Taxonomy of Agronomically Important Striga and Orobanche Species

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Summary

The taxonomy of the two most important parasitic genera in agriculture, *Orobanche* (broomrapes) and *Striga* (witchweeds) is summarized. The paper focuses on the most serious species and species clusters in these two genera. For witchweeds, discussion will center on *Striga asiatica* (L.) Kuntze and the putatively related species cluster (*Striga hirsuta* Benth., *Striga lutea* Lour., and *Striga elegans* Benth.); and on *Striga hermonthica* and related species [*Striga aspera* (Willd.) Benth., and *Striga gracilima* H. Melchior]; and *Striga gesnerioides* (Willd.) Vatke. (Synonyms: *Buchnera gesnerioides* Willd., *B. orobanchoides* R. Br., *Striga orobanchoides* (R. Br.) Benth., *Striga orchidea* Hochst., *Striga gesnerioides* var. *minor* Santapau).

Discussion of *Orobanche* includes the species cluster of *Orobanche crenata* Forskal, *Orobanche cernua* Loefl., and *Orobanche cumana* Wallr. and the cluster of *Orobanche aegyptiaca* Pers., *Orobanche ramosa* L., *Orobanche nana* (Reut.) Beck and *Orobanche mutelii* F. Schultz. Because of morphological reduction, parasitic plants exhibit tremendous reduction in their vegetative traits resulting in considerable variation. This limits the number of available characters used in distinguishing species within each group and pose taxonomic problems in parasitic plants especially species of *Orobanche*.

The accurate identification of parasitic plants comprises the first step in developing meaningful control strategies. Although most *Striga* and *Orobanche* species are not difficult to identify, the clusters of *Striga asiatica*, *Striga hermonthica*, *Orobanche crenata*, and *Orobanche aegyptiaca,* discussed in this chapter, are among the most confused species. Therefore we recommend that researchers have access to and use field guides that clearly distinguish these closely related species. All samples used in molecular studies and in other taxonomic studies must have vouchers and photos for verification.

La taxonomie des espèces de Striga et Orobanche important de point de vue Agronomique

Resumé

Le rapport explique la taxonomie de l'*Orobanche* et du *Striga,* les deux genres plus importants des plantes parasites dans l'agriculture. Le rapport se concentre sur les espèces et les branches d'espèces les plus sérieuses dans ces deux genres. Pour Striga, on mettra en relief la discussion sur le *Striga asiatica* (L.) Kuntze et les espèces putatives proches de cette branche (*S. hirsuta* Benth., *Striga lutea* Lour., et *Striga elegans* Benth.); et sur *Striga hermonthica* et spèces proches [*Striga aspera* (Willd.) Benth., et *Striga gracilima* H.

Melchior]; et *Striga gesnerioides* (Willd.) Vatke. (Synonymes: *Buchnera gesnerioides* Willd., *B. orobanchoides* R. Br., *Striga orobanchoides* (R. Br.) Benth., *Striga orchidea* Hochst., *Striga gesnerioides* var. *minor* Santapau).

La discussion sur l'*Orobanche* inclut les espèces *Orobanche crenata* Forskal, *Orobanche cernua* Loefl., et *Orobanche cumana* Wallr., mais aussi la branche de *Orobanche aegyptiaca* Pers., *Orobanche ramosa* L., *Orobanche nana* (Reut.) Beck et *Orobanche mutelii* F. Schultz. À cause d'une réduction morphologique, les plantes parasites montrent une énorme réduction dans les caractères végétatives ayant pour résultat une variation considérable.

Ceci limite le nombre de caractères disponibles utilisés dans des espèces pour leur différentiation dans chaque groupe et pose des problèmes taxonomiques des plantes parasites particulièrement d'Orobanche.

L'identification précise des plantes parasites est le premier pas pour développer des stratégies significatives de gestion. Bien que la plupart des espèces *Striga* et *Orobanche* ne soient pas difficile à identifier, les branches de *Striga asiatica*, *Striga hermonthica*, *Orobanche crenata*, et *Orobanche aegyptiaca,* discutés dans le présent rapport, sont souvent les espèces les plus faciles à confondre. Pour cette raison, nous recommandons que les chercheurs aient accès à l'utilisation des guides des champs qui montrent clairement la différence entre les espèces proches. Les échantillons utilisés dans les études moléculaires et dans les autres études taxonomiques devront avoir des bons et des photos pour la vérification.

