Spring 1994

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Recommended Citation

Mohamed, Kamal-Eldin I.. "Biosystematics and Diversification in the Genus *Striga Lour.* (Scrophulariaceae) in Africa" (1994). Doctor of Philosophy (PhD), Dissertation, Biological Sciences, Old Dominion University, DOI: 10.25777/g8f8-c352
https://digitalcommons.odu.edu/biology_etds/95

BIOSYSTEMATICS AND DIVERSIFICATION IN THE GENUS *STRIGA* LOUR. (SCROPHULARIACEAE) IN AFRICA

by

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A Dissertation Submitted to the faculty of
Old Dominion University in Partial Fulfillment
of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY
ECOLOGICAL SCIENCES

OLD DOMINION UNIVERSITY

May, 1994

Approved by:

Prof. Lytton J. Musselman (Director)

ABSTRACT

BIOSYSTEMATICS AND DIVERSIFICATION IN THE GENUS *STRIGA* LOUR. (SCROPHULARIACEAE)

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Of the 34 taxa of *Striga* (29 species) that occur in Africa, 25 are endemic. Species diversity differs from region to region. The subtropical zone has 74% of the taxa including 41% endemics. Within this region, the West African part (from Senegal to eastern Nigeria) has 62% of the total taxa including 24% endemics. South of the equator the number of taxa is 56% of the total with 21% endemics, a proportion slightly less than that for West Africa. The biogeography of *Striga* clearly reflects the importance of the subtropical zone, particularly West Africa as centers of distribution. I recognize 29 species based on extensive herbarium and field studies. A new species from Angola is described. *Striga yemenica* previously considered an Arabian endemic, is reported from Ethiopia. This is the first African record.

Multivariate Statistics was used to compare the effects of the groups (species, geographical separation, host) on 13 vegetative and floral features. The affinities within the different species groups and in polymorphic species were determined based on a large number of randomly (using a random table) chosen plants that represent the range and the various hosts parasitized by a given species or host-specific strain. In general, the autogamous species which constitute the majority of the taxa, are more variable than the

allogamous. Moreover, most of the intra- and inter-specific variabilities within *Striga* can be attributed to geographical separation rather than to host factors. *Striga asiatica* is divided into three species based on morphology, phenology, host range, and biogeography. The taxonomy adopted in the present study in general agrees with that of Hepper (1960) who recognized five subspecies of *S. bilabiata.* I recognize *S. ledermannii* as a fifth subspecies of *S. bilabiata* and not as a separate species as advocated by some workers, and propose *S. linearifolia* as the sixth subspecies of *S. bilabiata.* Special attention has been given to the problem of the development of host specific strains in *S. gesnerioides*, and *S. hermonthica*, wide ranging and serious pathogens of numerous crops in the sub-Sahelian Africa. While these strains may have distinct morphotypes, I accord them no taxonomic status.

The Phylogenetic Analysis Using Parsimony (PAUP) and the Lundberg Rooting were adopted to infer the phylogeny of *Striga.* Thirty characters were polarized and ordered prior to data entry following the Outgroup Algorithms of Maddison *et al.* (1984). Results suggested that *Striga* favored the natural global changes in climatic conditions towards less rains, and the destruction and disturbance of the natural grassland savanna of Africa by man and his livestock. The annual habit was probably evolved from the perennial as it might be of great survival advantage so *Striga* can complete its life cycle in a fairly short time; allocation of more energy to reproduction (r-selection); production of large number of tiny seeds; and highly specific germination requirements. It seems that in the early stages of the diversification of *Striga* species, two separate evolutionary lines emerged and diverged in different directions. The first evolutionary clade gave rise to species that parasitize broad leaved plants and the second clade produced the cereal-*Striga.*

I favor the argument of allopatric over sympatric speciation for *Striga*. For the allogamous species, available evidences support the idea that the geographical separation is more important than host in contributing to population differentiation. In autogamous species, although the chances of self-pollination (intrinsic factor) are high, this alone cannot guarantee the reproduction isolation necessary for speciation.

بسم الله الرحمن الرحيم

التصنيف والتنوع في نبات البودة في أفريقيا

ملخص البحث

هنالك عدة مشاكل أدت لصعوبة تصنيف نبات البودة. أهم هذه المشاكل العجز لتصور أنواع البودة كعناصر متجانسة منحدرة من أصل واحد. وعليه فإن تلك التصنيفات المبنية على أساس إقليمي قاصرة وتفتقر إلى الشمول لأنها لم تأخذ في الحسبان هذه الحقيقة. المشكلة الثانية هي أن بعض أنواع البودة الواسعة الإنتشار هي أيضا متغيرة على حسب البيئة ويصعب التعرف عليها. بناء على الدراسة الميدانية التي أجريناها فقد أمكن التعرف على تسعة وعشرين نوعاً من البودة. هذه الأنواع تشمل النوع الجديد والذي إكتشفناه خلال فحص عينات البودة الواردة من أنجولا. ولقد أثبتنا أن البودة المسماة باليمنية والتي كان يعتقد أنها محصورة فقط في جنوب الجزيرة العربية توجد في إثيوبيا.

من هذه الدراسة نخلص إلى أن خمسة وعشرين نوعاً وفصيلة من تلك الموجودة في أفريقيا محلية ولا توجد خارج القارة. في داخل القارة، عدد الأنواع والفصائل الموجودة يختلف من إقليم لآخر. المنطقة المعروفة بشبه السافنا يتواجد بها ٧٤٪ من الأنواع والفصائل وتشمل على ٤١٪ من الأنواع المحلية. منطقة غرب أفريقيا (من السنجال إلى شرق نيجريا) والتي تعتبر جزءاً من شبه السافنا تمثل ٦٢٪ من الأنواع الموجدة و٢٤٪ من الأنواع المحلية. أما مناطق جنوب خط الإستواء فبالرغم من إتساعها الجغرافي إلا أن عدد الأنواع والفصائل الموجودة بها لايمثل أكثر من ٥٦٪ وعدد الأنواع المحلية يمثل ٢١٪ من تلك الموجودة في القارة. من هذا نخلص إلى أن التوزيع الجغرافي للبودة يعكس أهمية منطقة غرب أفريقيا كمركز إنتشار لباقي القارة والعالم.

إستعملنا علم الإحصاء لتحديد أهمية الدور الذي يلعبه كل من النوع والموقع الجغرافي ونوع النبات المصاب بالبودة في التأثير على ثلاثة عشر صفة ورقية وزهرية. إنتماء الأنواع المتشابهة في مجموعة معينة وإنتماء الفصائل المختلفة في النوع الواحد حُددت بناءً على دراسة مجموعة كبيرة من النباتات التى تمثل المواقع الجغرافية المتعددة والمستضيف للأنواع والفصائل المختلفة. كشفت النتائج أن الأنواع ذاتية التلقيح أكثر إختلافا من ثنائية التلقيح. كما كشفت أيضا أن العزل الجغرافي يلعب الدور الأساسي في صفة التغير. قسمنا البودة المعروفة بالآسيوية لثلاث أنواع بناءً على المظهر ووقت الإزهار والنبات المصاب والتوزيع الجغرافي. فيما يخص البودة المعروفة بذات الشفتين (بايلابياتا) فقد تبنينا تصنيف (هيبر) والذى يقر بوجود خمس فصائل في هذا النوع. أيضا هذا التصنيف أثبت أن (ليدرمانياى) تمثل الفصيلة الخامسة

وليست نوعا منفصلا كما إقترح بعض خبراء البودة. نقترح إضافة (لينيريفوليا) كفصيلة سادسة جديدة للنوع (بايلابياتا). أجرينا دراسة تفصيلية فيما يخص تصنيف نوع البودة الذى يصيب النباتات ذات الفلقتين (جسنرويدز) والنوع الذى يصيب المحاصيل ذات الفلقة الواحدة (هيرمونثكا) لأهميتهما. من المعروف أن النوعين واسعا الإنتشار ويسببان خسارة إقتصادية هائلة للمحاصيل في المناطق شبه الصحراوية الأفريقية. فبالرغم من أن هذين النوعين نجحا في إنتاج شبه فصائل ذات أشكال مختلفة إلا أننا لم نعط أشباه الفصائل هذه أي صفة كما فعلنا في حالة البودة الآسيوية لعدم توفر الأدلة الكافية.

إستعملنا طريقة التحليل لبحث الأصول العرقية لإختيار أقوى الإحتمالات التي توضح الصلات العرقية بين نباتات البودة. لهذا التحليل إخترنا ثلاثين صفة بيئية وفسيولوجية ومظهرية بعد أن حُددت إتجاهات التطور فيها. أوضحت النتائج أن مشكلة البودة تفاقمت مع التغيرات الجوية العالمية والتغيرات التي أحدثها الإنسان والحيوان في البيئة والناتجة في قلة الأمطار وقصر فصل الخريف. هنالك إحتمال أن الدورة الحولية تطورت من الدورة فوق الحولية نتيجة هذه التغيرات والتي من المحتمل أنها قد لعبت دوراً حيوياً في نجاح البودة الذي يظهر في مقدرتها على إكمال دورة حياتها في زمن قصير (فصل المطر) وتخصيص معظم الطاقة لإنتاج البذور بدلاً عن إنتاج الأوراق وإنتاج كمية كبيرة من البذور الصغيرة التي لا تنمو إلا بعد توفر المناخ الذي يضمن نجاح حياتها. يبدو أن المراحل الأولى لتطور البودة إنقسمت لفرعين أساسيين. الفرع الأول نتجت عنه أنواع البودة التي تصيب النباتات والمحاصيل ذات الفلقتين مثل اللوبيا والتبغ. والفرع الثاني والأكبر عدداً نتجت عنه الأنواع الأخرى التي تصيب النباتات والمحاصيل ذات الفلقة الواحدة.

نرجح أن تطور الفصائل والأنواع الجديدة في البودة ناتج عن العزل الجغرافي وليس العزل الذاتي الداخلي الذي يعتمد على مقدرة النوع في الحفاظ على التلقيح الذاتي عبر أجياله. في البودة مزدوجة التلقيح، هنالك دليل يوضح أن العزل الجغرافي هو العامل الأساسي في إحداث التغيرات التي تؤدي إلى التطور. أما في البودة ذاتية التلقيح فلا يوجد دليل مباشر على ذلك ولكن يبدو أن التلقيح الذاتي وحده لايكفي لضمان عدم تبادل جينات من نبات آخر وعليه فلا يمكن لهذه الأنواع أن تتطور إلا عن طريق العزل الجغرافي .

DEDICATION

TO ZENAB, ABIER AND SHARIF
WITH MY ETERNAL DEVOTION AND LOVE

ACKNOWLEDGEMENTS

I specially wish to thank Professor Lytton Musselman my mentor, advisor and friend who gave me not only knowledge of scientific research, but also the valuable insight in the way of life. I owe him my greatest gratitude *Shookrun gezeelun,* Lytton! I also want to thank members of my guidance and dissertation committees for their sincere assistance and encouragement throughout this project. I am greatly indebted to Drs. Robert Eplee and Kneeland Nesius.

I would like to express my recognition and appreciation to the Department of Biological Sciences (ODU) and the University of Khartoum for financial assistance. Portions of this work were supported by the Office of International Cooperation and Development, US Department of Agriculture, Project number 58-319R-5-0006. Special thanks to the faculty and staff of the Department of Biological Sciences for their cooperation and support, the Department Chairman Dr. Daniel Dauer, the Program Director Dr. Frank Day, Drs. Rebecca Bray, Ray Birdsong, John Holsinger, Harold Marshall, Mrs. Rebecca Norris at the Whiteville Methods Development Center and Professor Faiz Bebawi of the University of Khartoum.

My sincere appreciation and thanks are due to the Director and staff of the Whiteville Methods Center for their friendly support during my internship and experimental stages of the project. Finally, and most important of all, I wish to thank my family, friends and colleagues for providing the assistance and encouragement throughout this study.

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CHAPTER ONE

AN OVERVIEW OF *STRIGA* BIOSYSTEMATICS, BIOLOGY, AND ECOLOGY

INTRODUCTION

The genus *Striga* (Scrophulariaceae), known by the English common name witchweed, has an estimated number of between 30 and 50 species depending on the author (Musselman *et al.* 1979, Hepper 1984, Musselman and Hepper 1986, Musselman 1987, Raynal-Roques 1987, 1991). Disagreement on the number of species in the genus suggests the need for further taxonomic work (Musselman 1984).

Although the parasitic behavior of all *Striga* species has not been documented it is safe to assume that all species are parasitic (Musselman 1987). In addition to the normal germination requirements of angiosperm seeds, *Striga* seeds require a period of conditioning at specific moisture and temperature regimes as well as a host stimulant. Preconditioned seeds not exposed to the proper stimulant revert to their original dormant condition when dry. This chemical stimulant is exuded by the roots of host and some nonhost plants. The *Striga* seeds germinate and parasitize the host only when a host's root is available within a certain distance from the seeds. Once they germinate, the seedlings attach themselves to the host root system via the organ of parasitism (haustorium) which forms the biological bridge between the host and the parasite.

Striga contains a low level of chlorophyll (Tuquet *et al.* 1990, Tuquet and Salle 1991) which reduces its photosynthetic capacity (Salle *et al.* 1987, Shah *et al.* 1987, Press *et al.* 1987a) and thus depends upon its host for the supply of carbon, water, minerals, and hormones (Parker 1984). *Striga* is considered one of the most serious constrains to food production in the semi-arid tropics. An annual average cereal grain losses have been estimated at about 40% across Africa (Lagoke *et al.* 1991). Production in highly affected countries like Sudan and Ethiopia suffers even more damage and is estimated at 65-100% (Bebawi and Farah 1981, Ejeta *et al.* 1992) and in India, an annual loss of 25,000 tons of sorghum has been estimated for the country (Setty and Hosmani 1981, Doggett 1988). Like other Scrophulariaceae that exhibit differences in vigor with different hosts (Atsatt and Strong 1970, Musselman and Mann 1977), reduction of crop yield may vary depending on *Striga* species. The dramatic impacts of *Striga* on its host growth were suggested to be due to a toxic or pathological effect (Parker 1984), reduction of gibberelin and cytokinin levels, by up to 90% in S. *hermonthica*, (Drennan and El Hiweris 1979), and the perturbation of the host growth mechanisms (Ramaiah and Parker 1982). This manifests itself in the host by dwarfing, yellowing, increased root production, reduced yield of grains, and in extreme cases death of the host. The problem of *Striga* is compounded by its high seed production (up to 500,000/plant) and the ability of the seeds to remain viable for up to 20 years (Doggett 1988).

BIOSYSTEMATICS OF STRIGA (SCROPHULARIACEAE)

The Scrophulariaceae is a large cosmopolitan family with about 250 genera and 5000 species. Members of the family are characterized by a superior ovary, actinomorphic or zygomorphic corollas, absence of stipules, and usually the presence of fewer stamens than corolla lobes. The current classification of Scrophulariaceae, in general, follows that of Wettstein (1891) who divided the family into the Pseudosolaneae, Antirrhinoideae, and Rhinanthoideae. These divisions are often presumed to be subfamilies although they were not designated as such by Wettstein. The Pseudosolaneae were given the initial position in the family (assumed to be primitive), apparently to emphasize their supposed affinities with the Solanaceae based upon the nearly actinomorphic corolla, alternate phyllotaxy, and the presence of five stamens in *Verbascum* (Thieret 1967). Robyns (1931) presented evidence that the long accepted affinity of the Verbaceae with the Solanaceae is apparent rather than real, and Pennell (1935) regarded the features of Verbaceae such as the nearly actinomorphic corolla, the frequent presence of five stamens, and the alternate leaves as derived rather than ancestral (primitive) features in the Scrophulariaceae, i.e. Verbaceae are not the "primitive" members of the family. Since the status of the subfamily Pseudosolaneae was based on the presumed affinity with the Solanaceae which proved to be artificial, Pennell (1935) abolished it and placed the three tribes of Wettstein's Pseudosolaneae (Verbaceae, Leucophylleae, Aptosimeae) in the subfamily Antirrhinoideae; the second subfamily Rhinanthoideae was left unchanged. This division of the family Scrophulariaceae into two subfamilies was based on a single feature, that is the relative position of the corolla lobes in aestivation. In the subfamily Antirrhinoideae the posterior corolla lobes are in an external position in aestivation as contrasted with the external position of the anterior corolla lobes in the Rhinanthoideae. Each subfamily was further divided into three tribes. The Antirrhineae, Cheloneae and Gratioleae were included in Antirrhinoideae, and the Digitaleae, Buchnereae and Euphrasieae were included in the subfamily Rhinanthoideae (Pennell 1935).

Search for the initial tribe (that shows the most plesiomorphic characters) took place within the Antirrhinoideae since the Rhinanthoideae appear to be the derived group based on the specialized habits of parasitism and elaborate zygomorphy. The Gratioleae were found to have the simplest seed structure, separate stigmas, usually septicidal capsule dehiscence, usually distinct sepals, racemose inflorescence, and opposite phyllotaxy and were therefore assigned to the initial position in the family (Pennell 1935).

Among the Rhinanthoideae, the Digitaleae retain the most plesiomorphic traits of distinct stigmas and septicidal dehiscence of the capsule. The Euphrasieae are considered to be the most derived tribe because they are specialized root-parasite, with loculicidal dehiscence, highly zygomorphic corolla, and laterally united sepals (Pennell 1935). The Buchnereae are intermediate between the two tribes. They are mainly tropical and characteristically specialized root-parasites as Euphrasieae, but share with the Gratioleae a number of presumably plesiomorphic characters: open throated zygomorphic corollas, five distinct sepals, similar racemes, and opposite foliage leaves. However, the dehiscence of the capsule has become loculicidal and the stigmas nearly always united.

