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PETIOLAR ANATOMY OF NORTH AMERICAN *ASTRAGALUS* SPECIES
(FABACEAE) WITH PERSISTENT PETIOLES

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ABSTRACT

The petiole and rachis anatomy of 11 North American *Astragalus* species that show a tendency towards persistent petioles is described and illustrated by line drawings of representative transections. The results are compared with those of a spine anatomical survey of 200 Old World *Astragalus* and *Astracantha* species. Attention was given to the anatomical characters previously determined to be taxon-specific such as the amount and position of sclerenchyma and distribution patterns of vascular bundles. Character evolution and the classification of species into sections are discussed. A fundamental difference between New World and Old World *Astragalus* s.l. species was found. Most of the sclerenchyma contributes to the stability of the persistent petiole by the inner vascular bundle sheath—primarily the median bundle—in North American *Astragalus* species. In the Old World species, however, the outer sclerenchymatous bundle sheaths form most of the sclerenchyma of the spine. In American as well as in Asian species, the persistence of petioles (and rachises) evolved several times in different sections by convergence. Species representing distinct stages of the evolution towards a spinelike organ occur in the three sections *Jejuni*, *Humillimi* and *Neonix*. Thus, unlike in the Old World species in which the petiolar anatomy of each section reached more or less the same evolutionary level, in the New World the sections investigated contain species with different levels of spine development.

Key words: *Astragalus*, *Astracantha*, *Fabaceae*, plant anatomy, comparative leaf anatomy, petiolar anatomy, spine anatomy.

INTRODUCTION

In the Old World, ca. 300 species of *Astragalus* L. s.str. and *Astracantha* Podlech (formerly *Astragalus* subg. *Tragacantha*, separated by Podlech 1983) out of 2000 *Astragalus* s.l. species have spines consisting of lignified petiole and rachis. Only 11 out of 400 North American *Astragalus* species (Barneby 1964) show a tendency towards persistent petioles (and rachises).

A survey of spine anatomy based on the investigation of 200 Old World *Astragalus* and *Astracantha* species was given by Engel (1990). In the present paper, the North American *Astragalus* species with persistent petioles are compared with the species in that survey.

In true spines of Old World Astragali, one half to three quarters of the length is rachis and only the rest is petiole (Engel 1990). In contrast, in North American Astragali the very short rachis is negligible in comparison with the persistent petiole.

The following anatomical characters of petioles (and rachises) were worked out as specific for the classification of *Astragalus* s.l. species: (1) transection portions of pith, cortex and vascular bundles in relation to the total transectional area at different levels of the petiole/rachis; (2) thickness of sclerenchymatous bundle sheaths in relation to the thickness of vascular tissue; (3) numerical proportions and distribution patterns of vascular bundles.

MATERIALS AND METHODS

All eleven North American *Astragalus* species, including some varieties that show a tendency towards persistent petioles, were investigated. Hand sections were made of the lower part of the petiole (and rachis) after they had been soaked and heated. The staining procedure with safranin, light green, and crystal violet followed Gerlach (1977). Representative transections were drawn, using the light microscope, with the aid of a drawing mirror. Line drawings show all relevant characters. All material was obtained from the Rancho Santa Ana Botanic Garden (RSA) herbarium.

List of Specimens Investigated

Section ERVOIDEL.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *coloradoensis* Jones: Utah, Kane County, Glen Canyon City, Barneby 13115.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *danaus* Barneby: California, Inyo Co., Sierra Nevada, 10,500 ft., F. W. Peirson 2802.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *elatus* S. Watson: Nevada, Washoe Co., 5350 ft., A. Tiehm 10613.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *implexus* (Canby) Barneby: Idaho, Custer Co., Lost River Mt., C. L. Hitchcock 15724.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *jessiae* (Peck) Barneby: Idaho, Owyhee Co., Ripley & Barneby 6526.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *kentrophyta*: Wyoming, Platte Co., C. L. Porter 4308.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *neomexicanus* Barneby: New Mexico, Sandoval Co., Barneby 12827.—*Astragalus kentrophyta* Nutt. ex T. & G. var. *ungulatus* Jones: Nevada, Eureka Co., Ripley & Barneby 9932.

Section HUMILLIMI.—*Astragalus cremnophylax* Barneby: Arizona, Grand Canyon, 7050 ft., M. E. Jones s.n.—*Astragalus gilensis* Greene: Arizona, Apache Co., White Mts., Ripley & Barneby 8443.—*Astragalus humillimus* Gray ex Brand.: Colorado, Mesa Verde, Brandegee 1087.—*Astragalus troglodytes* S. Watson: Arizona, Coconino Co., 12 miles S of Flagstaff, Ripley & Barneby 4897.—*Astragalus wittmannii* Barneby: New Mexico, Harding Co., 6000 ft., R. Gustafson 2315.

