: North and South America, bring in Eurasia, Africa, Australia; Boreal and Madrean subkingdoms, Andean Region of Neotropis.


Genus: Asperugo L. (1 species).

Areal: Eurasia, North America, North Africa; Boreal, Tethyan and Madrean subkingdoms.
Fig. 1. Types of the primary sculpture (pericarp ultrasculpture) of fruits and appendages of nutlets in the family Boraginaceae.  


Genus: Heterocaryum A.DC. (6 species).  
Areal: South-West Asia, Tethyan subkingdom.

Genus: Craniospernum (6 species).
Areal: Central Asia, Tethyan subkingdom.


Genera: 1. Echiochilon (incl. Sericostoma Stocks ex Wight.) (15 species); 2. Ogastemma Brummitt (=Megastoma Coss. et Dur.) (1); 3. Antiphytum DC. ex Meissn. (=Thaumatocaryum Baill.) (1); 4. Amblynotopsis Macbr. (1); 5. Amphibologyn Brand (1).

Areal: South-West Asia, North Africa, Mexico, Brazil, Uruguay; Tethyan and Madrean subkingdoms, Andean Region of Neotropis.

– Typus: Rochelia Reichenb.

Genus: Rochelia (15 species).

Areal: Europe, South-West and Central Asia, Tethyan subkingdom.


Genus: Pseudomertensia (9 species).

Areal: South-West and South-East Asia, Tethyan subkingdom.

DISCUSSION

The relationship between natural groups within Boraginaceae was variously interpreted in different systems. A. Engler school (Guerke 1893; Brand 1921, 1931) considered the tribe Cynoglosseae an initial group and put the tribe Lithospermeae (DC.) Guerke at the top of a fileme. Johnston (1924) and Gusuleac (1930) considered Lithospermeae a primitive group, and Cynoglosseae a more advanced one. Fedoseeva (1935, 1963), who studied anatomical characters of fruits and seeds of the borage family, recognized independence of these 2 lines of development. Based on a study of pollen characters of 216 species of Boraginaceae, Avetisjan (1952) concluded that the tribe Trichodesmeae Zak. ex Riedl was the most primitive as pollen grains of the ancient genera of that tribe had been 3-colpate (the genus Caccinia Savi) or 3-colporate with indifferenitated oras (the genus Trichodesma R. Br.), and all the rest of tribes with 6-10-corporate pollen grains with various arrangement of the apertures originated from it. She also considered the genus Poskea Vatke from the tropical subfamily Ehirtiliidae Guerke to be one of the ancient types.

Popov (1983) recognized two independent tribes as initial in the family: the tribe Eitririchieae DC. appeared, in his opinion, as a result of hybridization between Hydrophyllaceae Lindl. and Cordiaceae R. Brown ex Dumortier and distributed in North-West and South Africa and the tribe Trichodesmeae formed in crossing Solanaceae Juss. and Cordiaceae species in the eastern tropical regions of Africa. We agree with Popov (1983), but believe that the tribe Echiochileae must be placed at the base of Boraginaceae system together with them. Xeromorphic narrow-leaved dwarf shrubs, perennials and more seldom annual herbaceous plants of the tropical desert belong to this tribe (Langstrom & Chase 2002). The representatives of the tribe have pollen grains of a primitive type: 2-3-colporate with a perforated exine and large endoaperture with a granity ora surface (Scheel et al. 1996; Lonn 1999). Riedl (1968) noted evolutionary links between the Mexican-South-American genus Antiphytum from Echiochileae and Trigonotidae. The analysis of all characters suggests that development of the tribe Echiochileae is close to the evolutionary line of development of Ehirtiliidae and Heliotropiidae. Possibly not only the tribes Lithospermeae s. l. and Rochelieae, but also the subtribes Cryptanthinae, Allocaryinae and Anoplocaryinae in the tribe Eirtrichieae originated from the tribe Echiochileae.

An assumed phylogenetic scheme of evolutionary development of the tribe Eirtrichieae genera (the names are underlined) is given in Fig. 2. The relationship between different tribes, genera and species was discussed in various works (Ovchinnikova 2005, 2006a,b; 2007a,b,c), therefore attention is focused on the main directions and some examples of intergeneric hybridization. Apparently, Arnebia Forsk., Macrotomia DC., Pseudomertensia, Stenosolenium Turcz. (Lithospermeae), and Amsinckia (Amsinckiinae, Etrichiiinae) originated from the paleogene tribe Eirtrichieae. Peculiarities of the flower with 2-4 stigmas and orange pubescent or bright yellow corolla indicate to their Cordiaceae or waterleaf family ancestors. Fruit characters indicate to affinity with Eirtrichieae. Most of taxa of the family have their origins in the paleogene tribe Eirtrichieae. As a result of hybridization of the genus Trichodesma with uncertain partners, endemic genera Myosotidium in New Zeland, Caccinia Savi, Heliocarya Bunge, Heterocaryum in the Middle Asia and Craniospernum in Central Asia were formed. The whole tribe Cynoglosseae represented at present on all continents and in particular the genus Omphalodes Hill, the grandparent of all genera of Etririchiiinae and Echinoperminae, originated from this genus. Species from Allocaryinae and Anoplocaryinae were evidently
formed as a result of hybridization of the genus *Trigonotis* Stev. *Bilegnum* Brand, *Rindera* Pall., *Paracaryum* Boiss. (*Cynoglosseae*) and *Lepechiniella* (*Eritrichieae*) are close to the genus *Craniospermum*. The sections *Sclerocaryum* DC. et A.DC. and *Sinaicae* (Riedl) Ovchinnikova of the genus *Lappula* were formed under the influence of the genus *Rochelia*. The genus *Hackelia* affected species of the sections *Macranthae* (Riedl) Ovchinnikova and *Microcarpae* (Popov) Ovchinnikova of the genus *Lappula*.

**CONCLUSION**

A comparative analysis of all characters and chorology of species allowed to construct an assumed phylogenetic scheme of evolution of the tribe *Eritrichieae* genera. Each of its 6 subtribes is related by transitional taxa to 9 currently existing tribes of the *Boraginaceae* system, which confirms Popov's opinion of polytopic and hybrid origin of taxa and netlike character of evolution. As the youngest and progressively developing tribe, *Eritrichieae* must be the last in the hierarchical system of *Boraginaceae*.

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O poziciji tribusa *Eritrichieae* u sistemu *Boraginaceae*

Svetlana Ovchinnikova

Sistem tribusa *Eritrichieae* po prvi put uspostavljen na osnovu evolutivno-morfoloških i florišćko-genetičkih karakteristika obuhvata 6 podtribusa i 22 roda. Komparativna analiza svih karakteri i horologije vrsta omogućava pozicioniranje tribusa *Eritrichieae* u sistemu *Boraginaceae* i na osnovu svega izložen je njegov mogući evolutivni tok.

Ključne reči: Boraginaceae, tribus *Eritrichieae*, filogenetski sistem, evolucija, primarna struktura ploda.

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REZIME

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