Within the parasitic Scrophulariaceae, many genera are hemiparasitic but can hardly be recognized as so due to their broadly developed leaves and green colors as in *Cycnium, Melasma*, and *Aureolaria*. At the other extreme are the leafless genera such as *Harveya* and *Hyobanche* that completely lack chlorophyll and are obligate parasites. Intermediate taxa such as *Striga* show the gradual transformation from one extreme to the other (e.g. *Striga macrantha* and *S. gesnerioides*). Being root parasite, Wettstein (1891) placed *Striga* in the tribe Buchnereae, subfamily Rhinanthoideae, and considered it among the most advanced members of the scrophulariaceae. Only *Harveya* and *Hyobanche* are considered more derived than *Striga* due to the lack of chlorophyll and obligate parasitism.

The genus *Striga* was erected by Loureiro (1790). It is separated from other Rhinanthoideae by the unilocular anthers and bilabiate corollas with a pronounced bend in the corolla tube. This bend distinguishes the genus from the presumably related *Buchnera* (Musselman 1980) in which many species of *Striga* were first included. Other features of witchweeds include the herbaceous habit, dust-like seeds, and parasitism.

Based on the number of ribs on the calyx tube, Wettstein (1891) divided the genus into two sections, the Pentapleurae which have a five-ribbed calyx, and the Polypleurae characterized by approximately 10 ribs. Later Engler created the section Tetrosepalum to include members with approximately 15-ribbed calyx. As clarified by Musselman and Ayensu (1984), the reference is to the ribs which terminate at the tip of one of the five lobes, rather than terminating in a sinus between calyx lobes. Saldanha (1963) has noted that the number of ribs is not always consistent but no further work has been done to elucidate on the adaptive significance of this feature.

As in several other genera of parasitic angiosperms that exhibit reduction of vegetative parts, floral characters are the main basis for taxonomic characters in *Striga*. The characters used to key species include the number of ribs on the calyx tube, the way in which flowers are borne (dense heads or simple racemes), corolla color, dentation of leaves, and size characteristics (Musselman and Ayensu 1984, Musselman 1987). Other features are indumentum, relative sizes of calyx and of corolla tubes and sizes of bracts and bracteoles subtending each flower.

THE CENTER OF ORIGIN OF THE CEREAL-STRIGA

The theory of the probable center of origin and spread of the cereal-*Striga* was first proposed by Rao and Musselman (1987). They suggested that with the introduction of agriculture and domestication of cereal crops, the cereal-*Striga* species which were associated with cereals also became domesticated. In its new status sorghum (the crop with which the parasite is usually associated in its evolutionary history) appeared to be its primary host. They based this hypothesis on the fact that it is in sorghum among the various hosts of witchweeds that resistance mechanisms are best known. *Striga* appeared to have originated in the same region where sorghum originated, the Sudano-Ethiopian region (Musselman 1980, Harlan and Stanler 1976, Mulatu and Kebede 1991), and moved along the routes of introduction of its host from the Sudano-Ethiopian region to southern Africa, India, and elsewhere.

The nature of pollination biology in *Striga* may have influenced the spread of the genus. The self-fertilized species such as *S. asiatica* are far more widely distributed than the cross-fertilized species such as *S. hermonthica*. This is because a single plant of self-fertilizing species in isolation has a better chance of establishing a population than does a single plant of a cross-fertilizing species.

ECOLOGY OF STRIGA

Most of the *Striga* species are annuals with a relatively short life cycle. They appear a few weeks after their hosts are established following the commencement of the rain, and then set seeds and die at the end of the rainy season. The phenology of *Striga* differs from species to species and may also be habitat- or host-dependent. For example, in the South Kordofan area of the Sudan, Musselman and Hepper (1986) and Musselman *et al.* (1991), report that the first species to appear is *S. forbesii*, followed by *S. passargei, S. aspera, S. gesnerioides, S. asiatica,* and lastly *S. hermonthica*. In the same region *S. asiatica, S. aspera, and S. gesnerioides* were all flowering at the time when *S. hermonthica* was just emerging. Few *Striga* species are perennials. They produce a fleshy underground stem that bears scale leaves from which a new stem arises annually with the onset of the rainy season. Some of the perennial species include: *S. latericea, S. aequinoctialis, S. baumanii,* the six subspecies of *S. bilabiata, S. primuloides, S. fulgens, S. gastonii,* and *S. lepidagathidis*. Other species occasionally behave as perennials when permitted by their hosts. For example, all host-specific strains of *S. gesnerioides* are annual except the one parasitizing *Euphorbia*. Generally, I observed that annual parasites are leafy and faster growing than perennials. Because parasitic weeds depend on their hosts for survival we should not put too much emphasis on this feature at least when decisions are to be made on the phylogeny of the species.

The genus *Striga* is basically tropical and subtropical in distribution. Worldwide, it occurs between latitudes 30° N and 30° S reaching its northern limits in the Carolinas at 34° N. In Africa, the genus is typically restricted to the region between 14° N in the Sahel and 34° S in Cape province with *S. aspera* and *S. hermonthica* occupying the most northern limits and *S. bilabiata* and *S. elegans* occupying the most southern limits. Within this region, *Striga* is absent in areas of high rainfall except *S. hallaei* which is restricted to the openings and semi-shaded habitats of the rain forest in Gabon and Congo (Raynal-Roques 1969). There is no record of the presence of *Striga* north of latitude 14° N except *S. gesnerioides* in the Red Sea hills near Erkowit (Sudan) at 19° N and the local presence of *S. asiatica* and *S. hermonthica* in the Nile Delta at approximately 31° N. Generally, *Striga* can grow in areas with annual rainfall as low as 25 cm and as high as 150 cm with a decrease in the severity of the infestation in areas with high rainfall. Optimum temperature for seed germination of the species studied was found to be between 30° C and 40° C, with no germination at 15° C or lower or at 45° C or higher (Musselman and Ayensu, 1984). Optimum temperature for seed germination is affected by a number of factors such as soil moisture content (Babiker *et al.* 1987), temperature and the length of conditioning period (Patterson *et al.* 1982), and soil type. Bharathalakshmi and Jayachandra (1984) concluded that temperature effects on conditioning and germination of the three strains of *S. asiatica* they studied were correlated with climatic conditions at their sites of origin, suggesting some degree of local adaptation.

The weedy *Striga* species tolerate a relatively wide range of climatic and soil conditions. They grow just as well on rice under wet soil conditions as they do on grasses and millet on arid land with only 125 - 250 millimeters of annual rainfall (Verma and Bajpai 1963). In general, low soil fertility, nitrogen deficiency in particular, lighter well drained soils, and water stress accentuate the severity of witchweed attack in terms of damage to the host (Andrews 1945, Ramaiah 1981, Bebawi 1984, 1987). These are typically the environmental conditions under which *Striga*-hosts are grown in the semi-arid tropics on relatively light soils where rainfall varies in intensity and distribution. *Striga* causes less damage to hosts growing on fertile deep soils.

Some species show habitat preference. For example, S. *forbesii* prefers open wet areas and for this reason it is a problem in some irrigated crops like sugar cane. *Striga asiatica* is most common on light, sandy soils in southern Africa (Hattingh 1954), East Africa (Doggett 1965), and the United States (Nelson 1958). *Striga hermonthica* is a weedy species that is not particular to soil type or pH and reported to be abundant on shallow course structure soils in West Africa (Stoop *et al.* 1983) as well as on heavy soils in East Africa (Bebawi 1984, Ogborn 1987).

Typically, the genus prefers sunny, naturally disturbed grassland habitat in the semi-arid regions. Under these conditions the ruderal species like S. *asiatica,* S. *brachycalyx, and* S. *aspera* flourish and are found in high frequencies especially on the edges of small pools (depressions) within the grassland. Although this is the typical habitat of the subspecies of S. *bilabiata* they never are found in high frequences.

BIOLOGY OF STRIGA

Breeding systems:

Most *Striga* species are autogamous. This breeding pattern has been well documented for *S. asiatica* and *S. gesnerioides* (Musselman *et al.* 1982). Here, the pollen grains form a massive sticky layer that covers the stigma and possibly eliminates the chances of cross pollination. The transfer of pollens probably takes place even before the flowers open. Inbreeding in these species results in homogeneity of the population's morphology, genetics, and finally the development of host specific strains as is shown for *S. gesnerioides*, or the development of subspecies as evident in *S. bilabiata*. The second breeding strategy (allogamy) is common in *S. hermonthica* (Safa *et al.* 1984) and *S. aspera* (Musselman *et al.* 1991). The two species might share common insect pollinators at least in parts of Africa (Safa, personal communication). The work of Knepper (1989) and Knepper *et al.* (1991) show that *S. forbesii* produces two kind of flowers (distylous). In the first, the flowers have styles strongly exerted from the corolla tube exposing the stigma with a greater chance of being cross-pollinated. In the second form, stigmas are usually found amongst or just below the epipetalous stamens with increasing possibilities of self-pollination. However, the first form is rare and constitutes only about 3% of the total flowering population (Knepper 1989, Knepper *et al.* 1991)

Host range:

The genus *Striga* parasitizes a wide range of host plants. Among the cereal-*Strigas*, *S. hermonthica*, *S. asiatica*, and *S. forbesii* are considered the most important parasites in terms of damage done to agronomic crops. Each of the three species can attack various crops in different ecological zones. Affected agronomic crops include the different species of *Sorghum*, *Zea*, *Oryza*, *Saccharum officinarum*, *Arena sativa*, and *Triticum* *vulgare*. Several other wild grasses in fallow lands and field bunds, such as species of *Andropogon*, *Aristida*, *Brachiaria*, *Digitaria*, *Echinochloa*, *Eragrostis*, *Panicum*, *Paspalum* and *Setaria*, are also attacked by the various *Striga* species. On the other hand S. *gesnerioides*, S. *gastonii*, and S. *lepidagathidis* parasitize broad-leaved hosts. *Striga lepidagathidis* and S. *gastonii* have been reported to attack *Lepidagathidis* species (Raynal-Roques 1987). *Striga gesnerioides*, the only economically important species in this group, has a wide host range including *Vigna*, *Nicotiana*, *Ipomoea*, *Tephrosia*, *Euphorbia*, weedy Convolvulaceae, and *Lepidagathidis*. It is also reported to parasitize *Arachis hypogea*, *Glycine max*, *Medicago sativa*, and *Lupinus termis*.

Host specificity:

Host specificity is thought to be based on the need for germination stimulant, attachment, penetration, and the overall nutritional requirements of the parasite (Ramaiah 1987, Ejeta *et al.* 1992) and accordingly the needs of a specific parasite determine its host. For example S. *gesnerioides* has developed four well defined host-specific races, one each for *Euphorbia*, *Vigna*, *Nicotiana*, and the weedy Convolvulaceae. However, Wilson-Jones (1955) and Rao and Musselman (1987) acknowledged that host specificity broke down when cropping systems changed and favored the evolution of new "strains" adapted to new crops introduced into the area. Ramaiah (1984) studied host specificity in S. *hermonthica* parasitizing sorghum and millet and concluded that specificity is the outcome of the intensity with which a particular host crop is grown at the exclusion of the others, thus creating a reproductive barrier between sorghum- and millet-*Striga*. But as Ramaiah (1984) has stated, the genetic changes have not been fixed in these populations.

Intraspecific variability:

Striga is a genus of cosmopolitan distribution. As stated earlier, it grows well under a wide range of climatic and soil conditions. It is natural for the genus therefore, to show great morphological variations, especially in the widespread weedy species. Within the same species there are variations in vigor, branching habit, plant height, leaves, bracts, and bracteoles sizes, corolla shape and color, hairiness, and capsule size. Variation could be attributed to spatial distribution and climatic differences, soil characteristics, and hosts. These variations have caused some taxonomical difficulties.

EVOLUTION IN THE GENUS STRIGA

Parasitic plants form haustoria (specialized roots) which are defined by Kuijt (1969) as the physiological bridges that join host and parasite i.e. the specialized channels through which nutrients flow from one partner to the other. The origin of the haustorium in parasitic flowering plants is unknown but the topic has been reviewed by many authors (Kuijt 1969, 1977; Atsatt 1971, 1973, 1987; Atsatt and Hansen 1978; and Atsatt *et al.* 1978).

It is commonly assumed that haustoria are modified roots that evolved via the accumulation of selected mutation. In environments where resourses are limited, parasites are at an advantage compared to autotrophic plants because hosts provide the otherwise unavailable water and organic compounds. Also, the production of haustorium saves the parasite from producing a root. An alternative concept to mutation hypothesis is that haustoria evolved from pathogenically induced neoplasms (Atsatt 1973), a hypothesis which can be tested.

In search for the origin of the haustorium, root grafting has occasionally been suggested. However, Kuijt (1969) excluded it because root grafting is typical of many tree species, and all the non-Santalalean parasites are herbaceous. Root grafting is a phenomenon of secondary growth of older roots and therefore, it is difficult to think of the "primitive" haustoria in such areas rather than in the subapical parts of roots where haustoria usually originate. It is known that mycorrhizal fungi also act as an absorbing and conducting system between two vascular plants analogous to the haustorium. But since mycorrhizae are not reported for any kind of parasitism and the known autotrophic relatives of most parasites (Olacaceae, Scrophulariaceae, Convolvulaceae, and Lauraceae) are not among mycorrhizal families, Kuijt (1969) and Atsatt (1973) conclude that fungi are probably not involved in haustoria formation in annual parasites. Atsatt (1973) proposes a testable hypothesis, the Pathogen Model as a possible origin of haustoria. He suggests that haustoria were first produced in response to microbial parasitism, analogous to root nodules, and subsequently modified for the acquisition of water and nutrients from autotrophic hosts. In 1987, he developed circumstantial evidence supporting his pathogen model in which he considers the haustorium as a symptom of a highly regulated and beneficial disease. He stresses the fact that haustoria have more features in common with abnormal plant growth than they do with normal or "modified" roots.

No one has studied the evolutionary mechanisms in the genus *Striga* and there is very little information available on the phylogenetic relationships among the Rhinanthoideae and their affinities to the Antirrhinoideae and the Orobanchaceae. Among the Rhinanthoids, which are all root parasites, Wettstein (1891) considered *Striga* as one of the most derived genera and only *Harveya* and *Hyobanche* (both evolving towards the non-chlorophyllous Orobanchaceae) are more derived than *Striga*. Recently, Minkin (1987) provided evidence to support this notion. He used pollen grain ultra-structure to construct a dendrogram in which the genera *Lathraea*, *Harveya*, and *Hyobanche* have an intermediate position between the Rhinanthoideae and the Orobanchaceae and concluded that the three genera cannot be assigned to either family. Also Minkin's results showed that *Buchnera* and *Striga* are closely related taxa confirming Musselman's (1987) hypothesis.

As previously noted, the Sudano-Ethiopian region is the probable center of origin of *Striga* and its host. This hypothesis is supported by the high number of endemic species which represents 41% of the total number of taxa worldwide. The genus moved from its center of origin to different parts of Africa and eastward across the Red Sea and the Indian Ocean to the Arab Peninsula, Asia, and Australia where it underwent genetic isolation and further diversification. The fact that almost all witchweeds are autogamous could have increased the genetic separation of the newly established populations as well as their successful establishment in the new habitats.

BACKGROUND FOR THE STUDY

The genus *Striga* is predominantly an African taxon that reaches its greatest diversity and species richness in the semi-arid tropics. Three species, *S. hermonthica*, *S. asiatica*, and *S. gesnerioides*, cause serious damage to food crops. Of these, *S. asiatica* and *S. gesnerioides* are themselves among the most variable species. Despite the great economic importance of witchweed, little attention has been paid to the systematics of the genus as a whole, especially to the relationship among species. Such lack of systematic knowledge has resulted in misidentification and could lead to failure in applying the correct control measures and quarantine restrictions to confine and prevent the spread of witchweeds to new areas. As Hepper (1973) has stated it is a waste of time and skill for useful research to be conducted on unidentified or misidentified plants. There has been no comprehensive treatment of the genus and Musselman and Ayensu (1984) and Musselman (1987) have stressed the need for considerable field work and extensive studies to provide meaningful keys and description of all species to help resolve nomenclatural problems and present accurate determinations of species. The purpose of the key is to facilitate identification of a specimen and serves as a tool for taxonomic analysis since in their preparation one must select, evaluate, and arrange taxonomic characters.

Information on the distribution of *Striga* is very general and scattered. *Striga* species were assumed to be geographically speciated and thus comparing the distribution of closely related species may partly explain their phylogenetic relationships, and comparing the distribution and the inconsistent behavior (ruderal/weedy) of some species may uncover the physical and biological factors causing the different behaviors. Also, knowledge of species distribution is of great importance to food production, parasite management, and future planning. Unawareness of the presence of the parasite in certain localities may pose difficulties for future expansion of susceptible food crops. An example is S. *latericea*. This species was found to be a serious problem on sugar cane in Ethiopia although not previously known as such. Moreover, applications of successful quarantine measures depend on knowledge of the spatial distribution of the parasite.

In the genus there are some species that form complex groups. Examples are the complexes of S. *asiatica* and S. *elegans*, S. *hermonthica* and S. *aspera*, and S. *bilabiata*. There is confusion regarding the identity of these species which presents difficulties even to taxonomists. Taxa within each complex are morphologically similar and minor differences such as corolla colors, the degree of hairiness, sizes, and sometimes hosts are used to distinguish among them. Their genetics which may provide the bases for the observed morphology and compatibility (ability to interbreed) have not been fully investigated.

Although most *Striga* species are autogamous, only few of them are polymorphic. For example, S. *asiatica* and S. *gesnerioides* are considered to be among the most variable species. *Striga asiatica*, the most widely spread species, has at least three morphotypes with two different corolla colors: red and yellow. However, the flower color is not considered significant enough to justify recognizing them as separate taxa; more study is needed to determine their relationships. *Striga gesnerioides* on the other hand has at least four host-specific strains one each for *Vigna*, *Nicotiana*, *Euphorbia* and weedy Convolvulaceae. The taxonomic status of these "forms' remains to be investigated.

