

СИСТЕМАТИЧЕСКИЕ ОБЗОРЫ

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CONTRIBUTION TO THE TAXONOMY OF *ARABIDOPSIS* s. l. (CRUCIFERAE): THE STATUS OF *TRANSBERINGIA* AND TWO NEW COMBINATIONS IN *CRUCIHIMALAYA*

К СИСТЕМАТИКЕ *ARABIDOPSIS* s. l. (CRUCIFERAE): СТАТУС РОДА *TRANSBERINGIA* И ДВЕ НОВЫЕ КОМБИНАЦИИ В РОДЕ *CRUCIHIMALAYA*

Generic limits of the genus *Crucihimalaya* Al-Shehbaz, O'Kane et Price are revised. The genus *Transberingia* Al-Shehbaz et O'Kane is reduced to synonymy of *Crucihimalaya*. *Transberingia bursifolia* (DC.) Al-Shehbaz et O'Kane subsp. *bursifolia* and *T. bursifolia* subsp. *virgata* (Nutt. ex Torr. et Gray) Al-Shehbaz et O'Kane are transferred to *Crucihimalaya* which is recognized as a genus of 11 species of Asian (9 spp.), North American (1 sp.) and Transberingian (1 sp.) distribution. Morphological, geographical and molecular evidences of a New World origin of *Crucihimalaya* are discussed.

Introduction. It has been shown in the last decade that molecular markers help to clarify many problems in taxonomy, systematics and phylogeny of Cruciferae taxa (Koch et al. 2003). Combination of various molecular methods with the traditional morphological and geographical approaches thus appears to be the most prospective way of further taxonomical study of the family.

The genus *Arabidopsis* (DC.) Heynh. and its allies is still the most thoroughly analyzed group in the family. The comprehensive molecular and morphological studies covering all taxa ever assigned to the genus *Arabidopsis* (for general results see: Al-Shehbaz, O'Kane, 2002; O'Kane, Al-Shehbaz, 2003), with the single exception of *A. rupicola* (Kryl.) A.L. Ebel (German, Ebel, 2005) have totally confirmed the results of previous analyses of many experts (Ball, 1993; Yurtsev, 1975; Zyablitskaya, 1972, etc.) showing that the genus *Arabidopsis* as traditionally delimited (= *Arabidopsis* s. l.) is artificial, i. e., polyphyletic.

It turned out that *Arabidopsis* s. str. includes only 9 species mostly native to Europe (O'Kane and Al-Shehbaz, 1997) (in fact, the number of species is likely to be somewhat higher since some taxa treated by these authors as subspecies may well

deserve species rank: see, for instance, Dorofeev, 2002; but this problem is out of focus of the present study). Recent *Arabidopsis* s. l. studies have resulted in considerable taxonomic rearrangements: apart from nine species representing *Arabidopsis* s. str. (including all members of *Cardaminopsis* Hayek and *Hylandra* A. Löve), the majority of *Arabidopsis* s. l. taxa have been placed into other genera or have been recognized as new genera (Al-Shehbaz, Junussov, 2003; Al-Shehbaz, O’Kane, 2002; Al-Shehbaz et al., 1999; O’Kane, Al-Shehbaz, 2003; Price et al., 2001). It further turned out, these genera must necessarily not be closely related to *Arabidopsis* s. str. These newly defined genera represent monophyletic species groups strongly supported by molecular and morphological markers and a well defined distribution area. These are: *Beringia* Price, Al-Shehbaz et O’Kane (Price et al., 2001), *Crucihimalaya* Al-Shehbaz, O’Kane et Price, *Olimarabidopsis* Al-Shehbaz, O’Kane et Price, *Pseudoarabidopsis* Al-Shehbaz, O’Kane et Price (Al-Shehbaz et al., 1999).

In this paper the taxonomic revisions just mentioned are generally followed with two exceptions, i. e., the generic limits of *Crucihimalaya* and the status of the genus *Beringia*. Alternative interpretations are argued for herein.