Section JEJUNI.—*Astragalus jejunus* S. Watson: Nevada, Elko Co., Goshute Valley, 6.3 road miles NE of Hwy 80 on Hwy 30 to Montello, 1.2 miles E, A. Tiehm & M. Williams 9665.—*Astragalus limnocharis* Barneby: Utah, Kane Co., Navajo Lake, Ripley & Barneby 8596.

Section NEONIX.—*Astragalus johanniis-howellii* Barneby: Nevada, Mineral Co., A. Tiehm 8133.—*Astragalus mulfordae* Jones: Idaho, Washington Co., Crystal, Ripley & Barneby 6134.—*Astragalus peckii* Piper: Oregon, Deschutes Co., NW of Plainview, 3200 ft., Ripley & Barneby 6651.

RESULTS

All vascular bundles have an outer sclerenchymatous bundle sheath that is, in transection, at least as thick as the vascular tissue (Fig. 1–11). The persistence of the petiole can also be attributed to the inner sclerenchymatous bundle sheath, especially that of the median (= dorsal) bundle. A unicellular parenchymatous bundle sheath outside the outer sclerenchymatous bundle sheath can be found in most species investigated. This, in some cases, extends between the vascular bundles and can be a closed ring in transection (Fig. 2, 4, 5, 7–10).

Pith parenchyma as described for Old World *Astragalus* s.l. species (Engel 1990) is lacking in most species investigated here but is present in the section *Neonix* (Fig. 10, 11). In some species of section *Humillimi* one or two cavities are formed in place of the parenchymatous tissue between the lateral bundles and the median bundle (Fig. 2, 4, 5). Cortex parenchyma is always present. Its thickness is more or less constant around the whole petiole and follows the shape of the transection which is generally incised at the ventral side.

