

On the History of the Genus *Ephedra*

K historii rodu *Ephedra*

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Abstract -- The origin and history of the genus *Ephedra* has been recently discussed in "Botaničeskij žurnal" by I. T. VASILČENKO and the present author. Considering the flower morphology of *Ephedra*, its recent distribution and palaeogeography of Eurasia, the author has come to the conclusion that the genus *Ephedra* originated in Central Asia during the Cretaceous period and then migrated to N. and S. America and to the Mediterranean.

The origin and history of the genus *Ephedra* and the family *Ephedraceae* is a problem which has been interesting botanists for many years. Recently a discussion of this problem was started in the „Botaničeskij žurnal“ in an interesting paper by VASILČENKO (1950), and my critical notes on his deductions (HADAČ 1964); the reply of VASILČENKO (1965) in the same journal brought forth several new aspects. It would be desirable if also other botanists acquainted with this problem would take part in the discussion. I shall, therefore, recapitulate some points of our discussion and simultaneously present some more material on this problem.

In his first paper (1950) VASILČENKO has shown that the morphology of the seedlings their ability to form green leaves even in darkness, several morphological features in flowers of *Ephedraceae* as well as the results of serological experiments - all that speaks for their close affinity to *Coniferae*. According to his opinion the most ancient group of the genus are the *Scandentes* of STAFF (*E. foliata*, *E. fragilis*, *E. altissima* etc.), mainly climbing plants, living in the area of the ancient Mediterranean sea. The origin of the genus may be placed, according to VASILČENKO, toward the end of the Cretaceous, or later.

I had the opportunity of studying several species of *Ephedra*, such as *E. foliata* in the "ahraš forest" on the banks of the Tigris and *E. alata* in the Syrian desert. In studying their morphology I came to the conclusion that *E. foliata* and its allies, with their filaments fused to an „andropodium“ and bracts forming drupes, must belong to the most developed forms, whereas *E. alata* with relatively free filaments and free bracts is evidently relatively a very primitive form. But this is just the opposite of VASILČENKO's deductions!

Comparing VASILČENKO's theory of the origin of the genus *Ephedra* in the ancient Mediterranean (Tethys), I was struck by the fact that most of the recent areas of the *Scandentes* group were covered by sea during the Paleogene and even in the second half of the Cretaceous period. These and other observations led me to the assumption that the centre of origin of *Ephedraceae* must be somewhere in the continental parts of Central Asia. These parts were dry land with a decidedly continental climate during that time. From

this centre they migrated across the Beringia to the Northern and Southern America and after the retreat of the Tethys sea to the coasts laid bare by the regression (HADAČ 1964).

My deductions, concerning genus *Ephedra*, are thus similar to the results of the studies by E. G. BOBROV (1965) concerning genus *Nitraria*. "On the basis of the comparison of the recent areas of *Nitraria* species with the data of palaeogeography of the deserts of Asia a conclusion was drawn that the ancient centre of speciation of *Nitraria* associated with the savannahs of the Paleogene, if not of the Upper Cretaceous, was situated in the Central Asia." (BOBROV 1965, p. 1067, summary.)

In his reply VASILČENKO (1965) adduces the flower morphology of *Ephedra*. He shows that forms with free floral parts need not always be the most primitive, and forms with floral parts fused the most derived ones. He illustrates this with the results of the studies by M. G. POROV (1950) on *Calligonum*. This view is quite acceptable, even if it is clear that in most cases the "fused" is derived and "free parts" are primary.

Against my hypothesis speaks, according to VASILČENKO, likewise the fact that the section *Alatae* (the most primitive in my view) is also in North America well represented by numerous species, having free bracts but practically sessile anthers. But just this led me to believe that the centre of evolution of *Ephedra* could only be in Central Asia, where *Ephedras* with both free bracts and filaments are thriving, whereas forms, emigrated to America, have "antherophors".

VASILČENKO shows that members of the *Alatae* section in Central Asia (*E. strobilacea* etc.) are nowadays living in territories that are very young from the geological point of view (the sands of Balkash and Kara-Kum etc.). This is of course true, but it does not necessarily mean that *Ephedra* species in Central Asia had no other places where to live before these sands were formed. VASILČENKO quotes several authorities showing that in the Tethys sea many islands were present during the Cretaceous and Tertiary periods, affording many possibilities for the ancient *Ephedraceae*. But I don't think that small areas can become centres of origin for a whole family — they may contribute to forming endemic species or subspecies, but hardly to giving rise to a new family of world-wide distribution.

VASILČENKO (1965) enumerates the existing theories on the origin of *Ephedra*:

1. according to M. G. POPOV, the centre of origin of *Ephedras* was South Africa,
2. according to S. A. NEVSKI and I. T. VASILČENKO the Palaeomediterranean,
3. according to HADAČ Central Asia,
4. according to M. M. ILJIN the whole territory of the Asiatic and North American continents
5. according to E. P. KOROVIN the S. W. Asia, and
6. according to a new tentative theory of VASILČENKO (1965) North America.

