



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

Svetlana OVCHINNIKOVA*

Central Siberian Botanical Garden, SB RAS, Zolotodolinskaya st., 101, Novosibirsk, 630090, Russia

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. .

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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. Erems 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) 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; KHATAMSAZ 2001; 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* Guerke – *Heliotropioideae* Guerke. The line of pollen types with diorate oras in the subtribes *Eritrichiinae* and *Echinosperrinae* 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

*correspondence: sv-ovchin@yandex.ru

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 BARTHOLOTT (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*, *Heterocaryeae* 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.

Trib. *Eritrichieae* Benth. et Hook. f. in Gen. Pl. 2: 836 (1876), Popov in Fl. USSR 19: 524 (1953), Riedl in Rech. f., Fl. Iran. 48: 63, p. p. (1967). Syn.: trib. *Cryptantheae* Brand in Feddes Repert. 21: 249 (1925), Brand in Engler, Pflanzenr. 4, 252: 1, p. p. (1931). – Typus: *Eritrichium* Schrad.

Subtrib. 1. *Eritrichiinae* Riedl in Rech. f., Fl. Iran. 48: 63, p. p. (1967). Syn.: trib. *Eritrichieae* subtrib. *Cynoglossinae* Popov in Fl. USSR 19: 387, descr. ross., p. p. (1953). – Typus: *Eritrichium* Schrad.

Genera: 1. *Eritrichium* (76 species); 2. *Amblynotus* I.M. Johnston (1); 3. *Tianschaniella* B. Fedtsch. (1); 4. *Hackelia* Opiz (45); 5. *Microcaryum* Johnst. (1); 6. *Chionocharis* I.M. Johnston (1); 7. *Metaeritrichium* W.T. Wang (1); 8. *Stephanocaryum* Popov (2); 9. *Microula* Benth. (= *Tretocarya* Maxim.) (29).

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

Subtrib. 2. *Echinosperrminae* Ovczinnikova in Bot. Zhurn. 90, 8: 1157 (2005). Syn.: trib. *Eritrichieae* subtrib. *Cynoglossinae* Popov in Fl. USSR 19: 387, descr. ross., p. p. (1953). Syn.: trib. *Eritrichieae* subtrib. *Eritrichiinae* Riedl in Rech. f., Fl. Iran. 48: 63, p. p., excl. typo (1967). – Typus: *Lappula* Gilib.

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

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

Subtrib. 3. *Cryptanthinae* Brand in Feddes Repert. 21: 249 (pro subtrib. tribus *Cryptantheae* Brand), p. p. (1925), Brand in Engler, Pflanzenr. 4, 252: 22, p. p. (1931). – Typus: *Cryptantha* Lehm.

Genera: 1. *Cryptantha* (incl. *Johnstonella* 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.

Subtrib. 4. *Allocaryinae* Grigorjev ex Ovczinnikova in Bot. Zhurn. 92, 5: 753 (2007). Syn.: trib. *Cryptantheae* subtrib. *Cryptanthinae* Brand in Feddes Repert. 21: 249, p. p. (1925), Brand in Engler, Pflanzenr. 4, 252: 22, p. p. (1931). Syn.: trib. *Eritrichieae* subtrib. *Lithosperminae* Popov in Fl. USSR 19: 524, descr. ross., p. min. p. (1953). – Typus: *Allocarya* Greene.

Genera: 1. *Allocarya* (incl. *Echinoglochis* Brand, *Glyptocaryopsis* Brand) (40 species); 2. *Maccoya* F. Muell. (3); 3. *Echidiocarya* A. Gray (incl. *Allocaryastrum* Brand) (3); 4. *Plagiobothrys* Fisch. et C. A. Mey. (50).

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

Subtrib. 5. *Anoplocaryinae* Ovczinnikova in Bot. Zhurn. 92, 5: 754 (2007). Syn.: trib. *Cryptantheae* subtrib. *Cryptanthinae* Brand in Feddes Repert. 21: 249, p. p. (1925), Brand in Engler, Pflanzenr. 4, 252: 22, p. min. p. (1931). Syn.: trib. *Eritrichieae* subtrib. *Lithosperminae* Popov in Fl. USSR 19: 524, descr. ross., p. min. p. (1953). – Typus: *Anoplocaryum* Ledeb.

Genus: *Anoplocaryum* Ledeb. (4 species).

Areal: North Asia, Boreal subkingdom.

