

Problems in the Taxonomy of Tragacanthic Astragalus

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Abstract:

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In the course of a monographic revision of the genus *Astracantha* Podlech we have found many transitional species between this new genus and the genus *Astragalus* L. Many species in these two genera are so closely related to each other that generic delimitation can not be maintained. Contrary to the opinion of some authors, the results of thorn anatomy can not be used for separating the genera. The close similarity between species which are currently placed in two separate genera can not have resulted from mere convergence - phylogenetic relationships must play a part here. The genus *Astracantha* is most probably polyphyletic. It must be included in the genus *Astragalus* again. Molecular data support this conclusion. Some morphological evidence is discussed in detail.

Zusammenfassung:

Im Rahmen einer Revision der Gattung *Astracantha* Podlech wurde festgestellt, daß es viele Übergänge zwischen dieser Gattung und der Gattung *Astragalus* gibt. Die Arten an der Grenze zwischen den Gattungen sind zum Teil so nahe verwandt, daß eine weitere Trennung dieser Gattungen nicht beibehalten werden kann. Entgegen der Meinung einiger Autoren kann die Dornenanatomie nicht zur Unterscheidung beider Gattungen verwendet werden. Die Ähnlichkeiten von einigen Arten beider Gattungen sind so hoch, daß sie nicht durch Konvergenz entstanden sein können. Die Gattung *Astracantha* ist sehr wahrscheinlich polyphyletisch und sollte daher wieder mit *Astragalus* vereint werden. Molekular-phylogenetische Daten unterstützen diese Auffassung. Im Folgenden werden einige morphologische Hinweise diskutiert.

Introduction

In the first widely accepted classification of the genus *Astragalus* L., which was established by BUNGE (1868/1869), a main part of the thorny species of *Astragalus* was placed into the subgenus *Tragacantha* Bunge. This subgenus was characterized by its sessile flowers and inflorescences, which form a dense, compound synflorescence. Because many of those species produce tragacanth gum, lack black hairs at the calyx and possess unilocular fruits, which are mostly one-seeded, many taxonomists believe in the homogeneity and monophyly of the group. Therefore the subgenus was elevated to generic rank by some authors. BORISSOVA (1937, 1946, 1947, 1955) and some other Russian botanists, e.g. RASULOVA & SHARIPOVA (1978) treated it as genus *Tragacantha*. However, this name was not applicable for formal

reasons (see PODLECH 1983). PODLECH (1983) described the new genus *Astracantha* for this group. Today this name is generally accepted (GREUTER & RAUS 1986, REER & PODLECH 1986, GREUTER, BURDET & LONG 1989, ENGEL 1990 and 1991, LOCK 1989, LOCK & SIMPSON 1991, CZEREPANOV 1995, YAKOVLEV, SYTIN & ROSKOV 1996).

In the course of the work on *Astragalus* carried out by Podlech (Munich) and his group, the majority of thorny species of the genus has been investigated (DEML 1972, TIETZ 1988, TIETZ & ZARRE 1995, TIETZ 1996, ZARRE & PODLECH 1996). Within the framework of a revision of tragacanthic *Astragalus*, currently known as *Astracantha*, we found that generic rank for those thorny species of *Astragalus* is of no value and offers many problems in taxonomy. Moreover, this group seems to be polyphyletic.

This work is primarily based on the morphological analysis of herbarium material and numerous field observations during three excursions in Iran (by S. Zarre M.), which were supported by the Ministry of Culture and Higher Education of the Islamic Republic Iran.

The term tragacanthic *Astragalus* is used in this paper for the group of thorny species within the genus *Astragalus*, which were treated by Bunge as subgenus *Tragacantha*.

Morphological data

Maintaining an independent genus *Astracantha* is not possible due to the existence of many intermediates between tragacanthic *Astragalus* and some sections of *Astragalus*. Some important cases are listed as follows.