Materials and methods. The present study has been conducted based on morphological treatment of herbarium material deposited in LE, P, B, W, MW, TK, NS, ALTB as well as on observations of the species ecology and morphology during the field work in Russia (South Siberia), East Kazakhstan, West Mongolia and China (North Xinjiang). Results of molecular researches discussed here have been taken from the relevant literatures.

Results and discussion: *Crucihimalaya* s. str. versus *Crucihimalaya* s. l.

Morphological characters. As delimited by Al-Shehbaz et al. (1999), Appel and Al-Shehbaz (2002), Zhou et al. (2001), *Crucihimalaya* includes 9 closely related species distributed mainly in the Himalayas and neighboring mountain systems. The genus is well characterized by a set of morphological features (trichome structure, petal color, etc.) which distinguishes *Crucihimalaya* from all other genera of “Arabidopsoid affinities” (Al-Shehbaz et al., 1999). However, *Arabidopsis bursifolia* (DC.) Botsch. [*A. mollis* (Hook.) O.E. Schulz, *Halimolobos mollis* (Hook.) Rollins, arctic to subarctic regions of E Asia and America] remained “homeless” for the time being (Al-Shehbaz et al., 1999) and finally was recognized as a separate monotypic genus *Beringia* which also included *Halimolobos virgata* (Nutt. ex Torr. et Gray) O.E. Schulz (mountains of the west of N America) (Price et al., 2001). This illegitimate generic name has been replaced by *Transberingia* Al-Shehbaz et O’Kane later on (Al-Shehbaz, O’Kane, 2003). *Transberingia* (as *Beringia*) was stated to be most closely related to *Crucihimalaya*, but differs in three morphological characters from the latter: 1) biseriate seeds; 2) fruit valves with prominent marginal veins, and 3) presence of dendritic trichomes especially on basal leaves. In contrast, species of *Crucihimalaya* were reported to be characterized by uniseriate seeds, fruit valves with obscure marginal veins, and leaves with predominantly forked trichomes (Price et al., 2001).

To evaluate the diagnostic value of these characters used to distinguish these two genera, *Transberingia bursifolia* (DC.) Al-Shehbaz et O’Kane was compared with some representatives of *Crucihimalaya*, primarily with *C. mollissima* (C.A. Mey.) Al-Shehbaz, O’Kane et Price.

1. **Seed arrangement.** Generally, biseriate seeds are reported for *T. bursifolia* (Botschantsev, 1957; Price et al., 2001, etc.); only once Yurtsev (1975) mentioned that rarely seeds in a fruit appear to be almost uniseriate (semibiseriate; see the key for variations of *Arabidopsis bursifolia* in Yurtsev, 1975, p. 55). In contrast, the picture for *C. mollissima* is ambiguous: some authors report uniseriate seeds (Al-Shehbaz et al., 1999; Busch, 1926, 1939; Ovczinnikova, 1994; Zyablitzkaya, 1972), while others point out biseriate seeds in the species (Botschantsev, 1957, 1959; Vassilyeva, 1961; Yunussov, 1978). Analysis of herbarium material covering most of the distribution range of *C. mollissima* shows variation of this character, but no cases of uniseriate seeds were confirmed. Reports of uniseriate seeds in *C. mollissima* are obviously based on the study of fruits occasionally strongly compressed contrary to the plane of the septum under the herbarization (German, Ebel, 2005). Most typical are seeds arranged in two distinct rows in each locule (biseriate). However, in many specimens a special type of seed arrangement intermediate between uni- and biseriate is observed when two rows are developed but not completely distinct (seeds semibiseriate). Both variants are common in *C. mollissima*, but distinctly biseriate seeds predominate. However, no correlation with geographical distribution or ecological conformity of these variants has been detected¹.