Subtrib. 6. *Amsinckiinae* Brand in Engler, Pflanzenr. 4, 252: 204 (pro subtrib. tribus *Cryptantheae* Brand) (1931). – Typus: *Amsinckia* Lehm.

Genus: *Amsinckia* (20 species).

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

Trib. *Asperugeae* Zak. ex Ovczinnikova in Bot. Zhurn. 92, 5: 755 (2007). Syn.: trib. *Eritrichieae* Benth. et Hook. f. subtrib. *Asperuginae* Riedl in Rech. f., Fl. Iran. 48: 95, cum auct. epith. Zak. (1967). Syn.: trib. *Asperugeae* Zak. in Trudy Uzbeksk. Univ., Nov. ser. 28, 15: 4, 7, descr. ross. (1941), Popov in Fl. USSR 19: 529, nom. inval. (1953). – Typus: *Asperugo* L.

Genus: *Asperugo* L. (1 species).

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

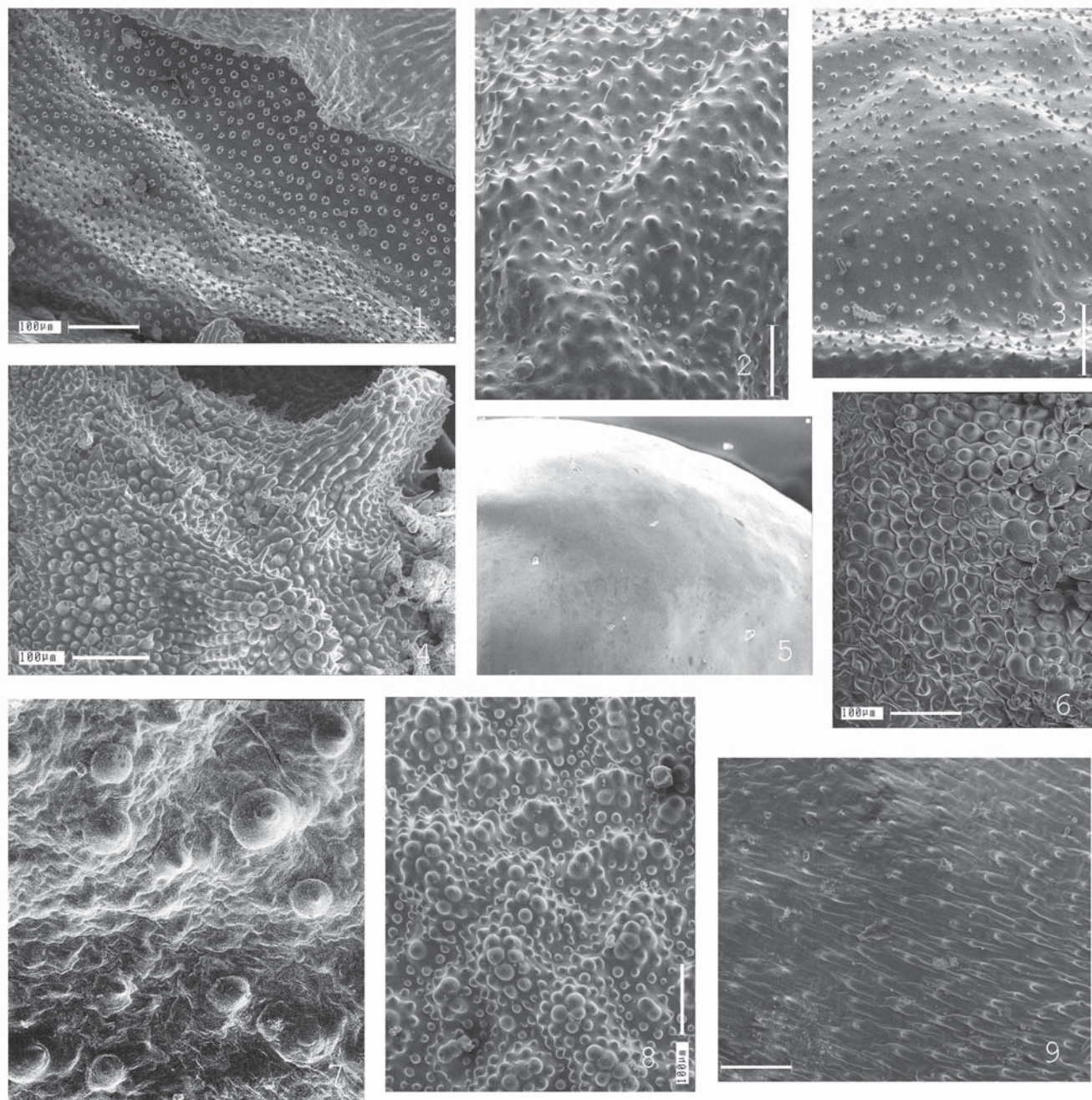


Fig. 1. Types of the primary sculpture (pericarp ultrasculpture) of fruits and appendages of nutlets in the family Boraginaceae. 1 – stellare-aculeate, 2 – aculeate, 3 – microaculeate, 4 – densepapillate-aculeate, 5 – nonexpressiate, 6 – pustulate, 7 – ruminata, 8 – tuberculate, 9 – striate-aculeate. Scale - 100 μm

Trib. *Heterocaryeae* Zak. ex Ovczinnikova in Bot. Zhurn. 92, 5: 755 (2007). Syn.: trib. *Eritrichieae* Benth. et Hook. f. subtrib. *Heterocaryinae* Riedl in Rech. f., Fl. Iran. 48: 84, cum auct. epith. Zak. (1967). Syn.: trib. *Heterocaryeae* Zak. in Trudy Uzbeksk. Univ., Nov. ser., 28, 15: 4, 7, descr. ross. (1941), Popov in Fl. USSR 19: 536, nom. inval. (1953). – Typus: *Heterocaryum* A.DC.

Genus: *Heterocaryum* A.DC. (6 species).

Areal: South-West Asia, Tethyan subkingdom.

Trib. *Craniospermeae* Popov in Fl. USSR 19: 531 (1953). Syn.: trib. *Borragaeae* subtrib. *Craniospermeae* DC. in Prodr. 9: 467 (1845). Syn.: trib. *Cryptanthaeae* subtrib. *Cryptanthinae* Brand in Engler, Pflanzenr. 4, 252: 22, p. min. p. (1931). – Typus: *Craniospermum* Lehm.

Genus: *Craniospermum* (6 species).

Areal: Central Asia, Tethyan subkingdom.

Trib. *Echiochileae* Langstrom et M.W. Chase in Plant Syst. Evol. 234: 149 (2002). Syn.: trib. *Eritrichieae* Benth. et Hook. f. subtrib. *Echiochilinae* Riedl in Rech. f., Fl. Iran. 48: 57 (1967). Syn.: trib. *Trigonotideae* Riedl subtrib. *Antiphytinae* Riedl in Rech. f., Fl. Iran. 48: 53 (1967), Riedl in Osterr. Bot. Zeitschr. 115: 296, p. p. (1968). – Typus: *Echiochilon* Desf.