The first theory is opposed by the absence of *Ephedra* species in South Africa. I do not see any reason why they could not exist there now, if they did exist there in the past. Let us now assume that the centre of origin of *Ephedra* was the Palaeomediterranean and that a group migrated to East (to Asia) and to West (to America) — but why not by the easiest way through the mountains of Ethiopia and Central East Africa to the Capensis? On the other hand, if they originated on the Asiatic continent (Central or S. W. Asia, theory 3 or 5), they could easily migrate to America through Beringia, but they came to North Africa too late to penetrate further to the south. It is difficult to say anything against or in favour of the fourth theory; I think that the presumed territory of origin is too broad — in my opinion it must be either Asia or America, not both. To find which of those two is more probable, I tried to bring in correlation the morphology of flowers and the

geographical distribution of the respective sections and subsections. The result may be seen in Fig. 1. I have used data from STAPFS Monograph.

ANTHERAE

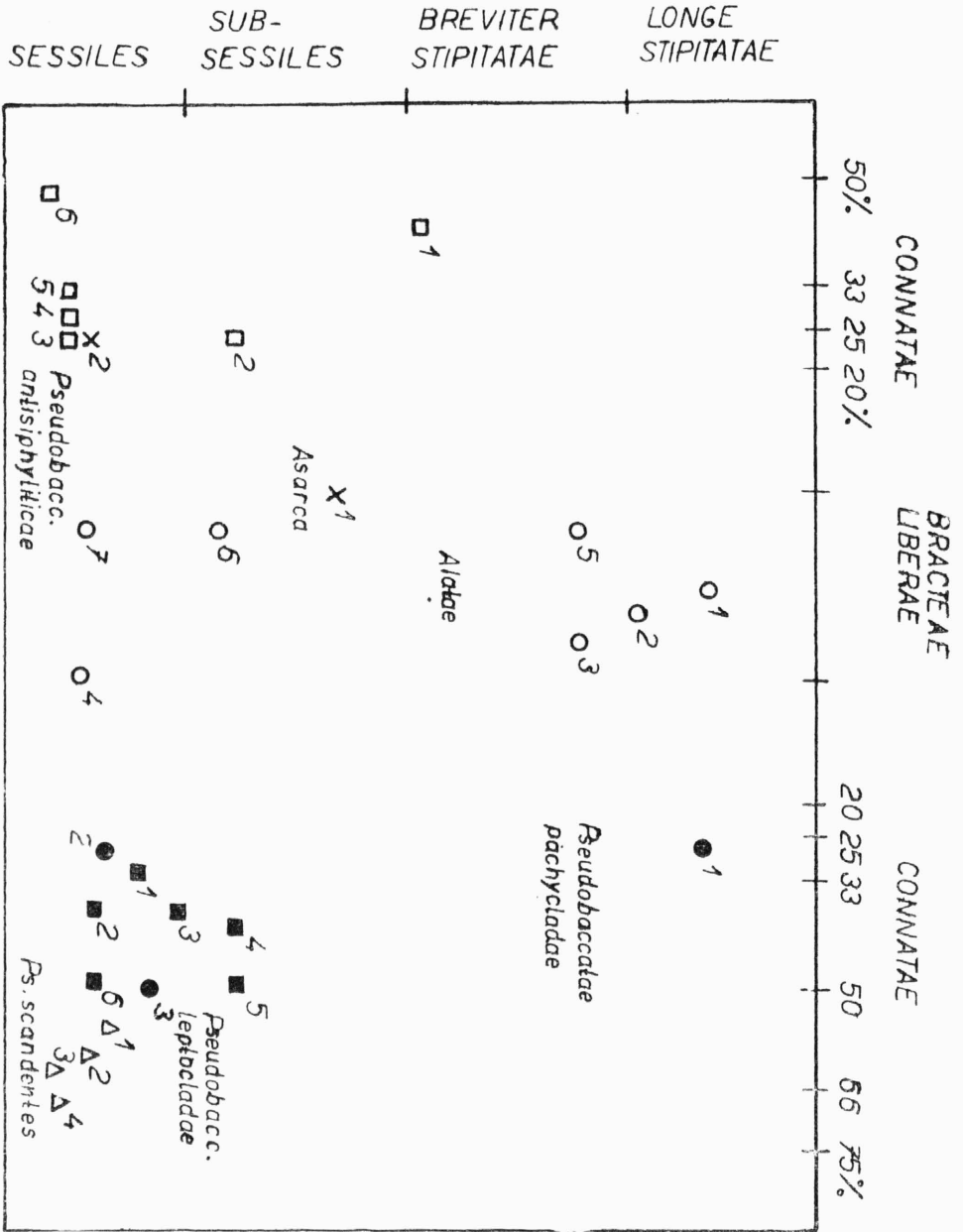


Fig. 1. — The correlation between flower morphology in different sections of *Ephedra* and their geographical distribution. (For explanation see p. 8.)