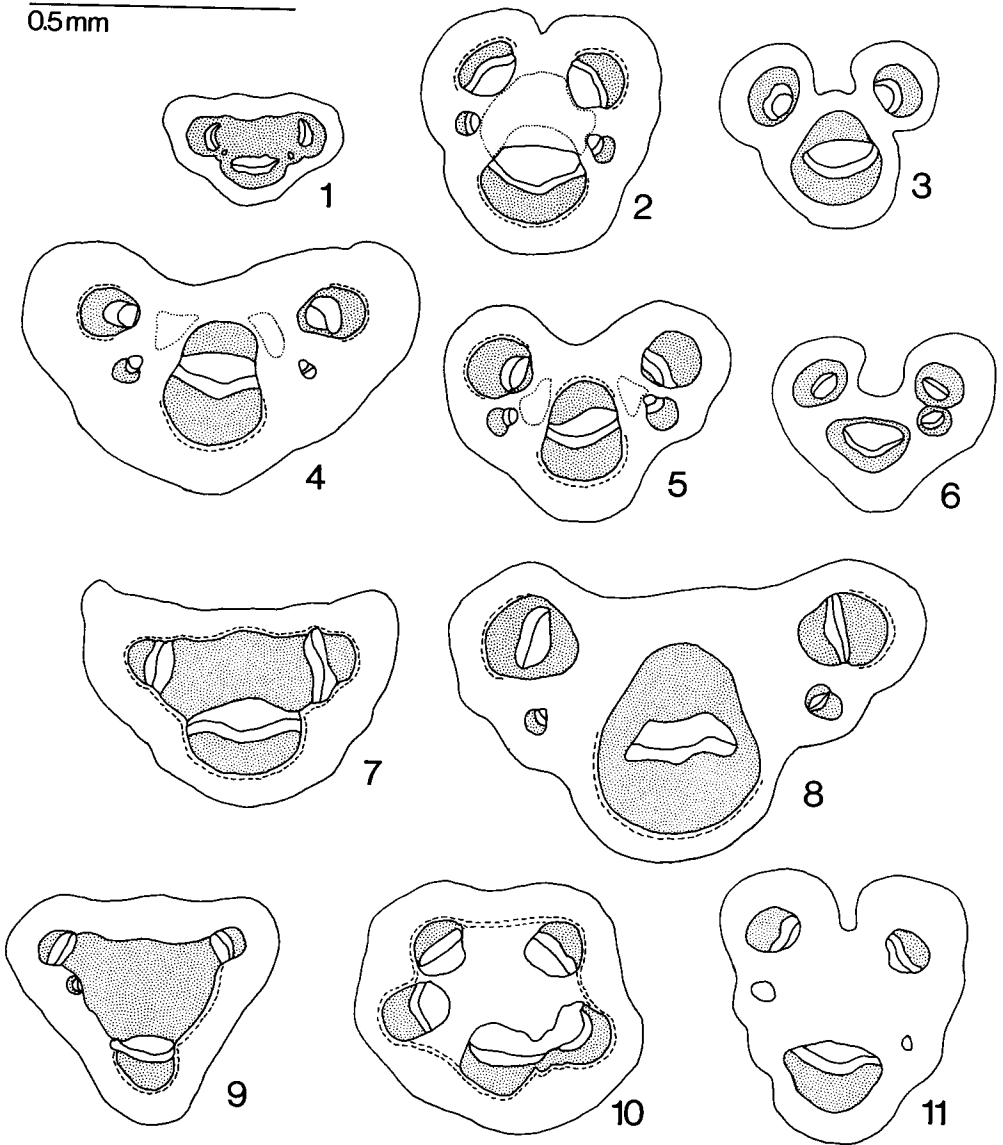


Fig. 1-11. Line drawings of selected transsections from the upper part of the petiole (dotted area = sclerenchyma; broken line = parenchymatic bundle sheath; dotted line = boundary of a cavity; white area in the vascular bundles: inner portion = xylem; outer portion = phloem; the rest of the white area = parenchyma).—1-5. Section *Humillimi*.—1. *A. humillimus*.—2. *A. troglodytes*.—3. *A. gilensis*.—4. *A. wittmannii*.—5. *A. cremnophylax*.—6-7. Section *Jejuni*.—6. *A. limnocharis*.—7. *A. jejunos*.—8. Section *Ervoidei* subsection *Submonospermi*, *A. kentrophyta* var. *elatus*.—9-11. Section *Neonix*.—9. *A. peckii*.—10. *A. johannis-howellii*.—11. *A. mulfordae*.

Unlike the majority of the Old World *Astragalus* s.l. species (Engel 1991), North American *Astragalus* species investigated do not have ventral vascular bundles in the petiole (Fig. 1-11). Rather there are the median (dorsal) bundles

and two major lateral bundles, and in the more distal part of the petiole as well as in the rachis there are two smaller lateral bundles. The nomenclature of the vascular bundles follows Howard (1979): M = median bundle; L = lateral bundles; $^{1/2}$ = decreasing hierarchy; $_{d/g}$ = right/left.

Despite some differences even between closely related species, the anatomical results are arranged in the order of the sections.

Section Humillimi

ASTRAGALUS CREMNOPHYLAX (Fig. 5), A. GILENSIS (Fig. 3), A. HUMILLIMUS (Fig. 1), A. TROGLODYTES (Fig. 2), A. WITTMANNII (Fig. 4).—All species have outer sclerenchymatous bundle sheaths that are as thick as or slightly thicker than the vascular tissue. An inner sheath is present in all species at the median bundle only. The sheaths are not closed. In *A. humillimus* the inner sclerenchymatous bundle sheath fills the whole center of the petiole. In *A. cremnophylax*, *A. troglodytes*, and *A. wittmannii* there are cavities in the center of the petiole above or at the sides of the median vascular bundle. The latter, with its inner sclerenchymatous bundle sheath, reaches the dorsal portion of the cortical parenchyma in four species, but not in *A. troglodytes*.

Section Jejuni

ASTRAGALUS JEJUNUS (Fig. 7), A. LIMNOCHARIS (Fig. 6).—*Astragalus jejunus* has the most lignified petioles in this section. In both species the outer sclerenchymatous sheaths of the median and of the two lateral bundles are as thick as the vascular tissue. They do not completely surround the vascular tissue in *A. jejunus* while in *A. limnocharis* the outer sclerenchymatous sheath is continued by a narrow sclerenchyma on the phloem side of the bundle. The largest amount of sclerenchymatous tissue in *A. jejunus* consists of the inner bundle sheath of the median vascular bundle that completely fills up the center of the petiole. In that place *A. limnocharis* has a small portion of unlignified pith parenchyma with a transition to the upper cortex parenchyma.

Section Ervoidei subsection Submonospermi

ASTRAGALUS KENTROPHYTA (Fig. 8), several varieties.—Only in some petioles—and mostly in the upper part—two smaller bundles ($L^2_{d/g}$ and $L^2_{g/d}$) were found in addition to the two larger lateral bundles ($L^1_{d/g}$ and $L^1_{g/d}$) and the very large median bundle. The median bundle is separated from the lateral bundles by several rows of parenchymatous cells. It usually extends from the dorsal to the ventral cortical parenchyma.

The sclerenchymatous sheath of the median bundle is closed in nearly all cases though the lateral part may only have two cell rows. The sheaths of the lateral vascular bundles are closed only in few cases. The inner and outer part of the sclerenchymatous bundle sheath are equal in the median bundle and approximately three times as thick as the vascular tissue. In the lateral bundles the outer part is slightly thicker than the inner part and both are equal to up to three times the thickness of the vascular tissue.