Sect. *Microphysa* Bunge:

Section *Brachycalyx* Bunge of tragacanthic *Astragalus* is an isolated section in the group. While most of tragacanthic species possess a turbinate calyx *A. brachycalyx* Fisch. (lectotype of sect. *Brachycalyx*) has a tubular-campanulate calyx identical with young calyces of *A. microphysa* Boiss. (lectotype of sect. *Microphysa*). *A. chartostegius* Boiss. & Hausskn. is another species with close relationship to *A. microphysa*. It was placed in sect. *Acidodes* Bunge by BOISSIER (1872). Shape of the leaflets, glabrescent stems, stipules and leaves, thinly membranous stipules, whitish corolla, similar form and size of the short hairy calyx are characters which are shared by all three species. The only difference between *A. brachycalyx* and the other above named species is the absence of peduncles. We have no doubt that *A. brachycalyx* and *A. chartostegius* must be placed in the same section. Interestingly, the number of inflorescences in *A. chartostegius* on each axis is high, so that they seem to build a dense compound synflorescence. In our opinion, this high degree of similarity is unlikely to be the result of convergence.

Calyces in *A. microphysa* are inflated a short time after anthesis. Moreover, the standard of the latter is not platynchioid as in *A. chartostegius* and *A. brachycalyx*. Therefore the separation of the last two species from sect. *Microphysa*, or specially from *A. microphysa*, is well supported.

Relationship between sect. *Acidodes* and sect. *Adiaspastus* Bunge:

A. sempervirens Lam. is the lectotype of sect. *Acidodes* (PODLECH 1990) and *A. aureus* Willd. is the lectotype of sect. *Adiaspastus* (ENGEL 1990). In both species the calyx is tubular and not rupturing until maturity. Moreover, the shape of the standard is similar and characteristic in both species: the limb is gradually narrowed into the claw. Although many specimens of *A. sempervirens* have shortly pedunculate inflorescences, there are some specimens with sessile ones. Moreover, in both cases inflorescences build up a dense compound synflorescence. There is no doubt, that both species belong to one natural group, and both sections must by necessity be synonymized. However, there is a wide disjunction between the ranges

of the above named species. The most easterly locality of *A. sempervirens* is in Greece, where the species is known as *A. cephalonicus* C. Presl and *A. aureus* is endemic on the mountains around the Caspian sea. The latter is a hyrcanian element and the former a mediterranean one. However, many species exhibit disjunct distribution between the mediterranean and hyrcanian floristic regions (RECHINGER 1970 and 1989, ZOHARY 1973).

Different ideas on the delimitation of the above named sections have been proposed: DEML (1972) separated a part of species which were placed in former time in sect. *Acanthophaea* Bunge (e.g. *A. carduchorum* Boiss. & Hausskn., *A. macrosemius* Boiss. & Hohen., *A. sahendi* Boiss., *A. jodotropis* Bunge and *A. paraplesius* Bunge) and transferred them to sect. *Acidodes* of *Astragalus*. This treatment was followed by ENGEL (1992) and GREUTER & RAUS (1986). CHAMBERLAIN & MATTHEWS (1970) and TOWNSEND & GUEST (1974) on the other hand believed that these species belong to sect. *Acanthophaea*. Other species, such as *A. harefae* Sirj., *A. leiophyllus* Freyn and *A. ochrochlorus* Boiss. & Hohen. were relegated to sect. *Adiaspastus* of *Astracantha* by DEML (1972), GREUTER & RAUS (1986) and ENGEL (1990), to sect. *Acanthophaea* Bunge by CHAMBERLAIN & MATTHEWS (1970) and p.p. by TOWNSEND & GUEST (1974). So the correct position of the species between these sections remains problematical and requires more studies. However, there can be no doubt that the available systems for separating the species in this group are artificial and impractical, because of the close affinities between the species which are currently placed in different genera.

One of the above named species, *A. ochrochlorus* highlights the problem: The species shows considerable variability with regards to the length of its peduncles and inflorescence morphology. In some specimens peduncles of lateral inflorescences are easily visible, for example the specimen Amin 15365 (W) collected at Lar, Kharsang, E. Tehran, 2500 m. In this specimen peduncles are up to 4 cm long while most of the other specimen have sessile inflorescences. If this character is used for generic delimitation, some specimens must be placed in genus *Astragalus* and others in *Astracantha*. This explains the divergent ideas about the taxonomic position of this species. The same variability is found in *A. titziae* Ghahreman & Zarre (see also GHahreman & ZARRE 1994).