I. *Striga* species

The genus *Striga* is predominantly African in origin and distribution. Of approximately 40 described *Striga* species, about 30 are endemic to Africa (Mohamed *et al.* 2001). Based on molecular evidence, Olmstead *et al.* (2001) placed the hemiparasitic genera traditionally included in the Scrophulariaceae including *Striga*, into the Orobanchaceae with the result that both of these genera--*Striga* and *Orobanche*-- are now in the same family.

Striga species are distinguished from other root parasites by unilocular anthers and bilabiate (two-lipped) corollas with a pronounced bend in the corolla tube. In some species the corolla is bent within the calyx teeth as in *Striga hermonthica*, in others it is bent above the calyx as in *Striga asiatica*. Other features used in distinguishing agronomically important species include indumentum types [pubescence, hirsute, and whether hairs are ascending or retrorse (pointing backward)]; stem shape (round, obtusely square, and square in cross section); leaf lobing and dentation (whether leaf margins are lobed, serrate or smooth); inflorescence types (spike, raceme, and the length of the inflorescence relative to the vegetative stem); number of ribs on the calyx tubes and length of calyx teeth relatives to tubes; and corolla color and type of indumentum on corolla.

The *Striga asiatica* cluster includes *Striga asiatica*, *Striga hirsuta*, *Striga lutea*, and *Striga elegans*. The fourth species in this cluster is morphologically unique and will be discussed later. It is important to emphasize that the Southeast Asian forms of *Striga asiatica* are not included in this analysis since their relationship to the African species complex is not known.

The name *Striga asiatica* is used to describe the noxious red-flowered *Striga* species which overwhelms sorghum, maize, and other cereal crops in Africa. Unlike *Striga hirsuta* and

Striga lutea, the *Striga asiatica* plants are profusely branched with leaves up to five cm long, longer than the plant internodes. Also, the bract in *Striga asiatica* is longer than the calyx. The number of the calyx teeth is five but in *Striga asiatica* it can be up to eight with teeth of unequal length. Overall, *Striga asiatica* is more scabrous (rough to the touch) than either of *Striga hirsuta* and *Striga lutea*.

The number of rows of hairs on the lower surface of the leaves and bracts is a unique and dependable feature that distinguishes *Striga hirsuta* from *Striga lutea. Striga hirsuta* has a single row of stiff hairs running along the margins and the mid rib of its leaves and bracts. *Striga lutea* has two rows of hispid hairs along the margin and mid rib of its leaves and bracts. *Striga lutea* plants are characteristically tall (up to 40 cm) and usually are unbranched or rarely with two branches. *Striga hirsuta*, on the other hand, is typically branched and the plants are the shortest (10 cm) in this cluster. Flower color can be of various shades of red and yellow and is not a reliable guide for species determination. *Striga asiatica* flowers are typically red with yellow throat. Flowers of *Striga lutea* are usually yellow, those of *Striga hirsuta* typically red but any of these species may occasionally have flowers of various shades of red, sometimes on the same plant. This is not unusual as the corolla color is controlled by few genes.

There are also distinct differences in the range of these species, though this may change overtime as in the following example of *Striga asiatica*. Until the late eighties and early nineties *Striga asiatica* was very largely confined to south and central Africa, normally south of the equator (*Striga asiatica* was also introduced into southeastern USA). In these areas *Striga asiatica* is usually restricted to agronomic hosts. Then it was reported from Kenya in the late 80's and Togo in West Africa in the early 90's. Our *Striga* surveys in West Africa and Sudan in the 80's and in Ethiopia as recent as 2007 show that *Striga asiatica* is not established as serious a problem north of the equator as it is in southern Africa, though it does occur sporadically on crops in several countries in West and East Africa. In November 2007 we surveyed *Striga* in Ethiopia. We reached as far south as Caves Omar and Megalo southeast of the Bale Region (6° 30'N, 41° 00'E), North to Mekele just south of the Eritrean boarder (13° 50'N, 39° 40'E), and east to Dire Dawa Region close to the Somali borders (9° 50'N, 42° 20'E). We encountered *Striga asiatica* once (and only two plants) in a demonstration farm. However, in 1985/1986 Chris Parker collected small forms of *Striga asiatica* with bright scarlet flowers widespread in Ethiopia attacking grasses without harming crops. In the south and east, however, *Striga asiatica* with various corolla colors ranging from brown, red, orange, and yellow were sporadically attacking sorghum and maize. Similar forms of *Striga asiatica* with various corolla colors were found attacking sorghum and maize in Ethiopia but with the scarlet forms attacking only native grasses (Sherif et al. 1987). *Striga asiatica* was not previously reported as a problem in Ethiopia until recently (Parker 1988). It was also known from a few collections in the Nile Delta in Egypt. This clearly suggests that the presence of *Striga asiatica* north of the equator is relatively recent compared to its establishment in southern Africa. As suggested by Berner and his team (1994), contaminated crop grains are the main source of *Striga* spread in Africa. *Striga hirsuta* and *Striga lutea* are distributed through much of Africa but common in west and central parts of the continent, especially the savannah grassland from Senegal to Ethiopia (Mohamed et al. 2001). While *Striga asiatica* is predominantly confined to crop fields, *Striga hirsuta* and *Striga lutea* are rarely problems on crops and are confined to natural grasslands.