Semibiseriate seeds are also characteristic for *C. lasiocarpa* (Hook. fil. et Thoms.) Al-Shehbaz, O’Kane et Price and *C. ovczinnikovii* (Botsch.) Al-Shehbaz, O’Kane et Price. Consequently, either semibi- or distinctly biseriate seeds occur in 3 of 9 *Crucihimalaya* species. Thus, *Crucihimalaya* was correctly characterized by Al-Shehbaz et al. (1999 : 298) as having “seeds uniseriate or rarely biseriate”, but not in more recent publications where exclusively uniseriate seeds were reported for the genus (Al-Shehbaz, O’Kane, 2002; Appel, Al-Shehbaz, 2002; Zhou et al., 2001). This character seems to be the single one used in the identification keys to separate *Crucihimalaya* from *Transberingia* (as *Beringia*) (Al-Shehbaz, O’Kane, 2002; Appel, Al-Shehbaz, 2002).

2. **Marginal veins on fruit valves.** Both *T. bursifolia* and *C. mollissima* have valves with only one well-developed middle vein; in both cases the marginal veins, though visible, are much less developed, represented by a net of thin veins in lateral

¹In several specimens from Tajikistan (LE) uniseriate seeds were revealed. However, these specimens have untypically for *C. mollissima* narrow fruits ca. 0.7 mm wide with inconspicuous midvein, and in fruit structure these plants remind *C. himalaica* (Edgew.) Al-Shehbaz, O’Kane et Price. However, their indumentum is typical for *C. mollissima*. A hybridization could be assumed, but *C. himalaica* is not reported from Tajikistan so far; the rank of these specimens needs further elucidation. Besides these few specimens, within the whole distribution range of *C. mollissima* (including Tajikistan), uniseriate seeds are unknown in the species.

parts of the valves. No principal differences in venation of fruit valves of *T. bursifolia* and *C. mollissima* are revealed, and it is not possible to separate these two species based only on fruit morphology. In most of other species of *Crucihimalaya* the venation of fruit valves is in general less developed, marginal veins and sometimes even middle one are obscure. It appears that there might be a correlation between the degree of development of fruit valves and the width of siliques in this group: both *T. bursifolia* and *C. mollissima* have fruits 1–2 mm wide while other species of *Crucihimalaya* have in general fruits up to 1 mm wide. However, even some “narrow fruit species” of the genus, e. g., *C. rupicola* (Kryl.) A.L. Ebel et D. German, also have both prominent midvein and rather distinct net of marginal veins.

3. **Trichome structure.** *Crucihimalaya* species are reported to have stalked, 1- or 2-forked trichomes, often mixed with simple and stellate, but *never* dendritic trichomes (Al-Shehbaz et al., 1999; Zhou et al., 2001). Trichomes in *Transberingia* are simple, forked, and dendritic (Price et al., 2001). The presence of dendritic trichomes (especially on lower leaves) in *Transberingia* is the main diagnostic difference in the indumentum separating *Transberingia* from *Crucihimalaya*. A comparison of leaf trichome structure in *C. mollissima* and *T. bursifolia* shows that both taxa are characterized by branched trichomes (stalked, 1–2-(rarely 3), often irregularly, forked hairs, somewhat different in size and in branch length). In general, these are forked trichomes with simple or 1–2-forked branches (only one or both); rarely additional small ray can be developed on the stalk (below the first bifurcation). Some trichomes are stellate, i. e., they have 3 (not 2) principal branches originating from one point; sometimes this can be observed also at higher levels of branching. Furthermore, the length of terminal rays can differ, sometimes considerably, what is more typical in *T. bursifolia*. Depending on the degree of branching, the number of terminal rays ranges from 2 to 7 (rarely up to 8–9), but 2–6-rayed trichomes are most common. Those 2–3-partit trichomes with branched principal rays (i. e., with 4–5 and more terminal rays) can only be defined as dendritic (especially in case of irregular bifurcation). All these types of trichomes, including dendritic, can be observed both in *T. bursifolia* and in *C. mollissima*, but the ratio of trichome types mentioned above (in fact, they all differ only in the degree of branching) varies in both species. This is especially typical for *C. mollissima*, in some specimens of which 1-forked hairs predominate and an admixture of 2(3)-forked trichomes is inconsiderable; in others a role of 1- and 2-forked hairs is comparable, and an admixture of more branched trichomes is also rather high. In general, a role of 1-forked trichomes is higher in *C. mollissima*, and this is a main difference of the latter species from *T. bursifolia*. This means that differences in trichome types between the two species are quantitative. In addition, trichomes in *T. bursifolia* are somewhat larger (long-rayed) with shorter stalk and with the terminal rays more often unequal in length. Despite of these (quantitative) differences, the general scheme of trichome structure is the same, and thus the separation of these two species based solely on leaf indumentum characters is problematic.