Maintaining the genus *Astracantha* as a natural one is impossible, even by transferring sect. *Adiaspastus* to genus *Astragalus*. This section is characterized by non rupturing \pm tubular calyx and the shape of the standard (see above). The following species were attributed to this section by most of authors: *A. aureus*, *A. breviflorus* DC., *A. michauxianus* Boiss., *A. karabaghensis* Bunge, *A. polyanthus* Bunge, *A. acmophyllus* Bunge, *A. cerasocrenus* Bunge and *A. noeanus* Boiss. There are, again, different ideas about the delimitation of this section. For example, some authors include *A. gummifer* Labill., *A. crenophilus* Boiss. & Hausskn. (TOWNSEND & GUEST 1974), *A. caspicus* M. Bieb. and *A. caucasicus* Pall. (CHAMBERLAIN & MATTHEWS 1970, BOISSIER 1872: partly) in this section. But this last group differs in so many important characters, such as form and indument of calyx, size of flowers, shape of the standard from the *Adiaspastus* s.str. (see above). We do not believe that they belong to sect. *Adiaspastus*. Concerning *Adiaspastus* s.str.: In *A. acmophyllus* and *A. cerasocrenus* the standard shows a tendency towards differentiating limb and claw. In both species the standard limb is acutely dilated at the base, a character that is very common in the species of sect. *Rhacophorus* Bunge and *Pterophorus* Bunge of tragacanthic *Astragalus*. Moreover, in some species of the latter, e.g. *A. muschianus* Kotschy & Boiss. and *A. asaphes* Bunge, calyx texture is somewhat firm in the same way as in sect. *Adiaspastus*. Otherwise *A. cerasocrenus* (from sect. *Adiaspastus*) has thinly membranous calyces like the young calyces of sect. *Rhacophorus* and *Pterophorus*, although they remain unruptured. In some cases, if the plants are young, a determination between sections *Adiaspastus* and *Rhacophorus* is very difficult. Thus transferring sect. *Adiaspastus* to the genus *Astragalus* and keeping other tragacanthic *Astragali* in the genus *Astracantha* would be artificial.

Sect. *Hymenostegis* Bunge:

Although no single species of the sect. *Hymenostegis* has a close relative within tragacanthic *Astragalus*, there are many characters in which both groups are related. For example, habit is so similar that young sterile specimens can not be identified as to which group they belong. Moreover, the shape of the standard in most of tragacanthic *Astragalus*, specially species of *Rhacophorus* and *Pterophorus* is elliptic-panduriform as in all species of sect. *Hymenostegis*. Another very important character is the form and size of the fruits. We have studied the fruits in most of the species of tragacanthic *Astragalus*: They are usually dorsiventrally compressed, one-seeded, sessile and shorter than 9 mm, just as in sect. *Hymenostegis* (ZARRE & PODLECH 1996).

Moreover, some species of sect. *Hymenostegis* have very short peduncles, e.g. *A. hirticalyx* Boiss. and short pedunculate forms of *A. persicus* Fisch. & C.A.Mey. (ZARRE & PODLECH 1996). Such species can be mistaken for tragacanthic *Astragalus*. The best example for this is *A. mishoensis* Turill: It was originally described in sect. *Rhacophorus*, because the axis of the racemes are very short and the peduncles are partly absent in the type collection. But this specimen belongs really to *A. hirticalyx* Bunge.

Sect. *Hymenostegis* is a very homogeneous section and without doubt is one of the most natural groups in the genus *Astragalus*. Most probably this section is a sister group of tragacanthic *Astragalus* in the strictest sense (sect. *Rhacophorus* and *Pterophorus*).

A. distinctissimus Rech.f. & Edelh.:

This species belongs to sect. *Pelta* (PODLECH, in press). Sect. *Pelta* is related to sect. *Lithophilus* Bunge of subgenus *Phaca* Bunge in Bunge's system (PODLECH & DEML 1967). Without doubt this section is phylogenetically very far from tragacanthic *Astragalus*, because of the highly derived shape of its pods and imparipinnate leaves. However *A. distinctissimus* (nom. illeg., non Eig) possesses a cylindrical, dense compound synflorescence, which is composed of many lateral 2–4 flowered inflorescences same as in some tragacanthic species of *Astragalus*.