Cladistic analysis can serve as a useful tool to infer the phylogenetic relationship among *Striga* species. Cladistics became an important force within systematic biology following the English translation of Hennig's "Grundzuge einer Theorie der Phylogenetischen Systematik" (1950), which was updated in 1966 as "Phylogenetic Systematics." The basic principle defining cladistic theory is that natural groups are recognized by uniquely derived characters, termed synapomorphies, and only natural groups defined by synapomorphies can be monophyletic (i.e. descended from a common ancestor) are to be admitted into Linnaean classification schemes.

That biologist can cluster derived similarities (and therefore taxa) hierarchically confirms an evolutionary history for life. Two comparative methods are now used to evaluate character polarities, the use of the Ontogenetic Criterion and the Outgroup Criterion. Both approaches seek to establish the direction of transformation from a character that is "primitive" to one that is derived.

CHAPTER TWO

SPECIES DESCRIPTION, DISTRIBUTION, AND KEY TO STRIGA SPECIES

INTRODUCTION

The genus *Striga* is a natural taxon, with members resembling each other in morphological, ecological, and phenological features. They occupy a similar environment and parasitize the same group of plants in the arid and semi-arid tropics of the Old World. Typically, *Striga* species are annual, hirsute, or scabrid, stiffly erect, herbaceous plants. The leaves are opposite or subopposite and reduced to small scales at the base of the stem in most species. The inflorescence is a dense or lax spike. The calyx is tubular, with usually five equal or subequal teeth. The corolla is divided into a cylindrical tube and expanded two-lipped limb, the lobes of which are fused at least at their bases to form a bilabiate corolla. Stamens are four, didynamous, and with unilocular anthers. The style is terete, elongate, and persistent. Seeds are tiny, dust-like, with prominent ridges. Germination is hypogeal and cryptocotylar (except in S. *angustifolia*).

Striga is separated from other genera in the subfamily Rhinanthoideae by the unilocular anthers and the bilabiate corollas with a pronouned bend in the corolla tube. This bend distinguishes *Striga* from its apparently close relative, *Buchnera*. In fact, at least ten species of *Striga* were originally described as species of *Buchnera*.

Striga is a hemiparasitic plant, and as is the case with most root parasites in the Scrophulariaceae, its roots are greatly condensed. All species produce primary and secondary haustoria with variable sizes and numbers depending on species. In general haustoria are larger and fewer in S. *gesnerioides* than in other members of the genus. For example, Ba (1984), and Visser and Dorr (1987) have found that S. *gesnerioides* has a primary haustorium of up to 15 mm in diameter and weighed 150 grams compared to a 5 mm diameter secondary haustorium; on the other hand S. *hermonthica* produces a primary haustorium and as many as 80 secondary haustoria but they were all of the same size (1-2 mm). *Striga asiatica* primary haustoria may reach 5 mm in diameter and only 2mm for the secondary haustorium.

Of the 36 species present worldwide, 83% are present in Africa. The most important agronomically are S. *hermonthica*, S. *asiatica*, S. *forbesii*, S. *gesnerioides* and S. *aspera*. This has led many authors to believe that Africa is the center of origin of *Striga* (Musselman 1987, Rao and Musselman 1987, Raynal-Roques 1991). Lesser centers of diversity are the southern Arabian Peninsula (six species), India and tropical Asia (five species), and Australia (four species). A total number of only five species are present exclusively outside Africa (S. *densiflora*, S. *sulphurea*, S. *curviflora*, S. *multiflora*, and S. *parviflora*).

This research is aimed at providing a detailed description, distribution and keys for the African *Striga* species. Description is based on field work and herbarium specimens with the object of quantifying the plasticity of the species characters resulting from the wide distribution of some taxa and the parasitism of different hosts. The species complexes and the infraspecific forms within each taxon were given special attention for their morphological similarities and differences, key characters and their taxonomic status. Keys and maps were meant to provide the basic framework necessary to identify and document the spatial distribution of witchweed that may hopefully lead to a better understanding of the *Striga* problem.

MATERIALS AND METHODS

Key to *Striga* species

The construction and outline of keys was based on the phylogenetic relationship among species determined by a cladistic analysis. After all taxa were identified and described, the key characters with their contrasting states were selected for the related taxa (species complex). Then, within each group, subsequent characters were used to key out the species. In general the method of Radford *et al.* (1974) was adopted to construct the keys. The dichotomous bracket key was selected because it is generally useful for long keys, requires less room on a page, and has the advantage of keeping coordinate choices together.

Distribution and maps

Latitude and longitude of the localities were determined and used to generate maps for the general geographical range of *Striga* in Africa (the mainland). The genus does occur in the islands on both eastern and western coasts of Africa but, since these islands are small, difficulties were encountered in plotting the symbols used for the mainland and are noted in the details of the taxa. Specimens cited in Hepper, (1963); (1984); Musselman and Hepper, (1986); and Ralston et al. (1987) were used here to supplement the species range.

Collection sites were plotted on a large computer generated map which was subsequently reduced to standard size. SAS graphics, the program used to produce maps on the CMS main frame, plots longitude and latitude as curved lines that conforms with the curvature of the earth surface therefore, the reference map (Fig. 1) is included and should be borne in mind when reading the other maps. Closely related species or rare species were plotted together.

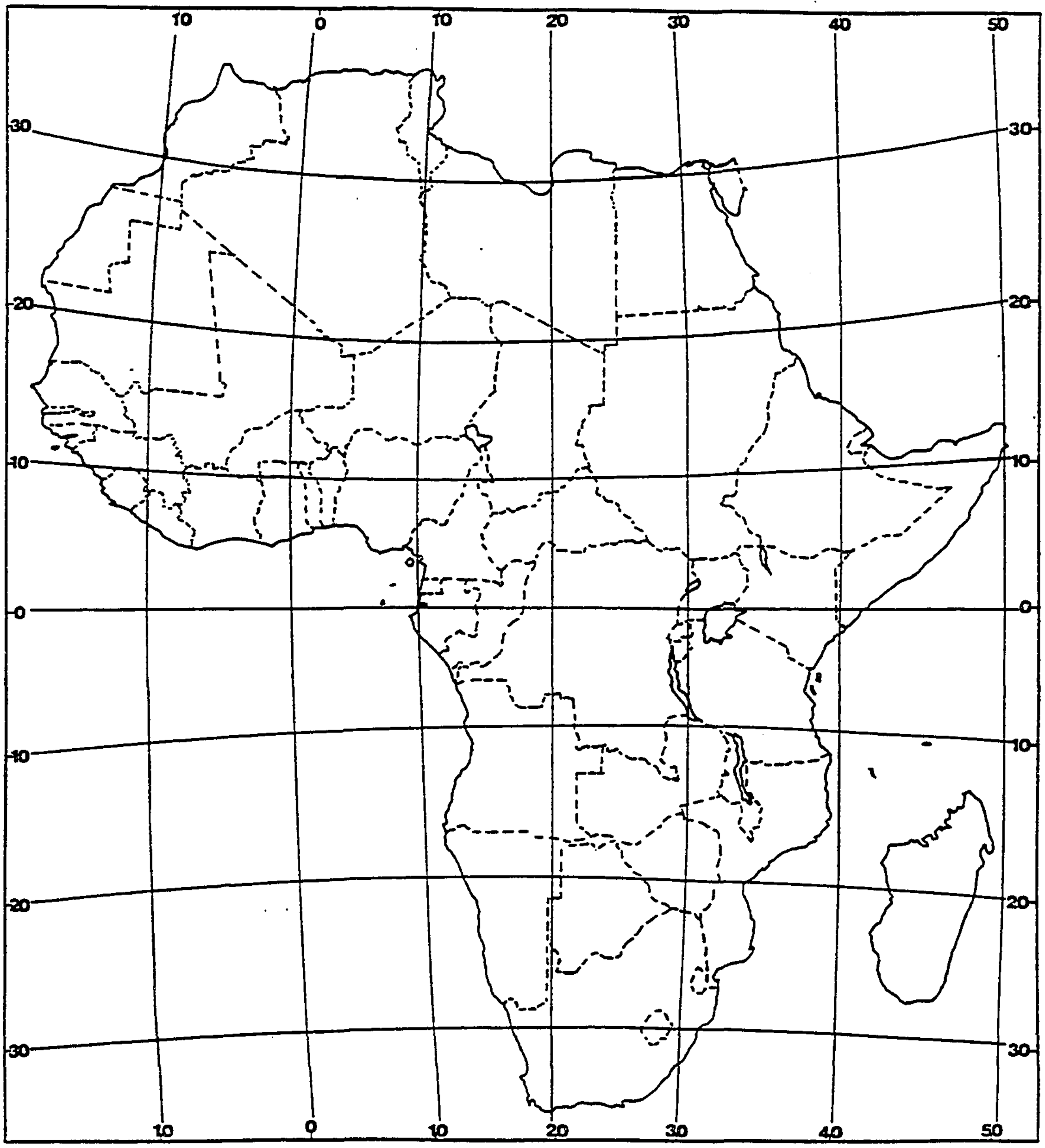

Fig. 1: Reference map.

Species description

The following morphological features were described for each species and subspecies: duration (annual/perennial), stem height and indumentum, the number of ribs on the calyx tube, the way the flowers are borne (in compact heads or simple raceme), corolla color, dentation and size of leaves, relative sizes of calyx and of corolla tubes, size of bracts and bracteoles subtending each flower, and capsule and seed sizes. For measurable characters, like length and width, the minimum and maximum values are given instead of averages. Description was based exclusively on herbarium materials, and in most cases on a large number of plants obtained from different gatherings and geographical locations except for the rare species like Striga *junodii*, *S. yemenica*, and *S. angustifolia*. Species known only from type specimen such as *S. pinnatifida*, *S. fulgens*, and the taxa proposed by Raynal-Roques are briefly described and included in the text with the other species.

In general *Striga* has square stems, but close observation reveals some deviations. Hence, I distinguished between three kinds of stems: square, obtusely square, and winged. The latter is square with sharp edges. In almost all species the basal leaves are consistently different from the upper leaves therefore they were described separately. The same applies to the floral bracts. In both cases "lower" refers to the basal 2-4 pairs. The three lower corolla lobes were considered of the same size even though the middle one is usually slightly broader or longer than the two lateral ones. Host-specific strains of *S. gesnerioides* are included although they were not accorded any taxonomic category (species, subspecies) to stress their similarities and differences. Taxa are arranged in alphabetical order.

Specimens used in this study were obtained from the Herbarium of Old Dominion University, Norfolk, Virginia (ODU); Herbarium of Missouri Botanical Garden, Saint

Louis, Missouri (MO); Gray Herbarium, of Harvard University, Cambridge, Massachusetts (GH); Swedish Museum of Natural History, Stockholm (S); Botanical Research Institute National Herbarium Pretoria South Africa (BRE); The Herbarium, Institute of Systematic Botany, University of Upplsala , Sweden (UPS); and The United States National Herbarium, Washington D.C. (US).

RESULTS AND DISCUSSION

KEY TO THE AFRICAN SPECIES OF *STRIGA*

a. Calyx 4-5-ribbed (section Pentapleurae) .... KEY ONE

b. Calyx 10- or more ribbed (section Polypleurae) .... KEY TWO

KEY ONE

1- Corolla strongly bilabiate i.e. lobes of the lower and upper lip are fused almost their entire length 2

1- Corolla weakly bilabiated i.e. lobes are fused only at their bases 8

2- Plant entirely glabrous except for few hairs on leaf margins and corolla tube .... *S. aequinoctialis*

2- Plant entirely scabrid hispid, or glandular pubescent 3

3- Corolla lobes obtuse 4

3- Corolla lobes acute 5

4- Leaves lanceolate, ascending, 10-25 mm long, 1-2 mm broad; bracts as leaves, 6-18 mm long, 1-3 mm broad .... *S. bilabiata* subsp *bilabiata*

4- Leaves linear, spreading, 20-100 mm long, 2-4 mm broad; bracts widely-obovate, acuminate, ciliate, 9-11 mm long, 3-4 mm broad .... *S. bilabiata* subsp *jaegeri*

5- Entire plant covered with appressed, gray, hispid hair; leaves scale-like, 3-7 mm long, 1-2 mm broad .... *S. bilabiata* subsp *linearifolia*

5- Entire plant pilose, hairs divergent; leaves developed, 10-55 mm long, 1-3 mm broad 6

6- Stem square and winged; calyx teeth half the tube length .... *S. bilabiata* subsp *rowlandii*

6- Stem terete, or obtusely square (not winged); teeth equal tube length 7

7- Leaves cauline, decussate, appressed, lanceolate; inflorescence less than half the stem length .... *S. bilabiata* subsp *ledermannii*

7- Leaves acauline, opposite, tortuous, linear; inflorescence longer than the rest of stem .... *S. bilabiata* subsp *barteri*

8-Leaves not nerved, margin entire 9

8- Leaves 3-nerved, margin toothed; otherwise reduced to small scales 13

9- Calyx teeth 5 unequal, acuminate, less than half the tube length 10

9- Calyx teeth 5 equal, narrow-lanceolate, at least half the tube length 11

10- Much branched plant; stem covered with ascending hairs; leaves 2-8(17) mm broad; corolla > 10 mm long, bent just above calyx, sparsely hairy .... *S. hermonthica*

10- Little branched plant (max. 2); stem covered with retrorse hairs; leaves 1-2 mm broad; corolla < 10 mm long, bent at apex, densely retrorsely pubescent .... *S. yemenica*

11- Leaves 10-45 mm long, 1-3 mm broad; upper bracts longer than calyces; inflorescence longer than the rest of the stem; flower sessile; corolla white rarely pink .... *S. passargei*

11- Leaves 10-35(50) mm long, 1(-2) mm broad; upper bracts shorter than calyces; inflorescence shorter than the rest of the stem; flowers shortly pedicellate; corolla pinkish/purple 12

12- Calyx tube 3-6 mm long; lower corolla lobes 4-8 mm long, 2-5 mm broad ... *S. aspera*

12- Calyx tube 1.5-3 mm long; lower corolla lobes 2-3 mm long, 1-2 mm broad .... *S. brachycalyx*

13- Plants stiffly erect, usually with single stem, more than 30 cm tall; inflorescence at the top of a leafy stem 14

13- Plants succulent, low, cespitose (much branched from base), less than 30 cm tall; inflorescence almost to ground level 15

14- Leaves shortly petiolate, elliptic, up to 7 × 3 cm; flowers shortly pedicellate, alternate forming lax raceme; corolla bright salmon-pink, corolla tube 22-25 mm long, lobes large .... *S. hallaei*

14- Leaves sessile, lanceolate; up to 3 × 1 cm; flowers sessile, opposite forming dense spike; corolla mauve, corolla tube 12-13 mm long, lobes small .... *S. angollii*

15- Corolla tube slender, 8-14 mm long, bent at top; corolla lobes ovate, tips round .... *S. gesnerioides*

15- Corolla tube wider at top, 9-12 mm long, bent just above calyx; corolla lobes lanceolate, tips acute 16

16- Entire plant glandular pubescent; capsule enclosed in the calyx tube at maturity .... *S. lepidagathidis*

16- Plant glabrous except that, corolla tube has few stipitate glands; capsule valves strongly recurved when dehiscing, the calyx then splitting into 5 parts *S. gastonii*

KEY TWO:

1- Leaf less than 3 mm broad, nerves obscure, margins entire 2

1- Leaf more than 3 mm broad, 3-nerved, margins toothed 3

2- Much branched plant, leaves up to 50 mm, longer than internodes; all bracts longer than calyces; inflorescence longer than vegetative stem .... *S. asiatica*

2- Little branched plant, leaves up to 30 mm, shorter than internodes; upper bracts shorter than calyces; inflorescence shorter than vegetative stem 7

3- Inflorescence lax; lower floral bracts 2-5(9) cm long; corolla salmon pink 4

3- Inflorescence dense; lower floral bracts 1-2 cm long; corolla pink or white 5

4- Stem hairs stiff; lower bracts 3-nerved, toothed, 3-12 mm broad; lower corolla lobes 6-9 mm long .... S. *forbesii*

4- Stem hairs soft; lower bracts not nerved, entire, 2-6 mm broad, lower corolla lobes 10-15 mm long .... S. *latericea*

5- Leaves linear, 2-3 cm long, 3 mm broad, hispid-setose; bracts up to 15 mm long, 3 mm broad; hair-base inconspicuous (not swollen) .... S. *dalzielii*

5- Leaves narrowly-elliptic, 3-16 cm long, 4-20 mm broad, scabrid-setose; bracts 10-22 mm long, 2-5 mm broad; hairs arising from swollen bases 6

6- Corolla pink, tube 10-13 mm long, bent just above calyx; lower corolla lobes 4-7 mm long, 2-4 mm broad; leaves longer than internodes, leaf-apex obtuse ...... S. *klingii*

6- Corolla white, tube 17-24 mm long, bent at top; lower corolla lobes 7-10 mm long, 2-8 mm broad; leaves shorter than internodes, leaf-apex acute .... S. *macrantha*

7- Flowers in pairs of two forming dense spike .... S. *elegans*

7- Flowers alternate forming lax spike 8

8- Flowers white or creamy-white 9

8- Flowers pink, purple, yellow, or dark-red 10

9- Calyx 8-12 mm long, teeth 3-6 mm long; corolla small, tube 10-15 mm long; lower lobes 4-8 mm long, 2-4 mm broad .... S. *angustifolia*

9- Calyx 13-21 mm long, teeth 4-12 mm long; corolla large, tube 20-35 mm long, lower lobes 12-20 mm long, 10-17 mm broad .... S. *pubiflora*

10- Leaves linear, or with linear segments, 10-30 mm long; calyx 10-16 mm long 11

10- Leaves lanceolate, reduced, less than 10 mm long; calyx less than 10 mm long 13

11-Calyx 15-ribbed .... S. *junodii*

11- Calyx 10-ribbed 12

12- Leaves pinnatifid, with linear segments; internodes 2-3 cm long; corolla tube 20 mm long, densely pubescent .... S. *pinnatifida*

12- Leaves not divided; internodes 1-5 cm long; corolla tube 10 mm long, nearly glabrous .... S. *fulgens*

13- Plants covered with stiff ascending hairs; flowers pedicellate 14

13- Plants entirely glabrous, or covered with soft divergent hairs; flowers sessile 15

14- Short plant, usually 6 cm tall (rarely 20); internodes less than 1 cm long; leaves linear, ascending; lower bracts longer than calyces; calyx teeth about equaling tube length; inflorescence longer than the rest of the stem; .... S. *hirsuta*

14- Plant slender, 7-40 cm tall; internodes 1-2.5 cm long; leaves lanceolate, appressed; lower bracts shorter than calyces; calyx teeth half the tube length; inflorescence shorter than the rest of the stem;

.... S. *lutea*

15- Calyx 10-ribbed; plant annual, small, tufted (much branched from the base), less than 12 cm long; inflorescence dense .... S. *chrysantha*

15- Calyx 12-15-ribbed; plant perennial stiffly, erect, simple, or little branched, up to 90 cm tall; inflorescence lax 16

16- Plant densely pubescent; calyx 5-toothed; corolla tube glandular pubescent, 20-30 mm long, bent at top, lobes rounded .... S. *primuloides*

16- Plant entirely glabrous; calyx 4-toothed; corolla tube 5-11 mm long, obscurely bent within calyx teeth, indurate, lobes acute .... S. *baumanii*

SPECIES DESCRIPTION

1- *Striga aequinoctialis* A. Chev. ex. Hutch. & Dalz., Fl. W. Trop. Afr. ed. 1, 2: 227, (1931); A. Chev., Expl. Bot. Afr. Occid. Fr. 1: 476 (1920).