Striga elegans is the fourth species in this cluster. However it is rarely confused with any of the other related species. It has brilliant scarlet flowers with yellow throats and dense compact inflorescences. Limited to south and east Africa, it reaches its northern range in Kenya and has not been reported from crops. Our research (Mohamed 1994, Mohamed et al. 1996) showed that it is more closely related to *Striga asiatica* than other species in the cluster. No molecular study has yet been done to determine the phylogenetic relationships of the *Striga asiatica* species group but it is more likely that *Striga elegans* is the wild relative of *Striga asiatica*, they are sympatric in southern Africa. A group of researchers from Old Dominion University, University of Georgia, and State University of New York-Oswego are studying the systematics of the genus *Striga* and its various cluster groups.

Striga hermonthica is the largest, among the agronomically important species, and the most destructive of all *Striga* species. It is common in Sahelian Africa from Senegal to Ethiopia reaching its southern limits in Congo and Tanzania and causes more damage in sorghum, maize, and millet than any other crop pest. Also it is sporadic as an invasive in the Nile Delta and Yemen (where it may be native). *Striga hermonthica* has great within-species variation which is expected as it is an obligate out-breeder (Aigbokhan et al. 1998, 2000). Also *Striga hermonthica* collected from different geographical regions exhibits variability (Mohamed 1994). This species has developed strains specific to sorghum and millet. These are morphologically similar but have consistent floral variations. The millet-strain has smaller dull pink corollas and the sorghum-strain has a larger pink corolla. Floral variations may discourage cross pollinations between these strains and further enhance the differentiation of populations in *Striga hermonthica* as evidenced in recent molecular studies in which populations of *Striga hermonthica* collected from sorghum, millet, and maize showed genetic differences, the maize strains were more closely related to the sorghum-strain than to the millet-strain (K. I. Mohamed, unpublished).

Striga aspera is also an out-crosser and frequently hybridize with *Striga hermonthica* (Aigbokhan et al. 1998, 2000). It attacks maize in Ethiopia; maize, rice, and sugarcane in West Africa (Mohamed et al. 2001). Some of the damage attributed to *Striga hermonthica* in West Africa may in fact be due to *Striga aspera* with expansion of agriculture into natural grasslands exposing crops to parasitism. It is reported only from the savannah north of the equator both as a native and weedy species especially in West Africa.

Striga hermonthica, *Striga aspera*, and *Striga gracilima* are morphologically similar forming a species cluster. *Striga gracillima,* known only from southern Tanzania, Malawi, and northern Zambia, does not attack crops and is rarely sympatric with the other two species. *Striga gracillima* is determined by its short corolla tube (6-8 mm), bent proximally and covered with dense stiff hairs but never glandular-pubescent. It has the smallest corolla lobes (upper lip 4mm long, lower lip 1-3mm long). *Striga aspera* is exceptional in having a glandular pubescent corolla which is bent distally above the calyx teeth, longer calyx teeth (3-5 mm) which are about the same length as the calyx tube, and narrow leaves ($\leq$ 2 mm). *Striga hermonthica* also lacks glandular-pubescent hairs on the corolla with hairs less dense than in *Striga gracillima*; corollas are much larger than in the other two species. *Striga hermonthica* is the tallest and most robust of all these witchweeds.