The same scheme of trichome structure is common in other species of *Crucihimalaya*, including the type species – *C. himalaica*. Although hairs in most of the

species of the genus are in general less branched, predominantly 1–2-forked (i. e., 2–4-rayed), some species (*C. wallichii* (Hook. fil. et Thoms.) Al-Shehbaz, O’Kane et Price, *C. rupicola*) have more branched trichomes (with 5–7–9 rays)). Obviously, separation of the two genera based on trichome structure is impossible.

Thus, none of the three morphological characters discussed here (i. e., seed arrangement, marginal veins on fruit valves, trichome structure) allows the separation of *Transberingia* from *Crucihimalaya*. However, geographical and molecular data could be used to recognize both *Crucihimalaya* and *Transberingia* as different genera.

Geographical data. Various samples of disjunctive distribution are known for the flowering plants both at generic and species level; in Cruciferae this distribution pattern, comparable to that demonstrated by *Transberingia* and *Crucihimalaya*, is provided by such genera as *Braya* Sternb. et Hoppe (*B. humilis* (C.A. Mey.) Robins. [*Neotorularia humilis* (C.A. Mey.) Hedge et J. Léonard]) and *Parrya* R. Br. (*P. nudicaulis* (L.) Regel). Consequently, *Transberingia bursifolia* can be separated from *Crucihimalaya* at the generic level solely with use of molecular data.

Molecular data. Phylogenetic tree shown in O’Kane et Al-Shehbaz (2003), constructed based on the analysis of nuclear ribosomal DNA sequences (ITS), includes 7 of 9 species of *Crucihimalaya* and *Transberingia bursifolia* (as *Beringia bursifolia*). The species of *Crucihimalaya* form a highly supported monophyletic group (bootstrap support 99%) to which *T. bursifolia* is a sister taxon (O’Kane, Al-Shehbaz, 2003). *Transberingia* and *Crucihimalaya* also form monophyletic group rather well supported (bootstrap support 87%), too. Similar results have been obtained by Heenan et al. (2002) studied molecular systematics of the New Zealand and Tasmanian *Pachycladon* Hook fil. s. l., a genus which turned out to be (on the base of ITS-analysis) a sister group to the two genera in question.

Two contrary taxonomic decisions could be suggested in this case – either to keep both taxa apart, or to merge them, and the choice primarily depends on the morphological characters. The separation of *Transberingia* and its recognition as an independent genus would be justified if at least one or better a set of morphological characters would support such distinctness. As shown above, there are no morphological differences clearly separating *T. bursifolia* from the totality of *Crucihimalaya* species. As molecular data do not contradict the morphological uniformity of “*Crucihimalaya+Transberingia*” complex, it seems more correct to keep the whole group taxonomically united (as a single genus, i. e., *Crucihimalaya* s. l.). Moreover, because of lack of morphological differences it is even impossible to assign *T. bursifolia* to a separate subgenus (section) within *Crucihimalaya* s. l.: intrageneric division of this compact natural group is problematic. In spite of often surprising results of numerous recent molecular studies of the Cruciferae (e. g., Al-Shehbaz, Koch, 2003; Al-Shehbaz et al., 2002; Bailey et al., 2002; Heenan et al., 2002; Mummenhoff et al., 2005; O’Kane, Al-Shehbaz, 2003; Warwick et al., 2002, 2004; and many others) which break down traditional view on the taxonomic value of morphological markers and strongly change the limits of many genera in the Cruciferae, the author based on morphological treatment of assumable relatives of the analyzed taxa believes that no other species (or a species

group) could make morphologically uniform *Crucihimalaya* s. l. paraphyletic, and considerable achievements of molecular studies of “arabidopsoid affinity”, to which *Crucihimalaya* s. str. and *Transberingia* belong, support this opinion so far. As mentioned above, delimitation of monophyletic and morphologically coherent, natural groups and attributing them a relevant taxonomic rank was the primary goal of the study on *Arabidopsis* s. l. (O’Kane, Al-Shehbaz, 2003; Price et al., 2001).