Perennial erect 30-50 cm tall. Stem slender, square, winged, grooved, simple or sparsely branched mainly from the middle, glabrous to very sparsely pilose along leaf margins and on corollas, hairs divergent. Lower leaves opposite, lanceolate, reduced, 2-5 mm long, 1-2 mm wide; upper leaves decussate, filiform, ascending, 10-24 mm long, less than 2 mm wide. Internodes 1-3 cm, leaves usually shorter than internodes. Flowers decussate in loose spike, 2-4 flowers open per flowering branch, spike up to 20 cm long, slender, shorter than the rest of the stem. Lower and upper bracts similar, lanceolate, ciliate, incurved, exceeding calyces, 4-6(12) mm long, less than 2 mm wide. Bracteoles small, 2-4 mm long, less than 0.5 mm wide. Calyx 5-ribbed, tubular, 3-4 × 1 mm; calyx tube 2-2.5 mm long; teeth 5 unequal, tapering at apex, ciliate, about as long, or slightly shorter than tube, 1-2 mm long. Corolla pale mauve, densely retrorsely pubescent; corolla tube narrow, 10-12 mm long, less than 1 mm wide, bent and inflated at top; lobes of lower lip ovate, tips acute, longer than wide, 3-7 mm long, 2-3 mm wide, upper lip wider than long, obtuse, 3-5 mm long, 4-7 mm wide. Capsule ovate, 2 mm long, 1 mm wide; seeds brown, 377 × 212 microns. Style persistent, long, hairy.

Restricted to the moist montane grasslands of west tropical Africa. Known only from Guinea, Sierra Leone, Liberia and Ivory Coast. Also locally present in Angola (Fig. 2).

Striga aequinoctialis has a bilabiate corolla like the subspecies complex of *S. bilabiata*. It also shares some of their other characters like the decussate leaves, the slender

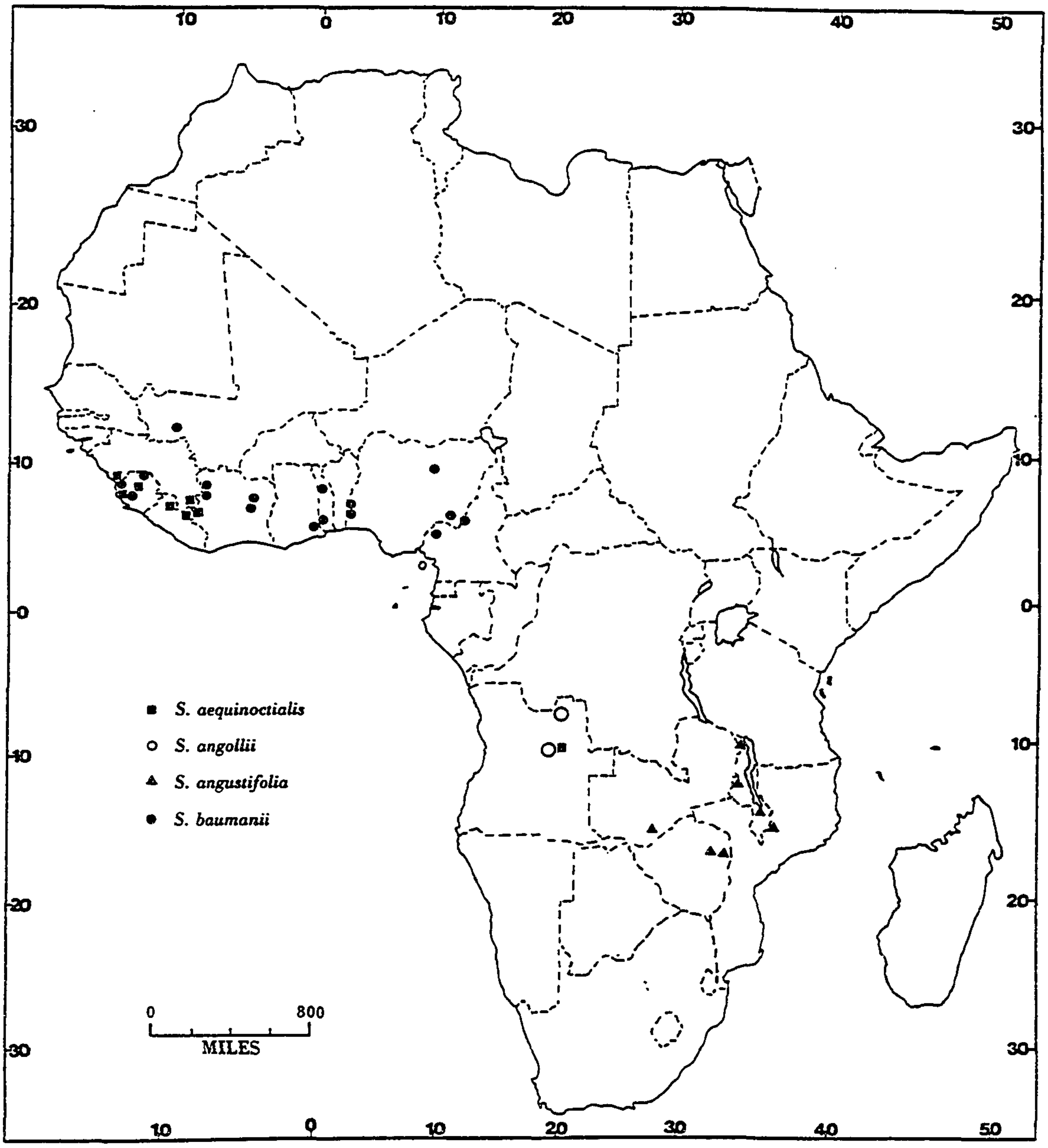

Fig. 2: Distribution of *Striga aequinoctialis*, *S. angollii*, *S. angustifolia*, and *S. baumanii*.

stem, the retrorsely pubescent corolla, and geographical range. However, it is distinguished by its glabrous stem, filiform leaves, and its small calyces, the smallest calyces in the whole genus.

Angola: Saurimo-Dala Rd., R. G. N. Young, 1300 (MO). Guinea: N'Zoo, N'Zerekore, J. G. Adam, 5111; 24653; 26531; 26054; 24386 (MO); Liberia: Granfield, Yekeba, J. G. Adam, 25550; 21457; 24039; 27478 (MO). Mont Nimba, Granfield, J. G. Adam, 21457 (UPS).

2- *Striga angollii* Mohamed & Musselman (Sp. nov.).

Summary: Stem stiffly erect, simple, densely glandular-pubescent. Leaves coarsely toothed, 3-nerved. Bracts lanceolate, abruptly different from leaves, shorter than calyces. Calyx four or five nerved; calyx lobes four equal or five subequal, about the same length of tube. Corolla mauve, bent and expanded at its top.

Type: Angola, Vila Luzo, R. Luena, Young, 1365 (MO).
Paratype: small river between R. Luachi & R. Lumeji, Young, 1261 (ODU).

Stiffly erect annual herb up to 70 cm tall. Stem unbranched, obtusely square, shallowly furrowed, densely glandular-pubescent. Lower leaves opposite, reduced, 5-10 mm long, 2-4 mm broad, linear, margin entire, tip obtuse; upper leaves alternate, ascending, or usually appressed, sessile, lanceolate, 10-35 mm long, 2-8 mm broad, glandular-pubescent, coarsely toothed, 3-nerved, tips subacute. Internodes 2-5 cm long, leaves longer than internodes at the lower part of the stem, becoming shorter above. Inflorescence up to 15 cm long, shorter than the stem, flowers sessile in pairs of two, inflorescence lax-flowered at its base, dense towards the apex. Bracts abruptly different from leaves, shorter than calyces, lanceolate, 5-8 mm long, 2 mm wide, margin entire, tips acute. Bracteoles subulate, 3-5 mm long, 0.5-1 mm wide. Calyx 4-5-ribbed, glandular-pubescent, tubular, 6-8 × 2-3 mm; calyx tube 2.5-4 mm long; teeth 4-5 equal or subequal, lanceolate, as long or slightly longer than tube, 3-5 mm long. Corolla mauve, densely glandular-pubescent; corolla tube narrow, 12-13 mm long, 1 mm in diameter, bent and expanded at its top; lobes of lower lip three, spreading, narrowly obovate, 7-8 mm long, 2 mm broad; upper lip obovate, slightly notched, or rounded, 5 mm long, 3 mm broad. Capsule ovate, apiculate, 5 × 2.5 mm, valves reflexed after dehiscence. Seeds brown 280 × 215 microns. Style persistent; stigma oblong, broader than style (Fig. 3).

The type and paratype are deposited in the herbaria of Missouri Botanical Garden (MO) and Old Dominion University (ODU) respectively.

Angola, where the new taxon was collected by Young (1932) together with Namibia constitute one of the most poorly collected regions in Africa. In seven relatively large herbaria there were only five records of *Striga* in the two countries. These were *Striga aequinoctialis*, *S. asiatica*, *S. gesnerioides*, *S. hermonthica* and *S. passargei*. Of these species, the latter is the first report of *Striga passargei* in Namibia known from the specimen number 1399 (S), collected by Lars E. Kers, from Ondangua, Ovamboland. Other species present in this region include *S. bilabiata*, *S. elegans*, *S. klingii*, and *S. lutea*.

The cladistic analysis for the genus *Striga* reveals that *S. angollii* is closely related to *S. hallaei*, *S. dalzielii*, *S. klingii*, and *S. macrantha*. All five taxa may have originated from a species similar to *S. latericea*. *Striga hallaei* (Raynal-Roques 1987), is restricted to equatorial Africa from Gabon to Zaire. *Striga angollii* and *S. hallaei* are the only two species among the Pentapleurae that possess toothed and nerved leaves, a feature common in at least six species of the Polypleurae. Other shared characters include: the simple, unbranched, erect stem and the corolla tube which bends near its top. However,

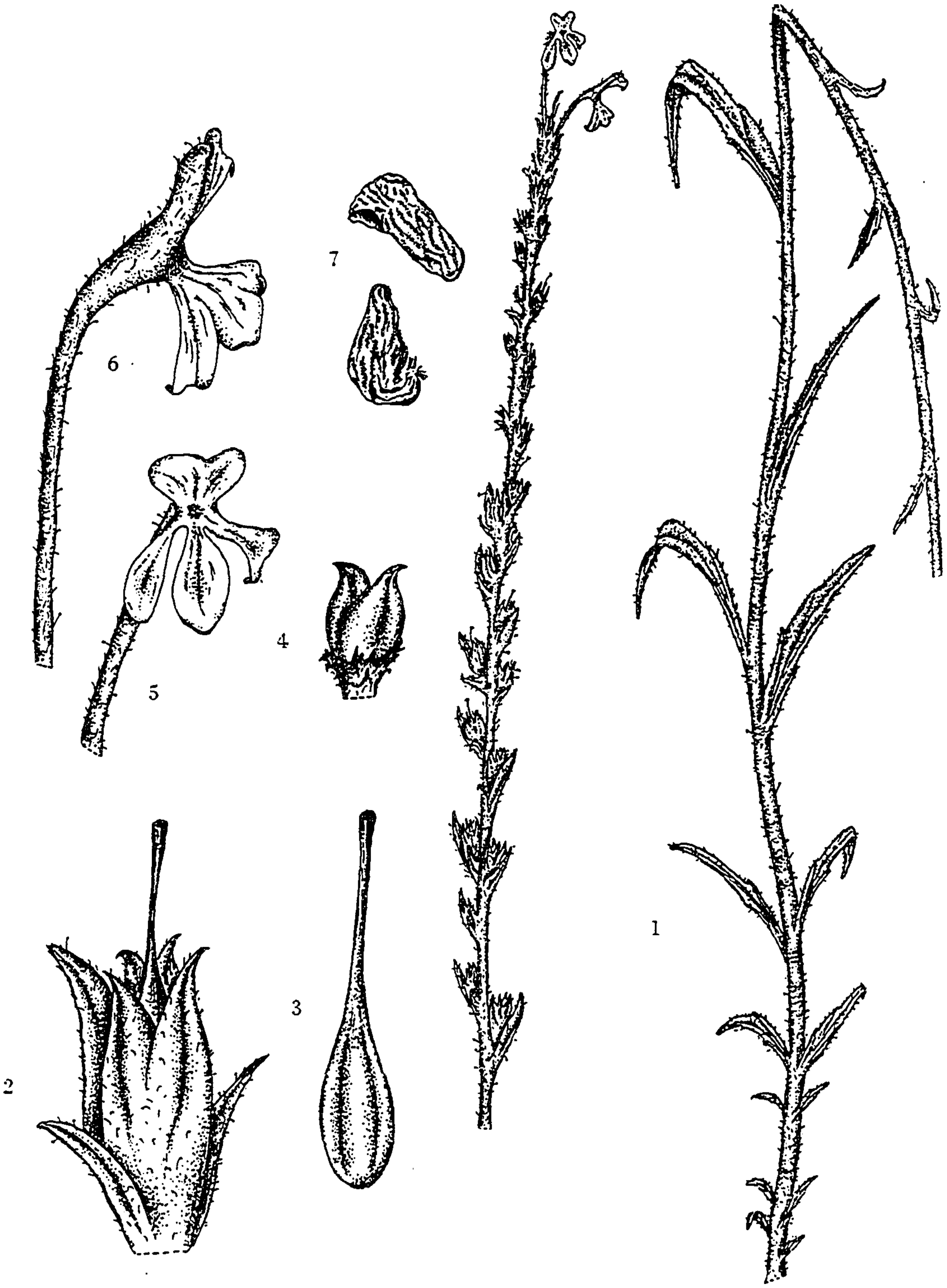

Fig. 3. *Striga angollii*: 1- habit × 1.5; 2- calyx with bracts and bracteoles × 7; 3- immature capsule with style × 6; 4- dehiscent capsule × 4; 5- corolla, face view × 3; 6- corolla × 5; 7- seeds × 40.

S. angollii and *S. hallaei* differ in a number of features: 1) their distribution, 2) presence of petioles 3) bracts length relative to calyx, 4) calyx teeth length relative to calyx tube, 5) inflorescence density, and 6) corolla tube and lobes sizes (compare these features in the two taxa).

In the section Polypleurae, *Striga dalzielii* shares with *S. angollii* a similar corolla tube that bends at its top, leaves which are 3-nerved but not toothed; both lack the stiff hispid hairs which usually arise from swollen bases. *Striga klingii* (Tetrosepalum), resembles *S. angollii* in its overall features. It shares with *S. angollii* the toothed, 3-nerved leaves, the presence of four to five calyx teeth, and the similar corolla dimensions except that the tube of *S. klingii* is bent just above the calyx. On the other hand both *S. dalzielii* and *S. klingii* differ from *S. angollii* in having leaf-like bracts which are longer than calyces at least at the base of the inflorescence and the dense leafy spike. In addition, only *S. dalzielii* has large corollas with tubes of up to 22-25 mm, and only *S. klingii* has harshly hispid stem with hairs arising from swollen bases.

Angola: River Luena, Vila Luzo, R. G. N. Young, 1365 (MO); small river between R. Luachi & R. Lumeji, R. G. Young, 1261 (ODU); (Fig. 2).

3- *Striga angustifolia* (Don) Saldanha in Bull. Bot. Surv. India 57(1): 70 (1963) & in Fl. Hassan Distr.: 526 (1976); Hepper, Taxon 35: 390 (1986); Musselman & Hepper Notes Roy. Bot. Gard. 45 (1): 45 (1988).

Buchnera angustifolia Don, Don. Prodr. Fl. Nepal: 91 (1825).