Striga gesnerioides is the only species attacking broad-leaf hosts. In addition to host preference, *Striga gesnerioides* tends toward holoparasitism reminiscent of *Orobanche*. *Striga gesnerioides* plants appear achlorophyllous (colorless) though they may have chlorophyll masked with other pigments. As a result, plants are white, shades of purple, and red --similar to *Orobanche* species. In addition, plants of *Striga. gesnerioides* have leaves reduced to scales-- a feature common to all *Orobanche* species.

Because of these characteristics, in addition to succulence, and tuftedness habit, *Striga gesnerioides* was never confused with other witchweeds. This species is the most widely distributed of all witchweeds. Its range includes Africa, Arabia, Asia, and the United States of America (where it has been introduced). *Striga gesnerioides* has developed host specific strains, the most important attack cowpea especially in West Africa and tobacco in Zimbabwe. Other reported host-specific strains includes *Indigofera* and *Tephrosia* in the Fabaceae Family, *Merremia*, *Ipomoea*, and *Jaquemontia* in the Convolvulaceae; and *Euphorbia* in the Euphorbiaceae. These host-specific strains do not damage crops but have the potential of becoming weedy, and agriculturalists should become aware of them. Some of these strains have unique distribution and known only in certain regions such *Merremia* strain reported only from southern Al Jazera Province in Sudan.

II. *Orobanche* species

Broomrapes are native to the Mediterranean region (North Africa, the Middle East, and southern Europe) and western Asia. Their range extends to similar climates in Asia, Africa, Australia, and North and South America where they also cause significant crop damage. Broomrapes are holoparasitic with more than 100 species (up to 170 spp according to Uhlich et al. 1995) but only a few of them are considered weedy. Important broomrape species include *Orobanche crenata* Forskal which is common on garden pea (*Pisum sativum* L.), lentil (*Lens culinaris* Medik), faba bean (*Vicia faba* L.), and garden vetch (*V. sativa* L.) and other hosts in the Mediterranean basin; *Orobanche cernua* Loefl. reported on carrot (*Daucus carota* L.), tomato (*Lycopersicum esculentum* Mill.), and tobacco (*Nicotiana tabacum* L.) in the Mediterranean basin extending eastward into Europe and Asia; *Orobanche cumana* Wallr. which is primarily a serious pest of sunflower (*Helianthus annuus* L.) in the sunflower-growing countries in the Mediterranean basin, Eastern Europe, and countries of the former Soviet Union; *Orobanche ramosa* L. is common on oil seed rape (*Brassica napus* L.) and many hosts in the Solanaceae including eggplant (*Solanum melongena* L.), tomato, tobacco, and potato in the Mediterranean region, Asia, Africa, Chile, and the United States; also reported on hemp and rape in western Europe; *Orobanche aegyptiaca* which has similar host range as *Orobanche ramosa* in Mediterranean region; *Orobanche mutelii* on tobacco in the Mediterranean region and Europe, Asteraceae in south Spain, Oxalidaceae in Crete and Lebanon; and *Orobanche nana* on Asteraceae, Solanaceae and Fabaceae in the Middle East (see also Parker 1991).

The holoparasitic life style of *Orobache* has resulted in dramatic reduction in morphological characters useful in field identification. Broomrape species have reduced leaves, almost uniform inflorescences, microscopic and uniform seeds, and very little variation in corolla color and shape, and often similar hosts. Taxonomists agree that the morphological features used in the classification of *Orobanche* are poorly defined. This paucity of characters to delimit species makes the development of meaningful keys difficult. Also because of the succulent nature of *Orobanche*, specimens deteriorate fast and preserve poorly.

Traditionally, the genus is divided into four sections of which Orobanche and Trionychon contain the noxious weedy species. Section Trionychon includes economically important species such as *Orobanche aegyptiaca*, *Orobanche ramosa*, *Orobanche nana*, and *Orobanche mutelii* while Section Orobanche contains *Orobanche crenata*, *Orobanche cernua*, and *Orobanche cumana*. These sections are mainly identified by the structure of the calyx and the presence or absence of bracteoles. Both Orobanche and Trionychon have zygomorphic calyces, but only Trionychon has bracteoles. Additional important distinguishing characteristics of the Section Trionychon are branched stems, an entire and campanulated (bell shaped) calyx, a blue or purple corolla, white anthers, and usually white stigmas. The Section Orobanche has a single stem; a calyx with two lateral segments; a white, yellow, brown, amethyst or red corolla; yellow, brown-grey or grey anthers; and yellow, orange, red, or purple stigmas (Pujadas-Salvà 2002, Plaza et al. 2004). Other features may include types of bracts, placentation, inflorescence types, cytology (chromosome number), host, and distribution. A combination of morphological characters rather than a single character are useful in identifying *Orobanche* species. Recent micromorophological (Andary 1994, Plaza et al. 2004), chemotaxonomical (Velasco et al. 2000), and molecular studies (Román et al. 2003, Manen et al. 2004) confirmed the integrity of these sections, some authors recognize them as separate genera.