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. *Amphibologyne* Brand (1).

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

Trib. *Rochelieae* DC. in Prodr. 10: 175 (1846), Popov in Fl. USSR 19: 548 (1953). Syn.; trib. *Harpagonelleae* Guerke in Engler u. Prantl, Nat. Pflanzenfam. 4, 3a: 130, p. p. (1893). Syn.; trib. *Eritrichieae* Benth. et Hook. f. subtrib. *Rocheliinae* (DC.) Riedl in Rech. f., Fl. Iran. 48: 89 (1967). – Typus: *Rochelia* Reichenb.

Genus: *Rochelia* (15 species).

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

Trib. *Lithospermeae* (DC.) Guerke subtrib. *Pseudomertensiinae* Riedl in Rech. f., Fl. Iran. 48: 58 (pro subtrib. tribus *Eritrichieae* Benth. et Hook. f.) (1967). – Typus: *Pseudomertensia* Riedl.

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 *Boraginoideae*, 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 indifferenced oras (the genus *Trichodesma* R. Br.), and all the rest of tribes with 6-10-

colporate pollen grains with various arrangement of the apertures originated from it. She also considered the genus *Poskea* Vatke from the tropical subfamily *Ehretioideae* Guerke to be one of the ancient types.

POPOV (1983) recognized two independent tribes as initial in the family: the tribe *Echieae* 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 grainy ora surface (SCHEEL *et al.* 1996; LONN 1999). RIEDL (1968) noted evolutionary links between the Mexican-South-American genus *Antiphytum* from *Echiochileae* and *Trigonotideae*. The analysis of all characters suggests that development of the tribe *Echiochileae* is close to the evolutionary line of development of *Ehretioideae* and *Heliotropioideae*. Possibly not only the tribes *Lithospermeae* s. l. and *Rochelieae*, but also the subtribes *Cryptanthinae*, *Allocaryinae* and *Anoplocaryinae* in the tribe *Eritrichieae* originated from the tribe *Echiochileae*.