Striga euphrasioides (Vahl) Benth. in Hook. Bot. Mag. 1: 364, (1836) & DC., Prodr. 10: 503 (1846). Skan in Fl. Trop. Afr. 4, 2: 412 (1906).

Annual herb 10-50 cm tall. Stem erect, obtusely square, furrowed, simple, or little branched from below the middle, pubescent, or densely hispid with short upward curved hairs. Lower leaves opposite, reduced, 5 mm long, 1 mm broad; upper leaves opposite at the lower part of the stem, alternate above, appressed, or ascending, linear to linear-lanceolate, 10-30 mm long, 1-3 mm broad. Internodes 2-5 cm long, leaves mostly longer than internodes. Inflorescence shorter than the rest of the stem, flowers shortly pedicellate, alternate, forming long lax terminal spike, 1-3 flowers open per inflorescence branch. Lower bracts leaf-like, linear, longer than calyx, 10-25 mm long, 1-2 mm wide; upper bracts linear, or subulate, shorter than calyx, 1-5 mm long, less than 1 mm wide. Bracteoles subulate, 1-4 mm long, less than 1 mm wide. Calyx 15-ribbed, ribs prominent, pilose along ribs, tubular, 8-12 × 2-3 mm; calyx tube 3-6 mm long; teeth 5-equal, linear to lanceolate, ciliate, as long, or just longer than tube, 3-6 mm long. Corolla whitish to creamy-white with greenish tube, densely pubescent; corolla tube narrow, 10-15 mm long, bent and inflated just above calyx; lobes of lower lip obovate, 4-8 mm long, 2-4 mm broad, upper lip broadly obovate, emarginate, or truncate, 3-4 mm long, 3-4 mm wide. Capsule ovoid 5 × 3 mm. Style persistent.

The species is known only from East Africa in the seasonally wet prairies of Tanzania, Malawi, Mozambique, Zambia, and Zimbabwe (Fig. 2).

Striga angustifolia is closely related to *S. pubiflora*, *S. junodii*, and *S. masuria*. They are in Tetrosepalum and known only from East Africa. *Striga angustifolia* and *S. masuria* are essentially Asian species. All together form a species complex. *Striga angustifolia* is not known as a problem to crops in Africa although it has been cited as a pest of cereals and sugar cane especially in India (Saunders 1933, Rao *et al.* 1986).
Malawi: Zomba Mt., Chivunde Valley, S. Region, I. F. La Croix, 2735 (MO).

4- *Striga asiatica* (Kuntze) K. I. Mohamed *comb. nov.*

Striga asiatica (L.) Kuntze, Rev. Gen. Pl. 2: 466 (1891); Hepper, Rhodora 76: 45-47 (1974).

Buchnera asiatica L., Sp. Pl.: 630 (1753).

Plants up to 40 cm tall. Stem erect, sparsely to densely branched from base and middle, sparsely to densely hispid, hairs ascending. Lower leaves opposite, appressed, lanceolate to broadly-lanceolate, 1-5 mm long, 1-2 mm wide; upper leaves opposite/ subopposite, spreading, or ascending, narrowly-elliptic, usually linear, 8-50 mm long, 1-3 mm wide. Internodes 1-3.5 cm, leaves usually longer than internodes. Inflorescence 8-24 cm, longer than the rest of stem, flowers alternate, shortly pedicellate in open raceme, 2-4 open per inflorescence branch. Lower bracts leaf-like, longer than calyx, 15-50 mm long, 1-3 mm wide; upper bracts narrowly-lanceolate, as long, or longer than calyx, 7-15 mm long, 2 mm wide, rarely 3-7 mm, shorter than calyx; all bracts hispid along margins and midribs. Bracteoles linear, 3-8 mm long, 0.5 mm wide. Calyx tubular, ribs hispid, 7-8(10) × 2-3 mm; calyx tube 5-7 mm long, teeth 5 equal, or 6-8 unequal, linear to narrowly-lanceolate, very short, less than 1/2 tube length, 2-3 mm long. Corolla red to bright-red, sometimes yellow, sparsely to densely glandular-pubescent; corolla tube 11-14 mm long, 1 mm or less wide, bent at top; lobes of lower lip obovate, longer than wide, 3-5 mm long, 2-3 mm wide; upper lip wider than long, 3 mm long, 3-4(7) mm wide; seeds light-brown, 326 × 172 microns.

The geographical range of S. *asiatica* includes southern and Central Africa south of the equator. An exception is the specimen collected from the Nile Delta, Egypt (Fig. 4). It is in southern Africa where *Striga asiatica* does most damage to crops like sorghum, maize, and millet especially in Botswana (Ralston *et al.* 1987). *Striga asiatica* is not known as a pest in Africa outside this region except in Kenya and its recent introduction in the Republic of Togo (Agbobli and Huguenin 1987, Agbobli 1991). It also parasitizes wild grasses.

Diagnostic features include: the densely branched stem (below the middle), with ascending hairs; linear, opposite or subopposite, spreading leaves, up to 50 mm long;

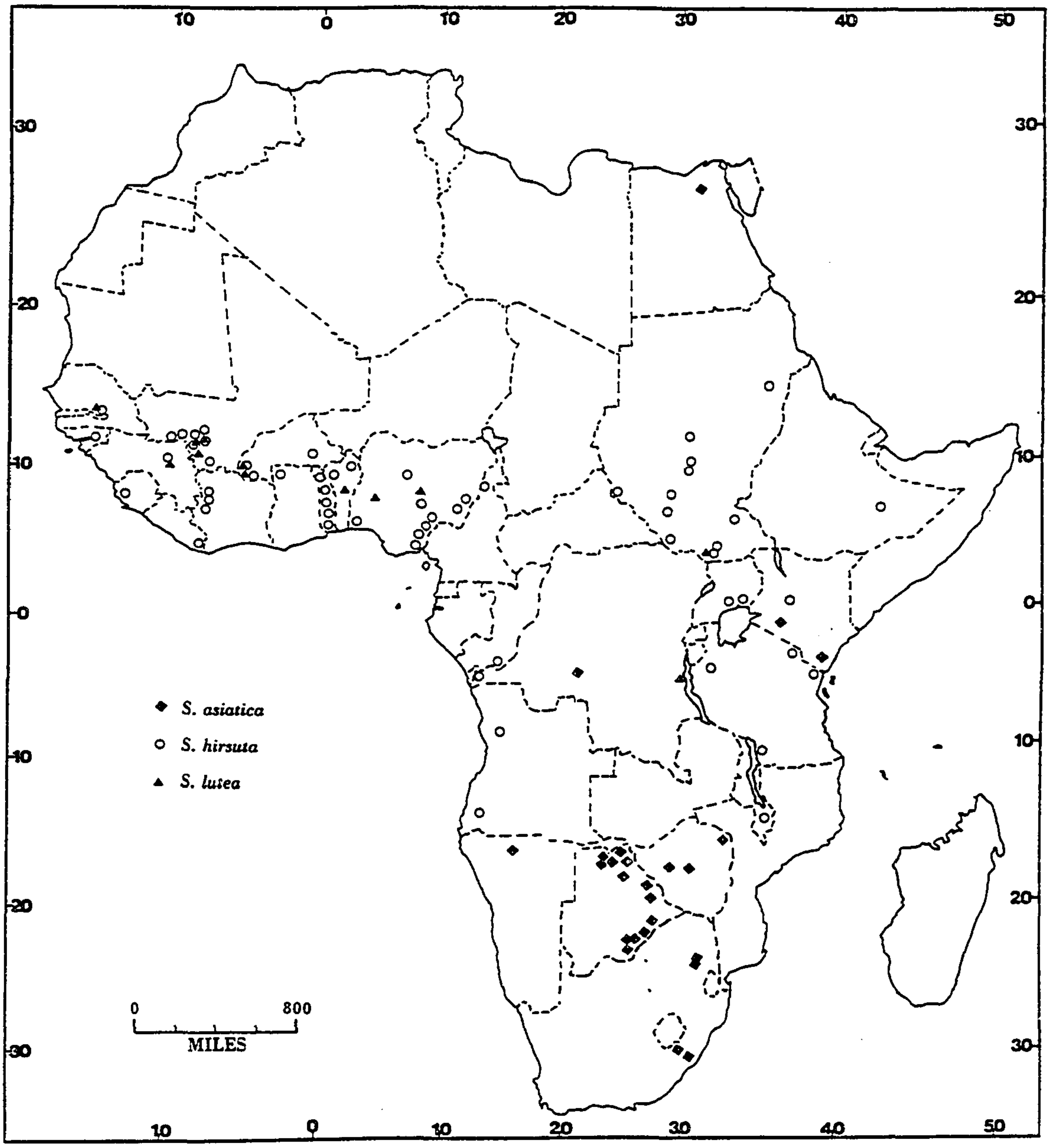

Fig. 4: Distribution of *Striga asiatica*, *S. hirsuta*, and *S. lutea*.

internodes 1-3 cm, shorter than leaves; inflorescence is a lax raceme with opposite or subopposite flowers, usually longer than the stem below it; floral bracts are leaf-like; calyx teeth are 5 equal or 6-7 unequal, about half the tube length; and corollas are large with larger lobes.

Botswana: Formabachena, near Pandamentenga, Chobe Region, L. J. Musselman, C. R. Riches, & D. M. Ralston, 9/4/86 (ODU); Mahalapye Lands 200 km N. of Gabarone L. J. Musselman, 7003 (ODU); Pandamentenga, L. J. Musselman, C. R. Riches, & D. M. Ralston, 9/4/86 (ODU); Sd, C. Parker, 2443 (ODU). Congo: Ganolajika, Chamjeidtive!, J. Lubrun, 2401 (GH). Egypt: Abu Zaabal, Nile Delta, N. Elhadi & A. Khattab, 90/188 (S). Kenya: Buffalo Hills, 60 miles SE Narok, A. G. Curtis, 707 (GH). Kedoug Valley, A. G. Curtis, 860 (GH); Mrima forest along the Mombasa-Lungalunga Rd, O. Hedberg 7022 (UPS); Madagascar: Katoala, S. of Ambovombe, R. Decary, 9014 (US); Sd, Blackburn, 1863 (GH). Malawi: Blantyre, Shire Highlands, Last, 1887 (US). Namibia: Sd, K. Dinter, 5749 (GH). South Africa: Clydis-dall, Griqualand East, K. Dinter, 5749 (GH); Cultis, prov. Valida, Transvaal, R. Schlechter, 4541 (GH); Griqualand East, W. Tyson, 1222 (GH); Kangwane Homeland, Nsikazi Reg., L. J. Musselman, 7022 (ODU); Kroonstad, D. Rogers, 96 (US); Natal, Appelsbosch, 1889 (UPS); J. M. Wood, 20 (US); vicinity of Nylstroom, W. Transvaal, L. J. Musselman, 7015 (ODU); Sydenham, Natal, J. M. Wood, 10873; 4/1908 (US); Umzimkulu, W. Tyson, 1504 (GH); Wonderfotein, Transvaal, Werdermann & Oberdieck, 2236a (US). Tanzania: Dar-es-Salaam, O. Kuntze, 7/iv94 (US); Zanzibar Isl.: Sd, K. Dinter, 5749 (GH); Sd, W. V. Duben, 1845 (S). Zimbabwe: near Makava, Midlands Region, Musselman et al., 4/17/86 (ODU).

5- *Striga aspera* (Willd.) **Benth.** in Hooker's Comp. Bot. Mag. 1: 362 (1836); Skan in Fl. Trop. Afr. 4, 2: 403 (1906); Andrews, Flow. Pl. Sudan 3: 145 (1956); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 372 (1963), Musselman & Hepper, Kew Bull. 41 (1): 209-211 (1986).

Euphrasia aspera Willd. Syst. 2: 776 (1801).

Striga aspera var. *schweinfurthii* Skan in Fl. Trop. Afr. 4, 2: 403 (1906); Fl. Sudan: 330 (1929).

Plants annual, usually slender, up to 53 cm tall. Stem delicate, obtusely 4-angled, grooved, or sparsely to densely profusely branched usually from the middle, densely hispid, hairs divergent at the base of stem, ascending above. Lower leaves reduced, opposite, appressed, lanceolate, or linear, 1-5 mm long, 1 mm or less wide; upper leaves linear, opposite, spreading, or ascending, usually very narrow, 10-35(60) mm long, 1 (rarely 2-3) mm wide. Internodes 1-3(5) cm, leaves longer than internodes. Inflorescence up to 15(26) cm, usually shorter than the rest of stem, flowers alternate, shortly pedicellate in loose spike, 3-10 flowers open per flowering branch. Lower bracts linear, spreading, longer than calyx, 8-40 mm long, 1 rarely 2 mm wide; upper bracts lanceolate to narrowly-lanceolate, appressed, ciliate, shorter than calyx, 2-8 mm long, 0.5-1 mm wide. Bracteoles linear, 2-7 mm long, less than 0.5 mm wide. Calyx 5-ribbed, ribs hispid, 5-10 × 1-2 mm; calyx tube 3-6 mm long; teeth 5 almost equal (adaxial more developed than in *S. hermonthica*), narrowly triangulate, acuminate, ciliate, as long, or just shorter than tube, 2-5 mm long. Corolla pinkish-purple; corolla tube sparsely glandular-pubescent, narrow, 12-16, (rarely 19) mm long, 1 mm wide, bent and inflated at top; lobes of lower lip obovate, spreading, 4-8(10) mm long, 2-5 mm wide, upper lip emarginate, or subtruncate, broadly obovate, 3-7 mm long, 4-7 mm wide. Capsule ovate to subovate 2-4 mm long, less than 1.5 mm wide; seeds dark-brown, 320 × 183 microns; style persistent, long, exceeding calyx; stigma with some stiff hairs on its surface.

Striga aspera is a widespread parasite in the Sahelian and Sudanian domains in Africa. It is the *Striga* species with the most northern distribution in Africa, reported in the region from Senegal to Sudan (Fig. 5), and from some isolated areas in Tanzania and Malawi (Hepper 1984). Although *Striga aspera* is confined to natural grasslands, it has the potential to attack agronomic crops (Safa, personal communication). With the extension of agriculture and the destruction of its natural habitat it may pose a real threat to cereal crops especially in West Africa where it is very common.

Striga aspera can be distinguished in the field from its relative *S. hermonthica* based on its delicate appearance, its slender stem, and the pinkish-purple corolla; however, it is difficult to pinpoint dependable key characters to separate the two species. Traditionally *S. aspera* is distinguished from *S. hermonthica* by its corolla tube being bent at its top while that of *S. hermonthica* is bent just above the calyx (Ramaiah *et al.* 1983, Raynal-Roques 1987). This character is useful and easy to notice but there are often intermediate specimens with corollas bent at half-way. I found the leaf width useful in separating the two species. In *S. hermonthica*, leaf width is usually greater than 2 mm whereas in *S. aspera* it is rarely 2 mm. The calyx teeth in *S. aspera* are almost equal to the tube length with the adaxial one being more developed while in *S. hermonthica* teeth are short, triangular and the adaxial one is less than 1 mm. The corolla tube of *S. aspera* is glandular pubescent while in *S. hermonthica* it is never glandular pubescent. I found this last feature as the most consistent character that should be considered when dealing with the differences between the two species. *Striga aspera* is also related to *S. brachycalyx* and *S. passargei* and the three species are sympatric in most of their range (Fig. 5, 7, and 12).

Burkina Faso: N. Banfora, S. B. Safa & L. J. Musselman, 10/13/87 (ODU); 5 km E. Godi, S. B. Safa & L. J. Musselman, 10/12/87 (ODU); 5 km N. Gourcy, S. B. Safa & L. J. Musselman, 10/10/87 (ODU); Ouada, L. J. Musselman, 6122; 6123 (ODU); 5 km N. Tenkodogo, S. B. Safa & L. J. Musselman, 10/25/87 (ODU); 74 km N. Togo border, L.

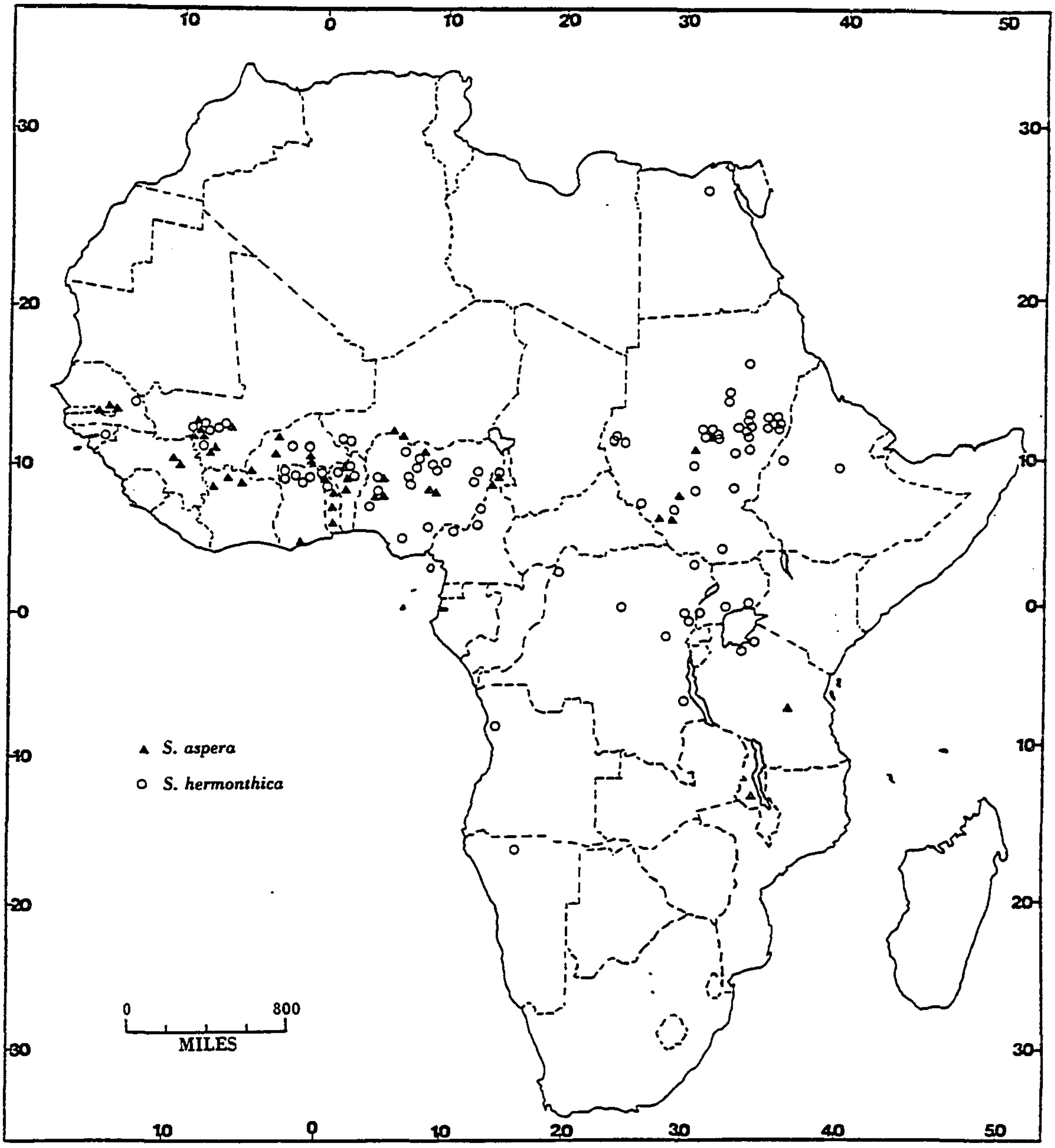

Fig. 5: Distribution of *Striga aspera* and *S. hermonthica*.