Moreover, in many other species of thorny *Astragalus* such as *A. susianus* Boiss. (sect. *Campylanthus* Bunge), *A. hirticalyx* (sect. *Hymenostegis*), *A. diopogon* Bunge (sect. *Megalocystis* Bunge), *A. microphyssa* and *A. callistachys* Boiss. (sect. *Microphyssa*) there is a tendency toward shorter peduncles and raceme axes. We believe that this process has occurred parallelly in different groups and can not be considered as an important synapomorphic character.

A. piptocephalus Boiss. & Hausskn.:

It is the only species of section *Polystegis* Boiss. Sessile lateral inflorescences and ovate and coriaceous bracts characterize the section. It was treated as a member of subgenus *Tragacantha* by BOISSIER (1872). TOWNSEND and GUEST (1974) considered it to be intermediate between sect. *Hymenostegis* (of genus *Astragalus*) and sect. *Macrophyllum* Boiss. (of genus *Astracantha*). No modern studies of the species have been published. Even in recent publications, in which the genus *Astracantha* is adopted, there are no data about the position of this species. The coriaceous bracts, tubular calyx, which is \pm closed at the mouth, and special and unique shape of the standard separate this section from the remainder of tragacanthic *Astragalus*. In our opinion, this species must be placed between *Astragalus* sect. *Hymenostegis* and sect. *Acidodes* and is not closely related to tragacanthic *Astragalus*. However it is yet another example for the tendency towards a shortening the the peduncles and raceme axes.

A. chionobiiiformis C.C.Towns.:

It was placed in sect. *Acanthophaea* by TOWNSEND & GUEST (1974) because of the presence of some black hairs on the calyx. It is a systematically isolated plant without close relatives and with a narrowly endemic distribution. It is likely to be a relic species like *A.*

piptocephalus. The species shows the same habit as most of tragacanthic species of *Astragalus*. Its standard is \pm platonychoid and relatively short, calyx hairs are shorter than 3 mm, peduncles and pedicels are not developed: characters by which the species is related to sect. *Platonychium* Bunge of genus *Astracantha*. Moreover, the species produces tragacanth gum (seen on Rechinger 11082 in W). The only difference of this species from other tragacanthic *Astragalus* species is the presence of black hairs on the calyx. A separation of this species from other tragacanthic ones only according to this character would be artificial.

Anatomical Data

Most of our knowledge about anatomical features of thorny *Astragalus* results from thorn anatomical and seed micromorphological studies done by ENGEL (1990 and 1991). According to his studies the structure of seed surface in most derived groups of thorny *Astragalus*, such as sect. *Hymenostegis* and *Poterion* Bunge is the same as in the majority of tragacanthic *Astragali*. Therefore the results of seed micromorphological studies do not support the separation of tragacanthic *Astragalus* from thorny ones. Contrary to that, cross sections of thorns can indicate some important characters for separating genus *Astragalus* from *Astracantha*. The following features characterize cross sections in genus *Astracantha* (ENGEL 1991):

- very thick outer sclerenchymatous bundle sheaths
- small pith, mostly with lignified cell walls, and
- clear dominance of the median vascular bundle.

However, some species of thorny groups of the genus *Astragalus*, which were also studied by Engel, show all of the above mentioned characters. As an example for this case we can give *A. hirticalyx* of sect. *Hymenostegis* and most other species of this section. As discussed above, the latter is also morphologically very close to tragacanthic *Astragalus*. Moreover, some species of sections *Microphysa* and *Campylanthus* also show thorn anatomical features of tragacanthic *Astragalus*.

A large median vascular bundle with its thick outer sclerenchymatous bundle sheet and very small and lignified pith characterizes sect. *Brachycalyx* of tragacanthic *Astragalus*. The same was observed in *A. flexilipes* Bornm. of sect. *Megalocystis* (Zarre, own data).

One of the most primitive sections of tragacanthic *Astragalus*, which is accepted by most of the authors as belonging to genus *Astracantha*, is the sect. *Macrophyllum*. Most of the species in this section have a thin outer sclerenchymatous bundle sheath, relatively large pith without lignified cell walls, and moderately dominant median vascular bundle, characters, which are not typical of tragacanthic *Astragalus*.

Conclusion: Although there is a tendency to have more lignified thorns within most groups of thorny *Astragalus* being reflected anatomically by the above named features, the differences are gradual and can not be used to separate the genera or even sections clearly.