An assumed phylogenetic scheme of evolutionary development of the tribe *Eritrichieae* 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*, *Eritrichieae*) originated from the paleogene tribe *Echieae*. 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 *Echieae*. Most of taxa of the family have their origins in the paleogene tribe *Trichodesmeae*. 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 *Craniospermum* 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 *Eritrichiinae* and *Echinosperminae*, originated from this genus. Species from *Allocaryinae* and *Anoplocaryinae* were evidently

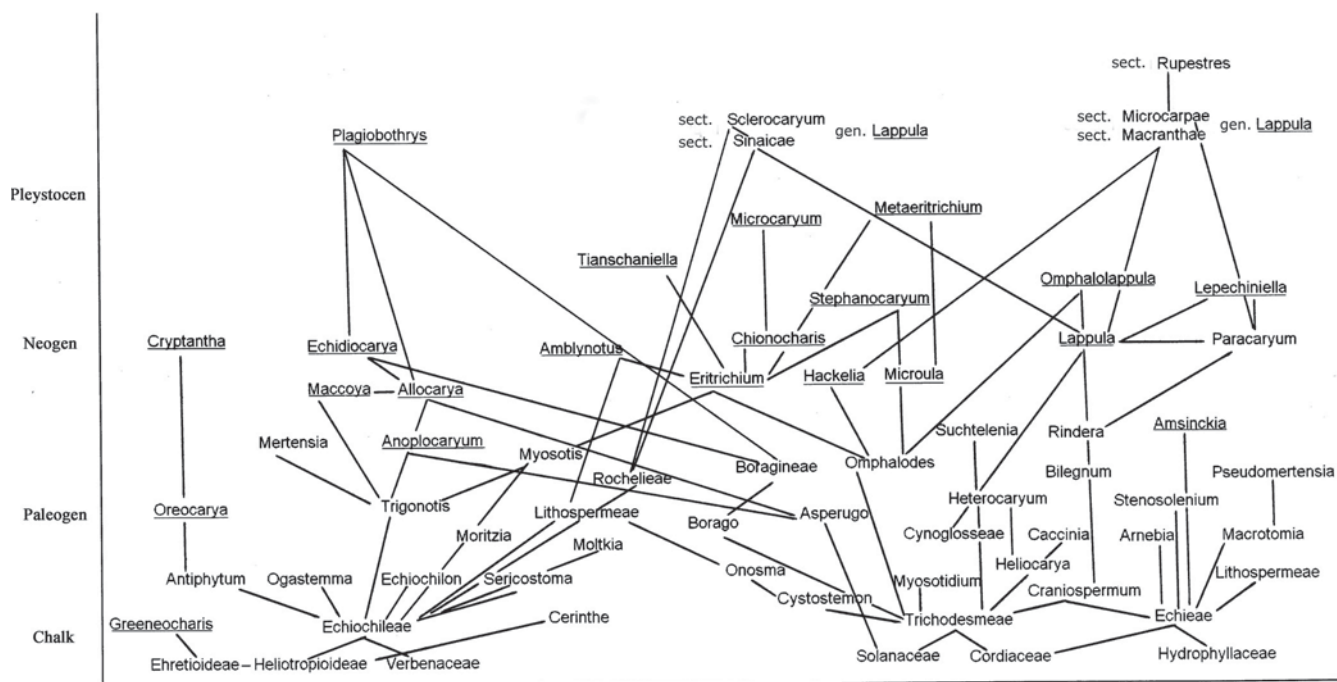


Fig. 2. An assumed phylogenetic scheme of evolutionary development of the tribe *Eritrichieae* genera (the names are underlined) in family Boraginaceae.

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) Ovczinnikova of the genus *Lappula* were formed under the influence of the genus *Rochelia*. The genus *Hackelia* affected species of the sections *Macranthae* (Riedl) Ovczinnikova and *Microcarpae* (Popov) Ovczinnikova 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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REZIME

O poziciji tribusa *Eritrichieae* u sistemu Boraginaceae

Svetlana OVCHINNIKOVA

Sistem tribusa *Eritrichieae* po prvi put uspostavljenom na osnovu evolutivno-morfoloških i florističko-genetičkih karakteristika obuhvata 6 podtribusa i 22 roda. Komparativna analiza svih karaktera 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. .