Rings: *Alatae Tropidolepides*: 1. *E. strobilacea*, 2. *E. alata*, 3. *E. Przevalskii*, 4. *E. alenda*.
Alatae Habrolepides: 5. *E. trifurca*, 6. *E. Torreyana*, 7. *E. multiflora*.
 Crosses: *Asarca*: 1. *E. aspera*, 2. *E. californica*.
 Squares: *Pseudobaccatae antisiphyliticae*: 1. *E. antisiphylitica*, 2. *E. nevadensis*, 3. *E. triandra*, 4. *E. Tweediana*, 5. *E. americana*, 6. *E. ochreatea*.
 Points: *Pseudobaccatae pachycladae*: 1. *E. sarcocarpa*, 2. *E. pachyclada*, 3. *E. intermedia*.
 Black squares: *Pseudobaccatae leptocladae*: 1. *E. nebrodensis*, 2. *Gerardiana*, 3. *E. distachya*, 4. *E. helvetica*, 5. *E. monosperma*, 6. *E. equisetina*.
 Triangles: *Pseudobaccatae scandentes*: 1. *E. foliata*, 2. *E. alte*, 3. *E. altissima*, 4. *E. fragilis*

We can see that the *Pseudobaccatae scandentes* group, supposed by VASIL-
 ŌENKO to be the most primitive one, is situated in the right lower corner
 and corresponds to the American group *Pseudobaccatae antisiphyliticae*,

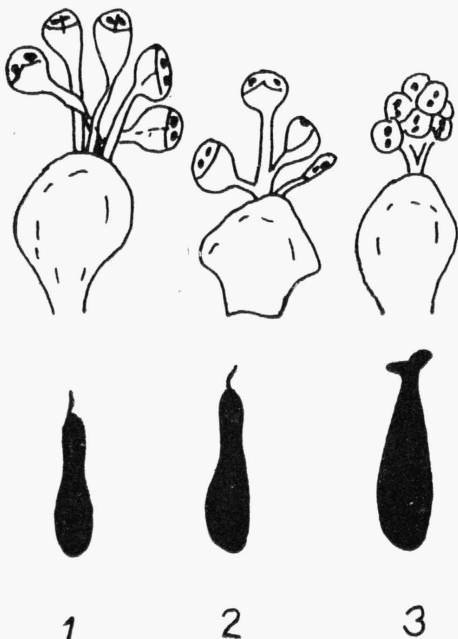


Fig. 2. — Male flowers and seeds of *Ephedra strobilacea* (1), *E. alata* (2) and *E. alenda* (3).
 (See p. 8.)

especially to their South American group. There is, for palaeogeographical reasons, very small probability of a connection between the Mediterranean and the American populations. The Mediterranean and the American *Ephedras* had thus developed independently. The trend of evolution in a plant group usually goes in one direction. In our case, we must suppose that the evolution of floral parts eventually went either by fusing of filaments to the „antherophor“ and by fusing of the floral bracts, or vice versa. Starting from the *Scandentes* group we may follow the supposed evolution over *Leptocladae* and *Pachycladae* to the Asiatic *Alatae Tropidolepides*. Here the supposed evolution from the antherophors to free filaments and from fused bracts to free ones is at its top — but how to explain further evolution in the opposite direction on the way to South America? If on the other hand we suppose that the *Alatae Tropidolepides* represent the most primitive recent group, we can see that the trend of evolution

from Central Asia is the same in both groups migrating West and East — from free filaments and bracts to fused ones.

In the group *Alatae Tropidolepides* the same trend may be followed. Let us compare *E. strobilacea*, distributed from Kara Kum to Iran, with stipitate anthers, *E. alata*, distributed from Iraq to Libya, with stipitate anthers, sometimes fused at the base, and the North African *E. alenda* with anthers sessile on the antherophor. The last one has seeds provided with hooks (for zoochorous distribution), an adaptation, which is without any doubt not a primitive feature. The trend of evolution goes even in this case from free to fused parts — from Asiatic to North African forms.

The history of the Genus *Ephedra* is still full of problems. I hope that my notes may contribute a little to their solution

Vznik a historie rodu *Ephedra* je předmětem diskuse, která dosud probíhala v časopisu „Botaničeskij žurnal“ mezi I. T. VASILČENKEM a autorem. Autor se na základě morfologie květu, recentního rozšíření a palaeogeografických poměrů v Eurasii domnívá, že rod *Ephedra* vznikl ve Střední Asii v křídové době. Odtud pak se rozšířil do Severní a Jižní Ameriky na jedné straně a do Středozeří na straně druhé.