J. Musselman, 6124 (ODU). Cameroon: near Guider, L. J. Musselman, 10/13/88 (ODU); 80 km S. Maroua, northern prov., L. J. Musselman & others, 10/13/88 (ODU); northern prov. L. J. Musselman, 10/13/88 (ODU). Ghana: Belgatanga, Hossain & Agyakwch, GC37829 (US); Sandema, U. E. R. Shanno, 88-39 (US). Mali: Baguineda, L. J. Musselman & K. I. Mohamed, 10/8/88 (ODU); Bakma, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); 11 km N. Didieni, L. J. Musselman & K. I. Mohamed, 10/6/88 (ODU); Kamesoba, between Bamako-Siby, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); Kati, 11 km NW Bamako, L. J. Musselman & K. I. Mohamed, 10/6/88 (ODU); Sanakoroba S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88 (ODU): between Siby and Kongula, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); Sotuba S. Bamako, L. J. Musselman & K. I. Mohamed, 10/1/88 (ODU); Zantiebougou, L. J. Musselman & K. I. Mohamed, 10/5/88 (ODU). Niger: Donkondonkou, C. Parker, 2314 (ODU); Kouroungosu, C. Parker, 3215 (ODU). Nigeria: Belawa, Kano State, D. A. Knepper, 9/21/89 (ODU); 8 km N. airport Jos-Wambo, D. A. Knepper, 9/23/89 (ODU); Jos-Plateau, D. A. Knepper, 8/25/89 (ODU); Jos-Shendam, D. A. Knepper, 8/26/89 (ODU); Kasaure, C. Parker, 2318 (ODU); L. J. Musselman and R. A. Mansfield, 5524 (ODU); Luna Rd, Hassan Estate, D. A. Knepper, 9/26/89 (ODU); Vom, S. Jos, D. A. Knepper, 9/23/89 (ODU). Senegal: Dialakoto, prov. Orientalis, L. J. Musselman, 7060 (ODU); Santion Meleme, Tambacounda, C. Parker, 1976; 1977 (ODU); 41 km NE Velingara, prov. Oriental, L. J. Musselman 7085 (ODU). Sudan: Jeriba Ghaffas, Djur region, G. Schweinfurth, 1992 (S); on R. Sue, between Peili and Wau, Equatorial prov., J. G. Meyers, 7329 (GH).

6- *Striga baumanii* Engl. Bot. Jahrb. 23: 515, t. 12 figs. O-T (1897); Skan in Fl. Trop. Afr. 4, 2: 414 (1906); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 731 (1963).

S. baumanii Pilger in Eng. Jahrb. 14: 215 (1910).

Perennial glabrous herb, up to 91 cm tall. Vegetative stem short, bearing two large rounded leaves; flowering stem square, stiffly erect, appearing leafless, usually simple, or, dichotomously branched from above the middle. Lower and upper leaves similar, opposite, scale-like, appressed, lanceolate, ciliate, tips acute, 2-7 mm long, 2-4 mm wide. Internodes 2-6 cm long. Inflorescence shorter than half the rest of stem below it, 15-35 cm long, flowers tubular, opposite in loose spike, 3-7 flowers open per inflorescence branch. Lower and upper bracts similar, appressed, lanceolate, broader but shorter than calyx, 4-6 mm long, 2-3 mm wide. Bracteoles linear, 5-6 mm long, less than 0.5 mm wide. Calyx tubular, 12-15-ribbed, three terminating each calyx tooth, calyx 6-11 × 1 mm; tube 4-7 mm long; calyx teeth four equal or essentially so, lanceolate, ciliate, about half the tube length, 2-4 mm long. Corolla indurate, persistent, pale brown (dark red), rarely exceeding calyx, inconspicuously bilobed within calyx teeth, glabrous, tube narrow, 5-11 mm long, 1 mm wide; lobes of upper and lower lips similar, small, tips acute, slightly recurved when dry, longer than wide, 1-3 mm long, 0.5-1 mm wide. Capsule linear, enclosed within the persistent corolla and/or calyx, 5 mm long, less than 2 mm wide; seeds light-brown, very large, 828 × 267 microns; style persistent.

Striga baumanii is restricted to the moist grassland savannas in Africa, roughly between latitude 00° and 8° . In West Africa it occurs in Sierra Leone, Ivory Coast, Mali, Ghana, Togo, Nigeria and Cameroon (Fig. 2) and also reported from Central African Republic, Chad, Kenya and Zaire.

Striga baumanii is a relatively tall, glabrous, perennial herb with tuberous roots. Corolla tube does not exceed the calyx length and inconspicuously bent within its teeth. Calyx very narrow with only four teeth. The nearly straight, short, indurate corolla tube, the glabrosity, and the presence of only four calyx teeth make *S.baumanii* a unique species within the genus *Striga.* It is the only known perennial species with a vegetative perennial and a reproductive annual stem (Raynal-Roques 1987). The former has two large round leaves that are fire adapted and the latter has reduced appressed leaves.

Ivory Coast: Ganse, G. J. H. Amshoff, 2115 (MO); Odienne, J. G. Adam, 27211 (MO). Nigeria: Abinsi, North Nigeria, J. M. Dalziel, 1912 (MO). Sierra Leone: near Falaba, G. F. S. Elliot, 5085 (GH); 2 miles W. Waterloo, F. A. Melville & T. Hooker, 329 (MO).

7- *Striga bilabiata* (Thunb.) Kuntze, Rev. Gen. Pl. 3(2): 240 (1898); Hepper, in Kew Bull. 14: 411-416 (1960)

The lack of dependable characters to separate S. *bilabiata*, S. *rowlandii*, S. *barteri*, S. *ledermannii*, and S. *welwitschii* led Hepper (1960) to reduce these species to the level of subspecies and to treat them as infraspecific taxa of S. *bilabiata.* Among the features on which Hepper based his study were the stem height, branching pattern, leaf position, and corolla characteristics which proved to be variable within and among the taxa he studied. The features which can be used to key out the subspecies of S. *bilabiata* are cited under each taxon in this Chapter and in Hepper (1960). The following is a brief account of S. *bilabiata*:

Striga bilabiata (Thunb.) Kuntze, Rev. Gen. Pl. 3(2): 240 (1898); Hepper in Kew Bull. 14: 411 (1960)

Plants perennial, 20-60 cm tall. Stem erect, simple or little branched, densely pubescent or scabrid hispid. Leaves appressed, lanceolate, reduced to small scales, 2-6 mm long, 1-2 mm broad; or leaves ascending, linear, 5-60(100) mm long, 1-2(5) mm broad. Calyx tubular, 5-ribbed. Corolla densely pubescent, tube expanded near top, lobes usually acute, short, the three lobes of the lower lip and the two lobes of the upper lip are fused to almost their entire length forming a strongly bilabiate corolla.

Striga bilabiata subspecies *barteri* (Engl.) Hepper, Kew Bull. 14: 414, (1960); and in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963); Musselman & Hepper, Kew Bull. 41 (1): 211 (1986).

Striga barteri Engl. in Engl., Bot. Jahrb. 23: 514, (1897).

S. glandulifera Engl. in Engl., Bot. Jahrb. 23: 514 fig. H-J (1897).

Plants perennial, up to 18 cm tall. Stem simple, or sparsely branched from base, or middle, terete, densely pilose, hairs divergent. Lower leaves opposite, appressed, linear, 2-5 mm long, 1 mm or less wide; upper leaves opposite, very narrow, linear, spreading, tortuous when dry, 10-40 mm long, 0.5-1 (rarely 2) mm wide. Internodes less than 1 cm, leaves longer than internodes. Inflorescence up to 20 cm, very much longer than the rest of stem, flowers alternate at the base of the inflorescence, opposite above forming a somewhat long lax spike, 1-2 flowers open per inflorescence. Lower bracts linear, spreading, pubescent, longer than calyx, 10-22(45) mm long, 1 mm or less wide; upper bracts narrowly-lanceolate, pubescent, shorter than calyx, 4-8 mm long, less than 1 mm wide. Bracteoles linear, 3-8 mm long, 0.5 mm wide. Calyx 5-ribbed, ribs and intracostal portion entirely pubescent, ovate, 6-12 × 2 mm; calyx tube 4(-8) mm long; teeth 5 unequal, linear, as long, or slightly shorter than tube, 3-4 mm long. Corolla pinkish or violet, densely pubescent, or glandular-pubescent, 12-14 mm long, 1-2 mm wide, bent and inflated at top; lobes of lower lip acute, 2-3 mm long, 1 mm wide, upper lip bifid, acute, 2-4 mm long, 2 mm wide. Capsule about 3 × 1.5 mm; seeds light-brown, 341 × 195 microns; style persistent, smooth, sticky, top inflated, covered with white pollen mass.

The geographical range of *S. bilabiata* subspecies *barteri* extends from Senegal to southern Sudan and south into Uganda and Tanzania (Fig. 6a). Within this region, it occurs only in isolated areas and in small demes being confined to the wet savanna.

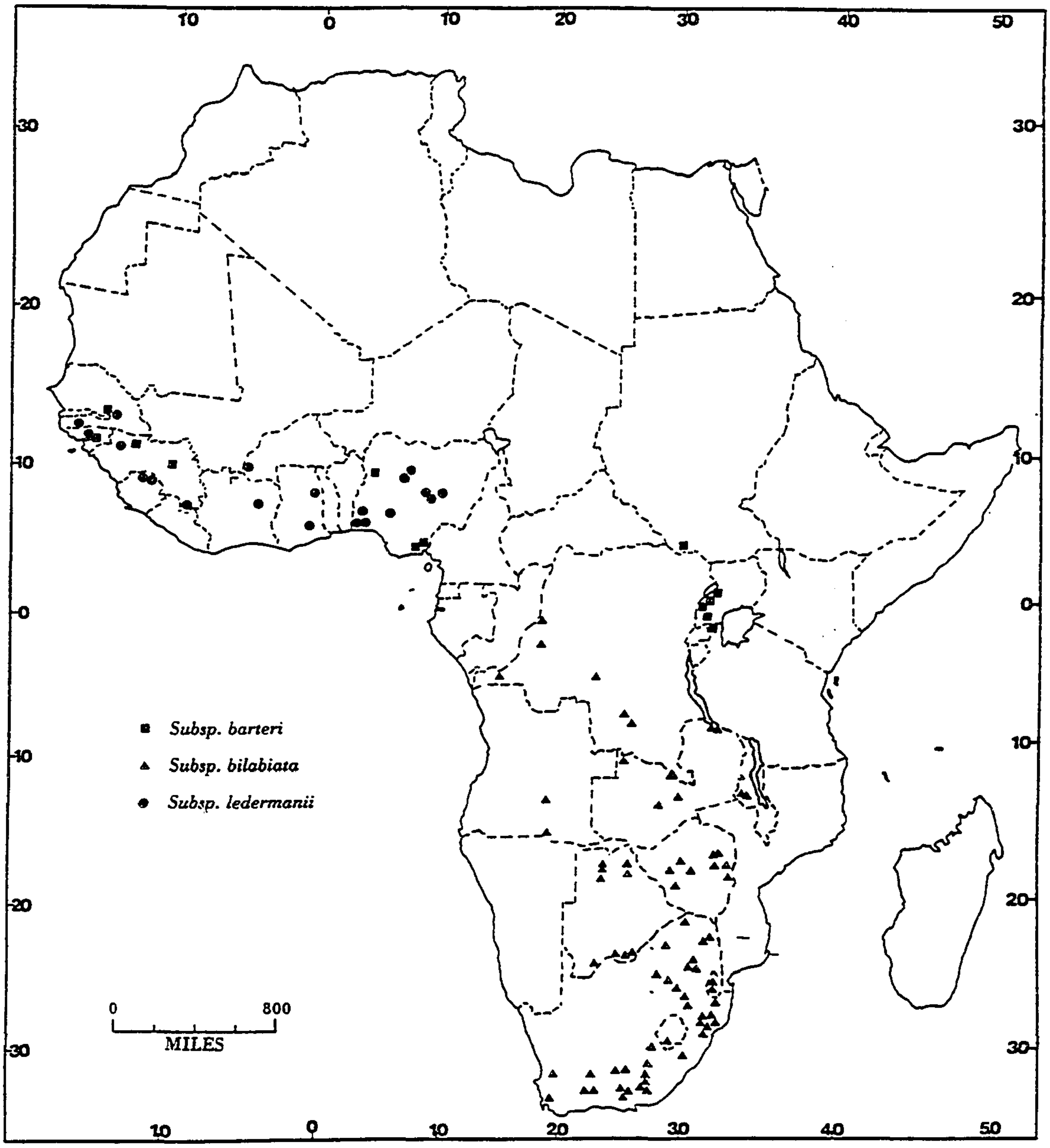

Fig. 6a: Distribution of *Striga bilabiata* subsp *barteri*, subsp *bilabiata* and subsp *ledermannii*.

The key characters of the subspecies include the terete densely pilose stem, the linear spreading tortuous leaves, the long and open spike that exceeds the length of the stem below it, and the long calyx teeth (about the same length of the tube).

Guinea: Village Banko, Kouroussa, J. G. Adam, 26896 (MO). Niger: Sd, C. Barter, 1170 (GH). Senegal: Hasirik, Tambacounda, J. G. Adam, 17917; 17934 (MO).

Striga bilabiata (Thunb.) Kuntze subspecies ***bilabiata***. Kuntze, Rev. Gen. Pl. 3(2), 404 (1898).

Buchnera bilabiata Thunb., Prodr. Pl. 100 (1800).

S. *thunbergii* Benth. in Hook., Comp. Bot. Mag. 1, 363 (1836); Fl. Trop. Afr. (2), 404 (1906).

S. *thunbergii* var. *grandiflora* Benth. in DC., Prodr. 10, 502 (1846).

S. *welwitschii* Engl. in Engl., Bot. Jahrb. 23, 514, t. 12, fig. F-G (1897).

S. *thunbergii* var. *grandiflora* Engl. in Baum, Kunene-Samb. Exped. 369 (1903), pro var. nov.

Plants perennial, 23 rarely 40 cm tall. Stem slender to medium thickness, simple, or little branched at base, square, grooved, scabrous, densely hispid, with divergent hairs. Lower leaves opposite, appressed, lanceolate, 2-8 mm long, 1-2 mm wide; upper leaves decussate, ascending, lanceolate, 10-30 mm long, 1-2(5) mm wide. Internodes up to 2.5 cm, leaves longer than internodes. Inflorescence up to 14 cm, flowers opposite in dense spike, 3-9 flowers open per inflorescence branch. Lower and upper bracts similar, lanceolate, recurved, ciliate, enclosing calyces, 6-18 mm long, 1-3 mm wide, as long, usually longer than calyx. Bracteoles linear, 4-8 mm long, about 0.5 mm wide. Calyx 5-ribbed, ribs hispid, tubular, 6-9(12) × 1-2 mm; calyx tube 3-5(7) mm long; teeth 5 unequal, ciliate, acuminate, as long, or just shorter than tube, 3-5 mm long, rarely 1/2 tube length, 1-2 mm long. Corolla white, mauve, or pinkish-white, densely glandular-pubescent, 10-15 mm long, 1 mm wide, bent and inflated just above calyx, or at top; lobes of lower lip obtuse, 2-4 mm long, 1-2 mm wide, upper lip without distinct lobes, longer than wide, 2-5(7) mm long, 2-4 mm wide. Capsule obovate, 2-3 × 1-2 mm; seeds brown, 366 × 219 microns; style persistent, long, densely hairy.

Striga bilabiata subspecies *bilabiata* is essentially a South African taxon. It is known only from the countries south of the equator- southern Zaire, Zambia, Angola, Zimbabwe, Botswana, and South Africa. There are no collection from the countries on the East African coast (Fig. 6a).

This subspecies has a square, grooved, and densely hispid stem; ascending, lanceolate leaves; lanceolate, ciliate bracts (enclosing calyces); long calyx teeth (about the same length of the tube); and a short dense spike.