Generic delimitation is well-known as traditionally the most difficult problem in the systematics of the Cruciferae (Al-Shehbaz et al., 1999; Bailey et al., 2002; Ebel, 2001; Koch et al., 1999; O’Kane, Al-Shehbaz, 2003, Yurtsev, 1975, etc.). Nowadays a highest role of convergent development of morphological structures in the evolution of the family is proved (Bailey et al., 2002; Koch et al., 2001, 2003; Mummenhoff et al., 1997, 2005, etc.), and this fact brings more difficulties in the systematics of the Cruciferae. Undoubtedly, these processes played certain role in the evolution of the group in question, but the remarkable morphological similarity of *Crucihimalaya* s. str. and *Transberingia* is first of all a reflection of the closest affinity of these two “genera” constituting *Crucihimalaya* s. l. what is obviously supported by the mentioned molecular data.

Taxonomic consequences. Based on the above discussion, *Transberingia* is reduced herein to synonymy of the earlier established *Crucihimalaya*; appropriate taxonomic arrangements are given below.

Crucihimalaya Al-Shehbaz, O’Kane et Price, 1999, Novon, 9 : 298. – *Transberingia* Al-Shehbaz et O’Kane, 2003, Novon, 13 : 396, **syn. nov.** – *Beringia* Price, Al-Shehbaz et O’Kane, 2001, Novon, 11 : 333, nom. illeg.

Type: *C. himalaica* (Edgew.) Al-Shehbaz, O’Kane et Price.

***Crucihimalaya bursifolia* (DC.) D. German et A.L. Ebel, comb. nov.** – *Nasturtium bursifolium* DC. 1821, Reg. Veg. Syst. Nat. 2 : 194. – *Transberingia bursifolia* (DC.) Al-Shehbaz et O’Kane, 2003, Novon, 13 : 396. – *Beringia bursifolia* (DC.) Price, Al-Shehbaz et O’Kane, 2001, Novon, 11 : 334, nom. illeg.

Type: “Kamtschatka. Fischer” (holo – G-DC, iso – LE?).

Distribution: NE Asia, N America (north), Greenland.

The detailed synonymy of the species is given in Price et al. (2001) and Aiken et al. (2003). Based on investigation of the holotype of *Arabidopsis tschuktschorum* (Jurtz.) Jurtz. (LE!), the present author follows Berkutenko (1983, 1997) and Price et al. (2001) in assigning this name to synonymy of polymorphic *C. bursifolia*.

Morphologically most close *Halimolobos virgata* has been treated as a subspecies of *C. bursifolia* (as *T. bursifolia*) by Price et al. (2001). This decision is likely to be the most appropriate but *H. virgata* is accepted here as an independent species based on 1) presence of the stable morphological difference in the indumentum supported by different distribution pattern and 2) intention to keep the single species concept within *Crucihimalaya* s. l. (otherwise taxonomic decisions for the pairs of closely related species *C. mollissima* – *C. ovzinnikovii*, *C. wallichii* (Hook. fil. et Thoms.) Al-Shehbaz, O’Kane et Price – *C. kneuckeri* (Bornm.) Al-Shehbaz, O’Kane et Price should be also revised).

***Crucihimalaya virgata* (Nutt. ex Torr. et Gray) D. German et A.L. Ebel, comb. nov.** – *Sisymbrium virgatum* Nutt. ex Torr. et Gray, 1838, Fl. N. Amer. 1 : 93. – *Halimolobos virgata* (Nutt. ex Torr. et Gray) O.E. Schulz, 1924, in Engler, Pflanzenreich, 86 (4, 105) : 294. – *Transberingia bursifolia* subsp. *virgata* (Nutt. ex Torr. et Gray) Al-Shehbaz et O’Kane, 2003, Novon, 13 : 396. – *Beringia bursifolia* subsp. *virgata* (Nutt. ex Torr. et Gray) Price, Al-Shehbaz et O’Kane, 2001, Novon, 11 : 335, nom. illeg.