Orobanche aegyptiaca, *Orobanche ramosa*, *Orobanche nana,* and *Orobanche mutelii* have similar morphologies and host ranges; these constitute a species cluster within the Section Trionychon. *Orobanche nana* and *Orobanche mutelii* were treated by some authors as infraspecific variants of *Orobanche ramosa. Orobanche aegyptiaca* can be identified by its relatively more branched stem, moderately dense to lax inflorescence, pubescent stamens, larger corolla (>25mm), and blue flowers. In contrast, *Orobanche ramosa* has smaller corollas (<20mm long), laxer inflorescences, glabrous stamens, and white to pale blue flowers at the base and blue distally.

Both *Orobanche ramosa* and *Orobanche nana* have a smaller calyx (4-7mm) and corolla (10-16 mm) distinguishing them from *Orobanche mutelii* with its larger calyx (7-15mm) and corolla (16-22mm). In addition, *Orobanche mutelii* has pubescent filaments and corollas, with pale blue-purple to violet corollas. *Orobanche ramosa* is distinguished from *Orobanche nana* by its height (17-35cm), longer and laxer inflorescence (10-25cm), and triangulate and acuminate calyx teeth. This contrasts with the usually dwarf plants of *Orobanche nana* (8-21 cm), which are less branched, and have shorter and denser inflorescences (5-7cm), and lanceolate to triangulate calyx teeth.

In addition to traditional taxonomy, Plaza et al. (2004) studied the micromophology of *Orobanche* seeds in the Iberian Peninsula and found enough variability to develop a key identifying *Orobanche* species including *Orobanche ramosa*, *Orobanche nana*, and *Orobanche mutelii*. In *Orobanche ramosa* the seed coat epidermal cells have unevenly thickened anticlinal walls while in the other two species these cells have evenly thickened anticlinal walls. *Orobanche nana* is characterized by smaller seed size (<0.40mm) compared to *Orobanche mutelii* (>0.40mm).

The second species cluster of agronomically important broomrapes is in the Section Orobanche which includes *Orobanche crenata*, *Orobanche cenua,* and *Orobanche cumana.* As expected, these species share many morphological characteristics such as the unbranched stem, absence of bracteoles, and calyx with two lateral segments. Among the three species *Orobanche crenata* has a unique morphology and easily separated from the other two species. *Orobanche crenata* has corolla lobes with erose or denticulate (irregularly notched) margins in contrast to the entire margins in *Orobanche cernua* and *Orobanche cumana.* Also, *Orobanche crenata* has dense inflorescence, fragrant flowers, and a long corolla (> 20 cm) which is usually white with purple veins.

Orobanche cumana is often confused with *Orobanche cernua.* While *Orobanche cumana* is almost exclusively confined to cultivated sunflower, *Orobanche cernua* is known from many hosts including wild plants. These two species differ in a number of ways. *Orobanche cumana* plants are taller (40-65cm), more slender, and with longer and laxer inflorescence than plants of *Orobanche cernua* (35cm tall). *Orobanche cumana* has entire, sometimes bifid calyx segments, glandular anther hairs, and white to pale blue flowers compared to *Orobanche cernua* which has bifid calyx segments, glabrous filaments, and blue, dark, violet or purple flowers. *Orobanche cernua* corollas are inflated at the base, upright, constricted in the middle, and bent at the tip while in *Orobanche cumana* corollas are not inflated (uniformly tubular) and markedly curved downward. The two species differ further in other morphological and ecological characteristics in addition to their oil and fatty acid contents (see Pujadas-Salvà and Velasco, 2000).

Overall, the genus *Striga* poses fewer problems in taxonomy and identification. The broomrapes, on the other hand, contain several species which require considerable effort to identify. Unlike the witchweeds, species of *Orobanche* have received considerable attention from taxonomists including a plethora of names of species, varieties, and even forms. The application of powerful molecular techniques used by several plant systematists working on the genus is providing increasing clarity of relationships and taxonomic levels.

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