L i t e r a t u r e

- BOBROV E. G. (1965): O proischoždenii flory pustyň starogo sveta v svyazi s obzorom roda *Nitraria* L. — Bot. Ž. 50/8 : 1053—1067.
 HADAČ E. (1964): Iz istorii roda *Ephedra* L. — Bot. Ž. 49/2 : 243—244.
 MARKOV K. K. (1955): Paleogeografie. — N. ČSAV Praha.
 STAFF O. (1889): Die Arten der Gattung *Ephedra*. — Wien.
 VASILČENKO I. T. (1950): Materialy po istorii proischoždenija efedry. — Bot. Ž. 35/3 : 263—273.
 — (1965): Prodloužení diskussii po efedre *Ephedra* L. — Bot. Ž. 50 : 867—870.
 (Further literature on this problem may be found in the last two papers.)

Zprávy o literatuře

Opera corcontica (Krkonoské práce) 1/1964

Pro Krkonoský národní park ve Vrchlabí vydalo Východočeské nakladatelství, Havlíčkův Brod 1965, 166 stran, 40 obr., 11 tab., cena brož. 18,— Kčs. (Kniha je v knihovně ČSBS).

První svazek, jehož vědeckým redaktorem je J. JENÍK a výkonným redaktorem J. FANTA, obsahuje deset základních prací a šest kratších sdělení. Nové výsledky geomorfologického, kvarterně geologického, petrografického a tektonického výzkumu v oblasti Krkonoského krystalinika přinášejí úvodní dvě studie, a to jednak J. SEKERY a jednak J. LÍBALOVÉ. Charakteristickými přírodními útvary Krkonosů jsou hřebenové rašeliniště. Je třeba chránit je před zásahy, jimiž se porušují hydrologické poměry hřebenů a zvyšuje se erozivní ohrožení. V. MEJSTŘÍK a K. ŠTRAKA podávají výsledky podrobného výzkumu Pančického rašeliniště, které svými klimatickými poměry a vegetačním krytem upomíná na rašeliniště skandinávská. Stanovili rozsah rašeliniště, objem, složení a stratigrafii rašeliny. Dále se zabývali hydrologickými a klimatickými poměry této přísné rezervace. Na území Krkonoského národního parku je třeba neustále udržovat rovnováhu a soulad mezi všemi složkami hospodářské, rekreační a sportovní činnosti. Varovným hlasem v tomto ohledu je závěr VRBOVY studie o sněhové akumulaci v lavinové oblasti Modrého dolu, kde se (jak je veřejnosti známo) počítá s vybudováním sportovního areálu a stavbou mezinárodní lyžařské sjezdové trati. Autor podává podrobný popis a zhodnocení pravděpodobně nejstaršího lavinového pole Sudet, vychází z dřívější literatury o této lokalitě a zpřesňuje především údaje o výšce sněhové pokrývky. Geobotanicou a problematikou Labského dolu se zabývá článek J. JENÍKA a J. KOSINOVÉ. Řeší topografii Labského dolu a zdůvodňuje potřebu podrobného topografického názvosloví tří morfologicky samostatných karů v závěru údolí. Těžišť článku spoívá v geobotanickém rozboru pozoruhodné lokality v severní části karové stěny Pančické jámy, kterou autoři navrhují pojmenovat „Schustlerova zahrádka“. Problémy racionálního zalesnění Krkonosů obsahuje studie T. LOKVENCE. Autor experimentálně řešil dávný problém vypěstování kvalitních sazenic kosodřeviny pro rekonstrukci křovitých alpských porostů. Volil několik výškových stupňů, v nichž na školkových kulturách provedl řadu měření a došel k závěru, že optimální zónou pro pěstování sazenic je závětrná oblast ve výšce 1000—1200 m n. m., což je zhruba alpská hranice lesa. Sborník obsahuje dále dvě práce polských autorů. A. DYRCZ studoval avifaunu polské části Krkonosů; F. RUDZKI podává ve svém příspěvku informace o organizaci výzkumu a zdůrazňuje hlavní úkol parku — ochranu přírody v nejširším slova smyslu. Hodnocení reliéfu a sněhové pokrývky z hlediska lyžování a turistiky na lyžích podal B. SÝKORA. Sborník uzavírá oddíl Zprávy a sdělení, v němž T. LOKVENC referuje o nově zjištěných lokalitách dřevin v alpské oblasti, A. PŘÍHODA upozorňuje na výskyt horských chorošů, J. ŠTURSA podává přehled synantropní vegetace v okolí Luční boudy a [růstových forem křeče a J. JENÍK popisuje ruderalní flóru na zbořeníšti Boudy Prince Jindřicha.

J. K o s i n o v á