Type: “USA, Rocky Mts., sources of Sweet Water of the Platte. Nuttall” (holo – BM, iso – GH, NY, PH).

Distribution: west of USA.

According to these novelties, *Crucihimalaya* includes 11 species nine of which occur exclusively in mountainous areas of Asia (to Sinai), one is restricted to the mountains of the west of North America, and one is distributed in arctic and subarctic regions of both E Asia and N America.

Notes on the origin and evolution of *Crucihimalaya* s. l.

Traditional point of view on the origin of *Crucihimalaya* s. l. was based on the fact of predominant concentration of species morphologically close to *C. mollissima* in the Himalayas and neighboring mountain systems. Consequently, it was quite logic to assume this area as a center of origin of the group, and *T. bursifolia* as a single species expanded its distribution area maximally northward and migrated through the Beringian bridge to N America (Berkutenko, 1997; Yurtsev, 1975). However, the topology of the discussed tree (O’Kane, Al-Shehbaz, 2003) contribute in favor of the contrary hypothesis assuming the New World origin of *Crucihimalaya* s. l. which is also supported by morphological, geographical and further molecular evidences. In fact, most of genera related to *Crucihimalaya* s. l. are of either completely or predominantly New World distribution, e. g., American *Halimolobos* Tausch and its affinity (“halimolobine clade”, following Bailey et al., 2002) and *Boechera* Á. et D. Löve with over 60 species confined to N America (Al-Shehbaz, 2003) excepting the single species of NE Asian distribution (German, 2004). The revealed prevailing genetic diversity of the American taxa detected in this group (Bailey et al., 2002; Heenan et al., 2002; O’Kane, Al-Shehbaz, 2003) indicates the New World roots of its non-American representatives, i. e., predominantly Asian *Crucihimalaya* s. l. and the New Zealand & Tasmanian *Pachycladon* s. l. Within this group (“crown Arabidopsoid clade”, following Heenan et al., 2002), many representatives share a set of characters with *Crucihimalaya* s. l. (forked to dendritic trichomes, often of different size, sessile and amplicaul cauline leaves, often biseriate seeds) (Appel, Al-Shehbaz, 2002; Bailey et al., 2002; Rollins, 1993).

Geographical distribution of states of some characters in *Crucihimalaya* s. l. allows to reconstruct some possible trends in the morphological evolution of this taxon: trichomes predominantly many branched (dendritic) – N America & Asia, trichomes generally less branched (predominantly 1–2-forked) – Asia; seeds biseriate to rarely semibiseriate – N America & Asia, seeds uniseriate to rarely biseriate or semibiseriate – Asia; valves with prominent midvein and developed net of marginal veins – N America & Asia, valves with obscure midvein and marginal veins – Asia; cauline leaves

auriculate – N America & Asia, cauline leaves auriculate or non-auriculate – Asia. Consequently, such changes as some diminishing of degree of trichome branching, gradual shift from biseriate to uniseriate seeds, decrease of development of valves venation, and, in some cases, the lost of auricles of stem leaves should be assumed as prevailing trends in the morphological evolution of *Crucihimalaya* s. l.