Botswana: Digkatlong Ranch, southern Dist., O. J. Hansen, 3016 (MO); sandy flood plains, at 19° 27' S, 22° 57' E, northern Dist., P. A. Smith, 1970 (MO); Okavango Swamp, Xhere Lediba, Dist. Ngamiland, P. A. Smith, 390 (MO); margins of small pan, L. J. Musselman, 7011 (ODU). Mozambique: Napub, Namaacha, Paschafer & Nuvuneg 6644 (MO). South Africa: Addo, Cape prov., Uitenhage Div., Ecklon & Zeyher, 10.11 (GH); J. F. Drege, 832649 (MO); Alexandra, Natal, H. Rudatis, 1829 (S), 543 (US); Alicedale Rd., Albany Dist. R. D. A. Bayliss, 8112 (MO, US); Amatole Mountains near Auckland, eastern Cape, P. B. Phillipson, 138 (MO): Clairmont, Natal, J. M. Wood, 10887 (US); Clydesdall, Griqualand East, Orientalis, W. Tyson, 894 (GH); Colenso, Natal, Wood, 911 (US); Durban, D. Rogers, 1493 (US); Dist. E. Transvaal, J. L. Sidey, 1589 (MO); Grassveld, near Highflat, Natal, Adele Lewis Grant, 3570 (MO); Haenertsburg, N. Transvaal. J. L. Sidey, 1287 (UPS); Transvaal, L. J. Musselman, 7040 (ODU); Inchzanga, Natal, J. M. Wood, 7252 (US); Itala Natural Reserve, Natal, O. M. Hilliard & B. L. Burtt, 10012 (MO); Jafelberge, Natal, J. Krauss, 213 (MO); Katberg pass, Katberg mountain, Cape, Adele Lewis Grant, 3141 (MO); Forest of Krakarkamna, between Port Elizabeth and Ranstsadesberg, Ecklon & Zeyher, 3.10 (MO); Letaba, Transvaal, J. G. Scheepers, 1048 (MO); Mtunzini Zululand, Natal, A. O. D. Moff, 5935.A.M. (MO); Natal, J. M. Wood, 4934 (MO); Ngoya Forest Reserve, Natal, B. J. Huntley, 192 (MO); Div. Nogsback, Pro. Stockenstrom, Cape, J. M. Leighton, 2948 (MO); Olifant River, Kapkolonio, R. Schlechter, 3814 (GH; MO); Olifantshock wood, between Bushman R. and Sundays R., Uitenhage Div., Cape prov., Ecklon & Zeyher, 10.11 (GH; MO); Palmiet, Natal, J. M. Wood, 9212 (GH); Sevenfontein, Natal, J. M. Wood 10,495 (MO); Strydpoort Mts. near Haenertsburg, L. J. Musselman, 7032 (ODU); Transvaal, Schlieben, 7668 (US); Tugela River bridge area, Stanger, Natal, C. H. Stirton, 401 (MO); Uitenhage, Ecklon & Zeyher, 10.11 (MO); Witberge, J. F. Drege, 832608 (MO); Sd, Ecklon & Zeyher, 10.11 (US); Swaziland: 5 km NW Mbabane, Hhohho Dist., E. S. Kemp, 701 (MO); 701 (US). Zambia: Abercorn, Lake Chila, W. Siame, 525 (MO). Zimbabwe: Dyke near Rod Camp Mina, Lomagundi Dist., R. O. B. Rutharford-Smith, 565 (MO); Matopo, O. B. Miller, 1590 (MO).

Striga bilabiata subspecies *jaegeri* Hepper, Kew Bull. 14: 415, (1960); and in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963).

S. welwitschii Engl. var. *longifolia* Berhaut, Fl. Sen. 84 (1954), French description.

S. brouilletii Mielcarek, Bull. Jard. Bot. Nat. Belg. Bull. Nat. Plantentuin Belg. 58: 121-127 (1988).

Plants perennial 30-40 cm tall. Stem square, ridged, simple or very sparsely branched from the base, stem indumentum of dense, divergent, hispid hairs. Lower leaves reduced, opposite, linear, 2-10 mm long, 1 mm wide; upper leaves mainly decussate or opposite, alternate towards the stem apex, linear or very narrowly-elliptic, spreading, with prominent midrib, 20-100 mm long, 2-4 mm wide. Internodes 2-3 cm long, leaves longer than internodes. Inflorescence dense, much shorter than the rest of stem, 2-4 cm long, flowers sessile, imbricate. Lower and upper bracts similar, widely obovate, acuminate, ciliate, enclosing calyces, longer than calyces, 9-11 mm long, 3-4 mm wide. Bracteoles narrowly-lanceolate, 3-5 mm long, 0.5 mm wide. Calyx 5-ribbed, tubular, 7-8 × 1 mm; calyx tube 5-6 mm long; teeth lanceolate, essentially 4 equal, or the fifth very much reduced, ciliate, less than half tube length, 2 mm long. Corolla densely pubescent, tube narrow, 15-17 mm long, bent at top; lower lobes acute, 2.5-3.5 mm long, upper lip obtuse 1.5-2.5 mm long; capsule oblong, 4-5.5 mm long, 2.5 mm wide.

Striga bilabiata subspecies *jaegeri* is a rare taxon known only from Senegal and Mali (Fig. 6b). It can be distinguished by the square, ridged, and the densely hispid stem; the linear spreading leaves has a prominent mid-rib; its bracts being broader than and enclosing calyces, widely obovate, acuminate, and ciliate; calyx teeth are short, less than half the tube length (2 mm), they are essentially four equal or the fifth being very much reduced; and the imbricate flowers form a short, dense, strobilus-like spike.

Senegal: Gouloumbou Tambacounda, J. G. Adam, 14861 (MO).

Striga bilabiata subspecies *ledermannii* (Pilger) Hepper, Kew Bull. 14: 413, (1960).

S. ledermannii Pliger in Engl., Bot. Jahrb. 45: 215, (1910).

Perennial, erect herb, 36 cm tall. Stem square, winged, scabrous, simple, or sparsely branched usually from the base, covered with long, dense, divergent, hispid hairs. Lower leaves lanceolate, opposite, scale-like, appressed, 2-7 mm long, less than 2 mm broad; upper leaves decussate, decurrent, lanceolate, appressed, inclosing stem, 10-23 mm long, 2-3(5) mm broad. Internodes short, 8-13 mm, leaves longer than internodes.

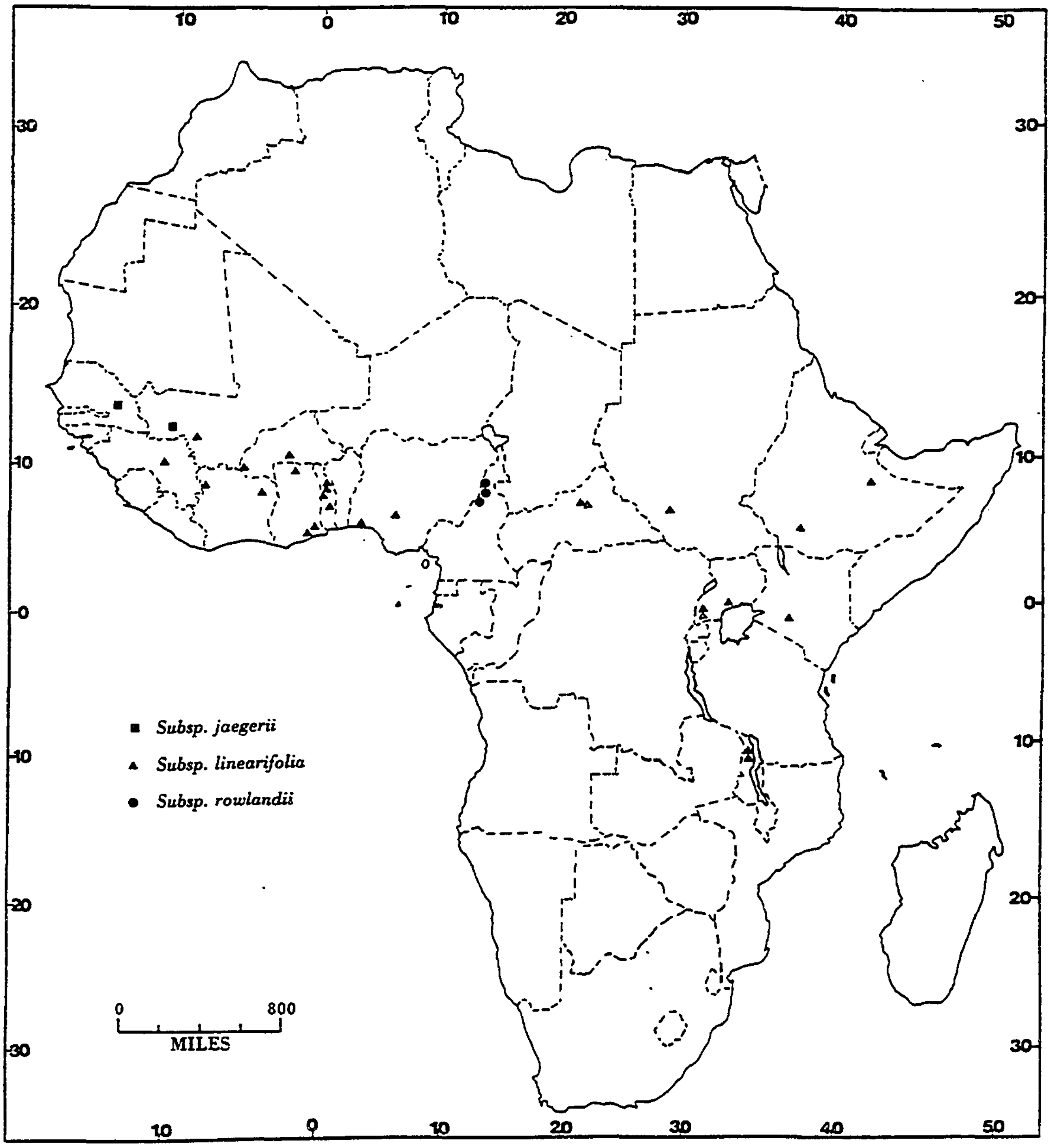

Fig. 6b: Distribution of *Striga bilabiata* subsp *jaegeri*, subsp *linearifolia* and subsp *rowlandii*.

Inflorescence 3-6(14) cm, very much shorter than the rest of stem, flowers imbricate, in dense spike, 2-5 flowers open per inflorescence. Lower and upper bracts similar, lanceolate, or narrowly-elliptic, longer than calyx, enclosing calyx, tips slightly incurved, margins ciliate, 8-15 mm long, 2-4 mm wide. Bracteoles minute, 2-3 mm long, about 0.5 mm wide. Calyx 5-ribbed, hispid along ribs, tubular, 5 × 1-2 mm; calyx tube 2.5-3 mm long; teeth linear, 5 unequal, about the same length of tube, 2-3 mm long. Corolla pink, densely pubescent, with divergent, usually retrorse hairs; corolla tube 12 mm long, densely hispid at orifice, bent and inflated at top; corolla lobes longer than wide, densely pubescent, lobes of lower lip 1-2 mm long, about 0.5-1 mm wide, tips acute to obtuse; upper lip obtuse, 3 mm long, 1-2 mm wide. Capsule very small, ovate to subovate 2 mm long, less than 1 mm wide; seeds brown, 331 × 165 microns; style long, persistent, pollen mass noticed on the sticky stigma.

Striga bilabiata subspecies *ledermannii* is endemic to the northern province of Cameroon (Fig. 6a). Similar to *S. bilabiata* subspecies *linearifolia*, it is infrequent and occurs only in small demes. Studying the biology of the two subspecies might reveals the reasons for the relatively inabundance and the smaller deme sizes which might be due to capsule eating insects, factors affecting the establishment of the parasite on its host, and any other factors relating to seed production, maturity, and dormancy.

This subspecies can be identified by its winged stem and its long hispid hairs; the decurrent, lanceolate, appressed leaves usually enclose the stem beneath it; the imbricate, lanceolate, and ciliate bracts also enclose the calyces; the linear calyx teeth; and the possession of a square, strobilus-like inflorescence.

Cameroon: near Koubout, northern prov., D. Thomas, 2452 (MO); 23 km. S Garoua, northern prov., L. J. Musselman & others, 10/16/88 (ODU).

Striga bilabiata subspecies *linearifolia* (Hepper) K. I. Mohamed *comb. nov.*

Striga linearifolia (Schum. & Thonn.) Hepper, Kew Bull. 14: 416 (1960) and in Fl. W. Trop. Afr. ed. 2, 2; 372 (1963); Musselman & Hepper, Kew Bull. 41 (1): 218 (1986).

Buchnera linearifolia Schum. & Thonn., Beskr. Guin. Pl.: 279 (1827); Skan in Fl. Trop. Afr. 4, 2: 415 (1906); Hepper, W. Afr. Herb. Isert & Thonning: 119 (1976).

B. euphrasioides (Vahl.)! Symb. Bot. 3: 81 (1794).

Striga canescens Engl., Pflanzenw. Ost-Afr. C: 361 (1895); Skan in Fl. Trop. Afr. 4, 2: 406 (1906).

Striga strictissima Skan in Fl. Trop. Afr. 4, 2: 407 (1906).

Plants perennial, up to 62 cm tall. Stem erect, slender, square, winged, looking leafless, usually simple, or if branched then from the base, rarely from the middle, densely hispid, with hairs being appressed, pointed upwards. Leaves reduced, decussate, decurrent, appressed, lanceolate; lower leaves 1-2 mm long, 0.5-1 mm wide; upper leaves 3-7(10) mm long, 1-2 mm wide. Internodes 1-6 cm, leaves shorter. Inflorescence up to 24 cm, usually much shorter than the rest of the stem, flowers opposite in dense spike, 2-6 flowers open per inflorescence. Lower and upper bracts similar, slightly broader than leaves, lanceolate, as long, or slightly longer than calyx, tips incurved, 5-7(10) mm long, 1.5-2 mm wide. Bracteoles linear, slightly shorter than calyx, 2-5 mm long, less than 0.5 mm wide. Calyx 5-ribbed, ribs hispid, transparent between ribs, tubular/obovate, 4-7 × 1-2 mm; calyx tube 2-3(4) mm long; teeth 5 unequal, linear, about the same length of tube, 1.5-3 mm long. Corolla whitish, or purplish to bluish purple, densely pubescent, hairs retrorse, corolla tube inflated and arched at 2/3 of its length, 7-14 mm long, 1-1.5 mm wide; lobes of lower lip finger-like, tips usually acute, 1-3(7) mm long, 0.5-1 mm wide, upper lip bifid, slightly rounded, 2-5 mm long, 2-4 mm wide, inner surface of lobes lined with divergent or appressed hairs. Capsule 3-4 mm long, 1 mm wide; seeds light-brown, 335 × 183 microns; style persistent, hairy, swollen at top.

Striga bilabiata subspecies *linearifolia* is widely distributed in Africa. It occurs in West and East Africa reaching its southern limits in Malawi. Reported from Guinea; Ivory Coast, Mali, Burkina Faso, Ghana, Togo, Benin, Cameroon, Nigeria, Niger, Chad, Central African Republic, Sudan, Ethiopia, Kenya, Uganda, Malawi and from a few collections in Angola (Fig. 6b).

Although the subsp. *linearifolia* occurs over a wide geographical range, it is confined to wet habitat in the grassy savannas. A common feature of this subspecies is the small population size which might not exceed a few plants in a given area. In a ten day vegetation survey in Mali, it was gathered once from a population of only two plants. The subspecies can be distinguished from the other subspecies of *S. bilabiata* by its appressed ascending hairs, white when dry; reduced leaves (< 10 mm long) which are similar the bracts (none of the subspecies of *S. bilabiata* has leaves of this size); and the obviously retrorse hairs on the corolla. It also flowers very early compared to *Striga*.

Burkina Faso: 5 km S. Banfora, S. B. Safa & L. J. Musselman, 10/3/87 (ODU); S. Sapones, S. B. Safa & L. J. Musselman, 10/21/87 (ODU). Central African Republic: 4 km N. of Camp Koumbala, N. of Gaumba Creek, J. M. Fay, 7057 (MO); Manovo-Gounda St., E. Camp Koumbala, J. M. Fay, 5479 (MO). Ethiopia: Gughe highlands, Gamu-Gofa Region, M. G. Gilbert and M. Thulin, 415 (MO); Harrar-Jijega, Harar prov., J. J. F. E. Wilde, 6399 (MO). Ghana: Akuse, Vigne, 4359 (US). Ivory Coast: along Iringou R., Gawi-seye, J. G. Amshoff, 225 (MO); Odienne, J. G. Adam, 27125 (MO). Kenya: Hobleys Volcano-Slope S. of West end of lake Naivasha, A. Agnew, 8700 (MO); Kenyatta College, Kahawa, Akestrid, 2527 (UPS). Malawi: Luwazi marsh, Nyika Plateau, northern prov., E. Phillips, 661 (MBGU); Radio transmitter, woodland, Nyika

Plateau, northern prov. E. Phillips, 1215A (MO); 27 miles N. Rumphi, Rumphi Dis., J. Pawek, 12317 (MO); Tazmia, Nyika Plateau, North prov., E. Phillips, 832 (MO). Mali: village Simidij, L. J. Musselman & K. I. Mohamed, 9/30/88 (ODU). Niger: Sd, C. Barter, 1263 (GH). Nigeria: Shere Mountains, NE States, J. B. Hall and B. O. Daramola, 67404 (MO). Uganda: Ibanda, Ankole Dist., Ragslane, 1251 (US); Kakonge, Dis. East Mengo, P. K. Rwaburindore, 580 (MO); Kanyamiyanga range, Dist. East Ankole, P. K. Rwaburindore, 817 (MO).