An outer parenchymatous bundle sheath was found at the peripheral side of the three major bundles in several varieties. A closed parenchymatous sheath around each of these three bundles was found in only a few transections.

Section Neonix

ASTRAGALUS JOHANNIS-HOWELLII (Fig. 10), A. MULFORDAE (Fig. 11), A. PECKII (Fig. 9).—The petioles of *A. peckii* are very similar to those of *A. jejuni* (sect. *Jejuni*, see the above description), and quite unlike the other two species of the section. Pith parenchyma in *A. johannis-howellii* and *A. mulfordae* covers approximately the same portion of the transection as all vascular bundles in sum. At the outer parts of the pith parenchyma there is a tendency towards lignification of the cell walls with transitions to the inner sclerenchymatous bundle sheath in *A. mulfordae*. In *A. johannis-howellii* four more or less equal lateral bundles are only slightly smaller than the median bundle while in *A. mulfordae* the larger lateral bundles (L^1_d and L^1_p) are half as big and the smaller lateral ones (L^2_d and L^2_p) are even much smaller than the median bundle.

The outer sclerenchymatous bundle sheath is more than twice as thick as the vascular tissue in *A. johannis-howellii* and *A. mulfordae*. The inner one is as thick as the outer one in the former and narrower in the latter. In both cases the sclerenchymatous sheaths are not closed.

In *A. johannis-howellii*, the parenchymatous bundle sheath completely surrounds the vascular cylinder (vascular bundles + pith) while in *A. mulfordae* it is only fragmentary.

CONCLUSIONS

Fundamental Differences between New World and Old World Astragalus s.l. Species

As described in detail by Engel (1990, 1991) the spines of Old World *Astragalus* and *Astracantha* species consisting of persistent petiole and rachis obtain their stability, for the most part, from the outer sclerenchymatous bundle sheaths. In addition, the pith parenchyma in the center of the spine has lignified cell walls and/or (depending on the infrageneric groups) the vascular bundles are closer and form a more compact and stable structure.

One can see from the results presented here that there is a fundamental difference concerning the ways in which both groups achieved the woody corpus of their petioles (and rachises). In contrast to the Old World *Astragalus* and *Astracantha* species, where the outer sclerenchymatous bundle sheaths are well developed and the inner ones only seldom are so, in North America *Astragalus* species the inner sclerenchymatous bundle sheaths are in most cases well developed and in some species contribute the largest part to the stability of the petiole. This can be deduced from transitions between the stages of evolutionary development of species usually considered to belong to the same section. In the section *Humillimi*, for instance, only one species, *A. troglodytes*, has no inner sclerenchymatous bundle sheaths (but at least a durable portion of parenchymatous tissue occurs between the median vascular bundle and the pith cavity), while in the other species, at least the median bundle has an inner sclerenchymatous bundle sheath that is as thick as the outer

one in *A. gilensis*, *A. wittmannii*, and *A. cremnophylax* and, in the extreme, fills the whole center of the petiole in *A. humillimus*.

This difference favors of the hypothesis of an early separation of the New World *Astragalus* species (at least the majority) from their Old World sister group.

Convergence of Persistent Petioli in North American Astragalus Sections

If one accepts the infrageneric classification of the North American *Astragalus* species by Barneby (1964), and if one does not overvalue the petiolar anatomical characters in using them for a new arrangement of the species, persistent petioles evolved several times convergently in different sections of the genus. Species with little sclerenchyma as well as species with a compact central sclerenchyma occur in three sections with dwarf, subcaulescent species (*Humillimi*, *Jejuni*, and *Neonix*), representing the evolution three times of this spinelike organ. In the fourth group examined, section *Ervoidei* subsection *Submonospermi*, comprising only one caulescent or subcaulescent species and its nine varieties, a distinct anatomical pattern evolved reflecting the more distant position of the group within the genus.

Convergence in the evolution of spines is also assumed for several groups of Old World *Astragalus* s.str. and *Astracantha* species (Engel 1990). However, only a detailed phylogenetic analysis would provide a reliable basis for this conclusion.

The Use of Anatomical Characters in Astragalus

There is more similarity between *A. humillimus*, *A. jejunos*, and *A. peckii*, representing three different sections of the genus *Astragalus*, than there is within the sections in the species investigated here. Thus, provided that the arrangement of species of Barneby (1964) reflects their phylogeny, the characters of petiole (and rachis) anatomy, particularly those of sclerenchyma, are not as useful for the infrageneric classification in the New World as in the Old World where a clearcut distinction of the sections from one another was achieved in most cases (Engel 1990, 1991). But, taking into account the complete set of characters provided by anatomy, an examination on a broad systematic basis could be expected to result in a valuable contribution to the classification of species, including those without persistent parts of the leaves.

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