Within *Crucihimalaya* s. str., phylogenetic relationships are not yet clear enough, and molecular data available (O’Kane, Al-Shehbaz, 2003) do not allow any sound conclusions on the phylogenetic position of its members for the reason of low resolution of the relevant part of the discussed tree. However, some suggestions can be put forward with use of the discussed above geographical and morphological evidences. As already mentioned, of all nine species of *Crucihimalaya* s. str., *C. mollissima* is most close morphologically to *T. bursifolia*, a taxon sister to *Crucihimalaya* s. str., and this worthy resemblance is likely to be the key point in unraveling the phylogeny of *Crucihimalaya* s. str. and s. l. The striking similarity of these species has been emphasized many times (Berkutenko, 1983, 1997; Botschantsev, 1957; Yurtsev, 1975). Moreover, the two have often been confused in the past: *C. mollissima* has been erroneously reported for NE Asia (Busch, 1926; 1939; Ledebour, 1841; Voroshilov, 1966) while *T. bursifolia* – for Central Asia (as *Arabis trichopoda* Turcz.) (Grubov, 1955; Maximowicz, 1889; for details, see: Botschantsev, 1957). *C. mollissima* has biseriate to semibiseriate seeds, rather broad fruits with well developed venation, auriculate cauline leaves, and indumentum of forked and dendritic trichomes, i. e., most of just mentioned morphological characters apparently basal for the genus. This is a single species of *Crucihimalaya* s. str. possessing the whole set of such characters typical also for *T. bursifolia*. Furthermore, *C. mollissima* has the most spacious and northern distribution of all species of *Crucihimalaya* s. str. (Altai, Tian-Shan, Pamir-Alai, Tibet, & Himalayas) (Al-Shehbaz et al., 1999; Zhou et al., 2001) with a considerable disjunction including Saur, Tarbaratai and Dzungarian Alatau (Bondarenko, 1974). The species is also highly variable in many aspects of morphology, e. g., seed arrangement and size, lack/presence of indumentum on fruits (a form with pubescent siliques occurs in Russian & Mongolian Altai – original data), petal color (white to purple). Altitudinal range of the species is between 600 meters a.s.l. in NE Kazakhstan (original data) to 4400 m in Himalayas (Zhou et al., 2001). Furthermore, *C. mollissima*, as well as *T. bursifolia*, is perennial while most of *Crucihimalaya* species are annuals or biennials (Al-Shehbaz et al., 1999; Zhou et al., 2001). Finally, *C. mollissima* can only be proposed to be the direct ancestor for at least two species – *C. ovczinnikovii*, local endemic to Pamir, and *C. rupicola* [incl. *C. mongolica* (Botsch.) Al-Shehbaz, O’Kane et Price] (German, Ebel, 2005), W Mongolian subendemic: no other species close to either of these two, occur in Pamir and in Mongolia; moreover, *C. rupicola* is a highly specialized ecologically (obligatory lithophytic) species. All these morphological and geographical evidences prove rather considerable age of *C. mollissima* and allow assuming this taxon as the most ancient of present-day *Crucihimalaya* s. str. members. It could originate on the base of any population of its ancestral species (evidently common also for *T. bursifolia*) succeeded to move from the Beringian area maximally southward

during one of the early ice ages. The present-day morphological similarity of *C. mollissima* and *T. bursifolia* but relatively big genetic distance between them is likely to be a consequence of the long-term stabilizing selection. Further evolution of *Crucihimalaya* obviously represented a burst of fast speciation and irradiation in the growing mountains of Asia which yielded a bunch of predominantly Himalayan *Crucihimalaya* species.

Alternative (or additional) suggestion explaining all-round similarity of *T. bursifolia* and *C. mollissima* is an admission of a hybrid origin of *C. mollissima* as a result of contacts of *T. bursifolia* with any species of *Crucihimalaya* s. str. caused by the glaciation cycles with subsequent substitution of the parental species and wide irradiation of the stabilized hybrid in mountain systems of Asia.

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РЕЗЮМЕ

Рассмотрены границы и объем рода *Crucihimalaya* Al-Shehbaz, O’Kane et Price, к его синонимам отнесен род *Transberingia* Al-Shehbaz et O’Kane. В состав *Crucihimalaya* переведены *Transberingia bursifolia* (DC.) Al-Shehbaz et O’Kane subsp. *bursifolia* и *T. bursifolia* subsp. *virgata* (Nutt. ex Torr. et Gray) Al-Shehbaz et O’Kane. Согласно такому пониманию, *Crucihimalaya* объединяет 11 видов азиатского (9), североамериканского (1) и амфиберингийского (1) распространения. Обсуждены морфологические, географические и молекулярно-генетические доказательства новосветского происхождения *Crucihimalaya*.