Molecular Phylogeny

Molecular data do not support tragacanthic *Astragalus* as a separate genus. LISTON & WHEELER (1994) have shown for the first time on the base of restriction site analysis of the chloroplast genes rpoC1 and rpoC2 that the recognition of the segregate genus *Astracantha* makes *Astragalus* paraphyletic. According to the cladogram reconstructed from the mapped restriction sites there two *Astracantha* species, *Ac. ambolepis* Fisch. and *Ac. eriocephala* Willd. (correctly *Ac. breviflora*, see PODLECH 1993) groups with *A. icmadophilus* Hand.-Mazz. The latter belongs either to sect. *Acidodes* (DEML 1972) or *Acanthophaece* (CHAMBERLAIN & MATTHEWS 1970) which are also morphologically similar to tragacanthic *Astragalus*.

So the close relationship between the above named sections and *Astracantha* is again well supported.

Moreover, nucleotide sequence variation in the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA for some species of *Galegeae* including *A. peristerea* Boiss. & Hausskn. also supports the traditional placement of the genus *Astracantha* within *Astragalus* (SANDERSON & LISTON 1995).

However, our knowledge in the field molecular phylogeny is still very poor and more comparisons especially between tragacanthic *Astragalus* and other thorny species of the genus *Astragalus* must be done (Liston, pers. comm.).

Results of Field Observations

Most of the tragacanthic species of *Astragalus* are cushion-forming plants of alpine or subalpine habitats. In the same way as other thorny *Astragalus* species they are adapted to dry and windy conditions. They are mainly late flowering and the fruits may remain attached to the plant up to november. This is also found in sections *Acidodes* and *Hymenostegis* of genus *Astragalus*.

Producing traganth gum is one of the very important characters which has been considered to be exclusive for this group. However, there are also some thorny *Astragalus* species which occasionally show this character, e.g. *A. susianus*, *A. chrysostachys* Boiss., *A. glumaceus* Boiss., *A. keratensis* Bunge and *A. macrosemius*. LUTZ (1910, 1922a, b) found this character also in *A. armatus* Willd. and *A. aristatus* L'Hér. (= *A. sempervirens*). On the other hand there are many tragacanthic *Astragalus* species which do not produce gum, for example *A. albispinus* Sirj. & Rech.f., *A. stenolepis* Fisch. and *A. michauxianus* (Zarre, own data). So this character can also not be used for delimiting the two genera.

Discussion

Segregation of some natural groups from the huge genus *Astragalus* could simplify a taxonomic determination of the species in this genus and has been tried many times in its taxonomic history. Segregation of the genus *Astracantha* was one of these attempts which gained popularity for a while. Unfortunately, the group is not natural and many species have close relatives within thorny *Astragalus*. As it has been shown above, the presence of compound synflorescences is taxonomically not reliable and can have been arisen polyphyletically in unrelated groups. Other characters, which have been considered characteristic for genus *Astracantha* are problematical, due to the existence of intermediates with other thorny *Astragalus*. The genus *Astracantha* in its current circumscription has close relationships to sections *Acidodes*, *Hymenostegis*, *Microphysa* and *Acanthophaea*. These morphological and anatomical similarities are probably phylogenetically informative and not the result of convergence, as one of us previously believed. These data concur with the findings of molecular phylogeny.

Even thorn anatomical studies showed that the majority of the most derived species of thorny *Astragalus* and tragacanthic *Astragalus* have similar patterns in the size of the sclerenchymateous bundle sheath and median vascular bundles, as well as the size of the pith and the lignification of cell walls.

The tragacanthic *Astragalus* species are not monophyletic and can thus not be maintained even at subgeneric level. As the taxonomic treatment of our results, we synonymize the genus *Astracantha* with the genus *Astragalus*.

Astragalus L. subgen. *Astragalus*. Lectotype (AGERER-KIRCHHOFF 1976): *A. christianus* L.
= *Astracantha* Podlech, Mitt. Bot. Staatss. München 19: 4. 1983 ≡ *Astragalus* subgen.
Tragacantha Bunge, Mém. Acad. Imp. Sci. Saint Pétersb. 11(16): 77. 1868, non *Traga-*
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