Striga bilabiata subspecies *rowlandii* (Engl.) Hepper, Kew Bull. 14: 415, (1960); and in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963).

Striga rowlandii Engl., Bot. Jahrb. 23: 513, (1897).

Plants perennial, erect, of medium thickness, up to 34 cm tall. Stem simple, or little branched from the base, square, winged, sparsely to densely pilose, hairs divergent. Lower leaves reduced, opposite, appressed, lanceolate, 2-7 mm long, 1-2 mm wide; upper leaves decurrent, decussate, ascending, rarely spreading, linear to narrowly-lanceolate, 7-55 mm long, 1-2 mm wide. Internodes 1-4 cm, leaves longer than internodes. Inflorescence 7-14 cm, usually very much shorter than the rest of stem, flowers alternate at the base of the inflorescence, opposite above in somewhat dense spike, 3-9 flowers open per inflorescence branch. Lower bracts lanceolate, entirely pubescent, longer than calyx, 7-10(18) mm long, 1-2 mm wide; upper bracts lanceolate, shorter than calyx, 3-7 mm long, 1-2 mm wide. Bracteoles lanceolate, 2-5 mm long, 0.5 mm wide. Calyx 5-ribbed, entirely pubescent, ovate, 6-7(10) × 1-2 mm; calyx tube 5-6(-8) mm; teeth 5 unequal, triangulate, very short, 1-2 mm long. Corolla pink, mauve or white, densely pubescent, 9-12(17) mm long, 1 mm wide, bent and inflated at top; lobes of lower lip acute, 2-4 mm long, 1 mm wide, upper lip bifid, acute, 2-4 mm long, 2-4 mm wide. Capsule obovate/tubular, 2-4 × 1-2 mm; seeds light-brown, 403 × 238 micron; style persistent, long, hairy.

Striga bilabiata subspecies *rowlandii* is endemic to the relatively wet, rocky, plateau grassland in West Africa. Its range extends from Senegal to Cameroon (Fig. 6b). The subspecies possesses a winged but (unlike subspecies *ledermannii*) sparsely to densely pilose stem; a linear, decurrent, ascending leaves; lanceolate, entirely pubescent bracts; a triangulate calyx teeth which are very much shorter than the tube (1-2 mm); and a short dense spike.

Burkina Faso: 18 km N. Banfora, A. J. M. Leewvenberg, 4357 (MO). Guinea: Seriba, Gaoual, J. G. Adam, 14812 (MO); N'Zoo, N'zerekore, J. G. Adam, 26898; 27661 (MO). Ivory Coast: 45 km NW Dabakala, C. Geerling & J. Bokdam, 2029 (MO). Niger: Sd, C. Barter, 1169; 1263 (GH). Nigeria: Bauchi-Plateau, North Nigeria, H. V. Lely, P83 (MO). Senegal: Bayotter, Ziguinchor, J. G. Adam, 13724 (MO); Niokolo-Koba, Tambacounda, J. G. Adam, 14200; 26891; 26897 (MO). Sierra Leone: Buyabuya, Scarcies, S. Elliot, 4279 (GH); Falaba, S. Elliot, 5207 (MO).

8- *Striga brachycalyx* Skan. Skan. in Dyer Fl. Trop. Afr. 4, 2: 403 (1906); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 372 (1963); Musselman & Hepper, Kew Bull. 41 (1): 211-213 (1986).

S. *warneckei* Engl. ex, Skan. in Fl. Trop. Afr. 4, 2: 414 (1906).

Annual, erect plants, up to 68 cm tall. Stem mostly slender, square, grooved, usually profusely branched from above the middle, sparsely to densely hispid, with divergent, short, stiff hairs arising from swollen bases. Leaves opposite to subopposite, tortuous, ascending, or spreading, glandular, scabrid-hispid; lower leaves small, linear, 1-6 mm long, less than 1 mm wide; upper leaves linear, 7-35(50) mm long, less than 1 (rarely 2) mm wide. Internodes 1-3 cm long, leaves longer than internodes. Inflorescence 8-20 cm, much shorter than the rest of stem, flowers alternate, shortly pedicellate in simple raceme, raceme somewhat open, 2-3 flowers open per inflorescence branch. Lower bracts linear, scabrous, ciliate, as long, or longer than calyx, 5-20 mm long, 1 mm or less wide; upper bracts acuminate, shorter than calyx, 1-5 mm long, 1 mm or less wide. Bracteoles minute, 1-4 mm long, less than 0.5 mm wide. Calyx 5-ribbed, ribs hispid, scarious between nerves, tubular, 3-6 × 1-2 mm; calyx tube 1.5-3 mm long; teeth 5 unequal, tapering at apex, ciliate, as long, or longer than tube, 1-3.5 mm. Corolla purple with white centre; corolla tube narrow, sparsely glandular-pubescent, (6)9-19 mm long, less than 1 mm wide, bent and inflated at top; lobes of lower lip small, tips rounded, 2-3(5) mm long, 1-2 mm wide, upper lip obovate, 1-2(4) mm long, 2-4 mm wide. Capsule ovoid, 3 mm long, 2 mm wide; seeds light-brown, 313 × 176 micron; style very long, persistent with some pollen on surface.

Striga brachycalyx is a widespread and frequently common parasite that occurs in large demes in the grassy savannas of West and Central Africa. It ranges from Sierra Leone west into Ivory Coast, Burkina Faso, Mali, Ghana, Togo, Benin, Nigeria, Niger and Cameroon reaching its eastern limits in Sudan (Fig. 7). This species is not known from south of the equator.

Striga brachycalyx is an annual, slender, diffusely branched herb. Leaves are long and narrow (<2 mm wide). Calyces are small with their teeth being of about the same length of the calyx tube. The only difference between this species and S. *aspera* is size.

The following specimens are deposited in (ODU) except the last one. Burkina Faso: 5 km S. Banfora, S. B. Safa & L. J. Musselman, 10/13/87; Faracoba, S. Bobo Dioulassou, S. B. Safa & L. J. Musselman, 10/13/87; 5 km E. Godi, S. B. Safa & L. J. Musselman, 10/12/87; 5 km S. Gourcy, S. B. Safa & L. J. Musselman, 10/10/87; 1 km S. of Kamboiense, L. J. Musselman, 6118; 7 km N. of Mia, L. J. Musselman, 6131; 3 km S. Niou, S. B. Safa & L. J. Musselman, 10/10/87; 10 km S. Sapones, S. B. Safa & L. J. Musselman, 10/21/87; 5 km north Tenkodogo, S. B. Safa and L. J. Musselman, 10/9/87. Mali:

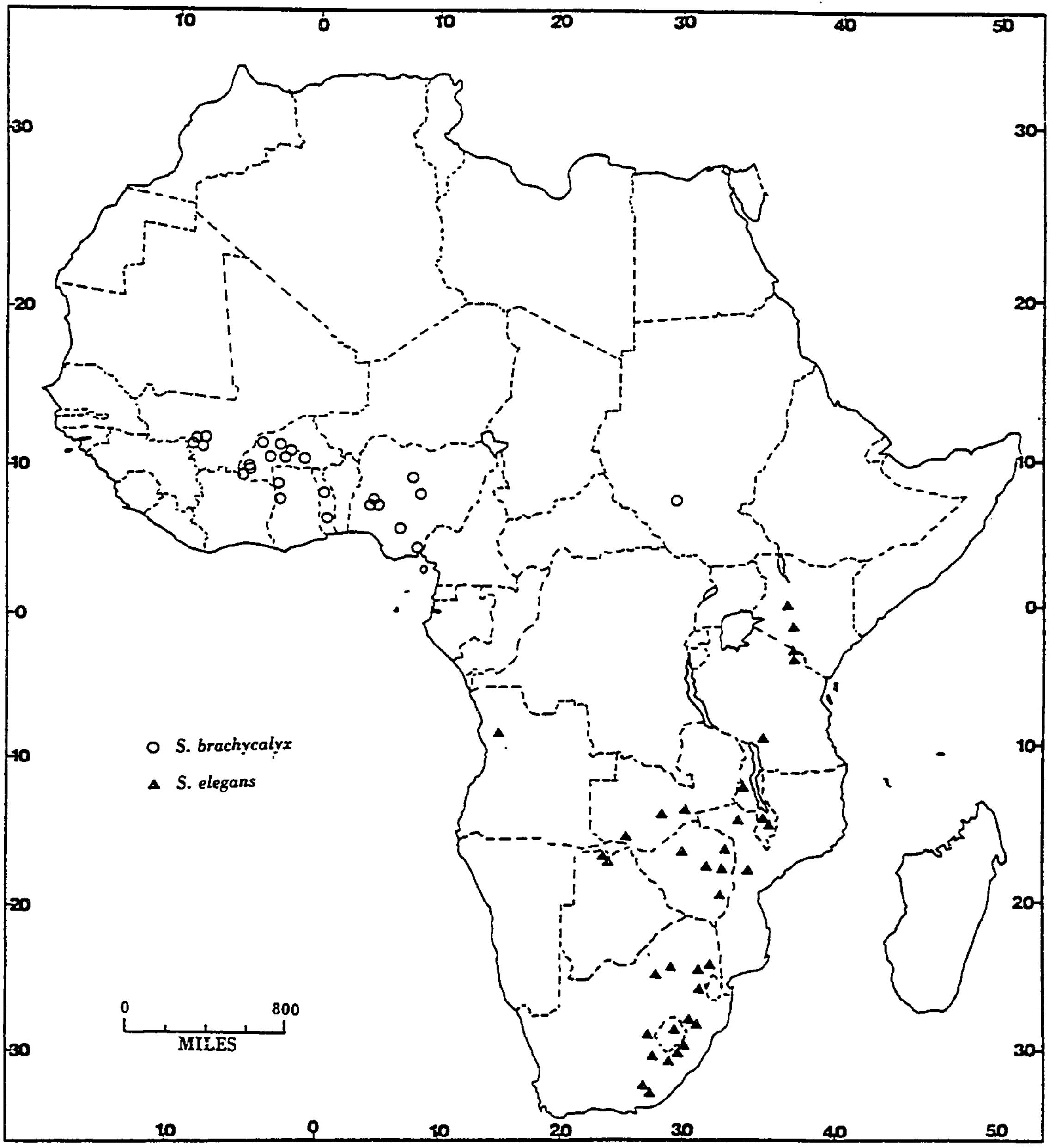

Fig. 7: Distribution of *Striga brachycalyx* and *S. elegans*.

village Bakma L. J. Musselman & K. I. Mohamed, 10/2/88; Dialakoro, 32 km S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88; Kati 11 km N. Bamako, L. J. Musselman & K. I. Mohamed, 10/6/88; Mafia, 11 km N. Koulikoro, L. J. Musselman & K. I. Mohamed, 10/1/88; 12 km N. Oulessebougou, L. J. Musselman & K. I. Mohamed, 9/30/88; Sanakoroba just S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88; Soulemanbougo, L. J. Musselman & K. I. Mohamed, 10/1/88. Nigeria: Bida/Mokwa junction, R. A. Mansfield, 9/4/78; Ilorin, Kwara State, V. Parkinson, 9/17/86. Togo: Togo Forest at 6° 29' N., 1° 09' E., Sd., (US).

9- *Striga chrysantha* A. Raynal, Bull. Jard. bot. natn. Belg. 39: 378, (1969).

Annual, small, tufted, densely pubescent plants. Leaves and bracts similar, scale-like, less than 10 mm long. Inflorescence a dense spike with alternate flowers. Calyx 10-ribbed, teeth 5, much shorter than tube. Corolla bright yellow; corolla tube slender, long, bent near its top, 20-25 mm long; lower lobes spreading, broadly rounded, upper lip reflexed backwards, bifid.

Endemic to Central African Republic and Zaire.

10- *Striga dalzielii* Hutch. in Hutch. & Dalz., Fl. W. Trop. Afr., ed. 1, 2: 225, (1931); Hepper in Fl. W. Trop. Afr. 2, 2: 371 (1963).

Plants annual, 19-35 cm tall. Leaves linear, or narrowly elliptic, becoming reduced along the stem, 15-35 mm long, 3-7 mm wide. Flowers sessile, opposite, forming very dense, short inflorescence. Lower and upper bracts similar, leaf-like, longer than calyces, 8-18 mm long, about 4 mm wide. Calyx 10-ribbed, tubular; teeth 5 unequal, shorter than the tube. Corolla pink, bent at top, 14-20 mm long; lower lobes broadly rounded, upper lip bifid.

Occupying the wet Guinea savannas in Guinea, Mali, and Nigeria. Related to S. *klingii.*

11- *Striga elegans* Benth. in Hooker's Comp. Bot. Mag. 1: 363 (1836); Skan in Fl. Trop. Afr. 4, 2: 408 (1906).

Plants annual, 30 (rarely 50) cm tall. Stem erect, obtusely square, furrowed, simple, or sparsely branched from the base, rarely from middle, densely hispid with divergent hairs. Lower leaves opposite, appressed, lanceolate, reduced, tips acute, 2-4 mm long, 1-2 mm wide; upper leaves scabrous, linear, or lanceolate, opposite, ascending, 6-20 mm long, 1-2 mm wide, rarely narrowly-elliptic, 35-50 mm long, 2-3 mm wide. Internodes 1-3.5(5) cm, leaves usually shorter than internodes. Inflorescence 2.5-10 cm, much shorter than the rest of the stem, flowers opposite, shortly pedicellate in a dense raceme, 4-12 flowers open per inflorescence branch. Lower and upper bracts similar, densely hispid, lanceolate, shorter than calyx, 3-12 mm long, 1-2 mm wide, or, rarely as long or longer than calyx, narrowly-lanceolate to narrowly-elliptic, 13-20 mm long, 1-5 mm wide. Bracteoles linear, 3-6 mm long, 0.5-1 mm wide. Calyx (10-15)-ribbed, one at least terminating each calyx tooth, hispid along ribs, tubular, 8-13 × 2 mm; calyx tube 6-7(9) mm long, teeth 5 equal, or 6 unequal, linear to lanceolate, 2-5 mm long. Corolla bright-red with a yellow throat, densely glandular-pubescent, bent at apex, 14-18 mm long, 1 mm wide; lobes of lower lip ovate, 5-10 mm long, 3-5(7) mm wide, upper lip bifid, wider than long, 3-5 mm long, 6-11 mm wide. Capsule 7 mm long, 2 wide; seeds 406 × 265 micron; style short, persistent, feather-like; stigma indistinctly bilobed, rough, not papillate. pollen somewhat sticky, perforate, persistent on stigma.

Striga elegans is common in East and South Africa. Its range extends from southern Kenya south into Tanzania, Malawi, Zambia, Zimbabwe, Mozambique, Swaziland, Botswana, Lesotho and widespread in the Republic of South Africa. Even in East Africa, its range does not extend north of the equator (Fig. 7).

Striga elegans superficially resembles *S. asiatica*. They occur sympatrically sharing the same geographical range in East Africa. *Striga elegans* can be distinguished from *S. asiatica* by its relatively short, dense inflorescence with opposite flowers, the large corolla lobes, and the yellow throat.

Botswana: North Dist., P. A. Smith, 2259 (MO). Kenya: Nairobi, A. B. Perceval, 1901 (MO); Rumuruti, Laikipia Dist. F. N. Hepper & A. Jaeger, 6618 (MO). Lesotho (Basutoland): Mont-aux-Sources, Adele Lewis Grant, 2212387 (MO). Mozambique: Paraia Sepulveda, J. Lavranos, 4265 (MO). South Africa: Ashbury, Dist. Pretoria, P. A. Smith, 1369 (MO); Boshasberg, L. MacOwan, 426 (GH); Caledon R., Bunke, 369 (GH); around Colenso, Natal, J. M. Wood, 92715 (MO); Crocodile R., Transvaal, R. Schlechter, 3979 (GH; MO); Farm "Erythrina", Trappes Valley, Bathurst Dist., R. D. A. Bayliss, 3080 (US); Fairfield, Dunvia, Natal, Awbeya, 1430 (MO); Garden Castle Nature Res. Underberg Dis. Magaliesberge, Transvaal, Schlieben, 7662 (US); Natal, O. M. Hilliard and B. L. Burtt, 7861 (MO); Garsfontein, Pretoria, L. C. C. Liebenberg, 8748 (MO); Griqualand, Orientalis, W. W. Tyson, 1368 (MO); Rte 528 near Haenertsburg, L. J. Musselman, 7038; 7039 (ODU); Kelland, Randburg, Transvaal, L. C. C. Liebenberg, 8581 (MO); N Kokstad, Natal, W. Haygarth, 92714 (MO); between Kraarivies and Witbergen, J. F. Drege 92713 (MO); Percy Fyfe Nature Reserve, Transvaal, B. J. Huntley, 2033 (MO); Pilgrim's Rest, Transvaal, W. Greenstock 1613834 (MO); Pretoria, Transvaal, Johannes, 26-1-22 (US); Raylon Pretoria, Rogers, 20943 (US); Southwell, eastern Cape, R. D. A. Bayliss 7468 (MO); Strydpoort Mountains, near Haenertsburg, L. J. Musselman, 7030 (ODU); near Umtata Falls, Transkei, Cape prov., Adele Lewis Grant, 3505 (MO); Woest Hill, Albany Dist. Cape, R. D. A. Bayliss, 4526 (GH; MO); Sd, Sd., 2069; 2482 (GH). Swaziland: Goedgegun, Louwsberg, J. H. Ross, 1743 (MO). Tanzania: Kullama, S. Kilimanjaro K. G. Linoblom, 1911 (S); S. slope Kilimanjaro, Moshi Dist. Greenway, 7840 (S); N. Lake Nyasa, Kyimbila Dist. A. Stolz, 2494 (GH; MO). Zimbabwe: Circular drive, Harare, N. K. Hughes, no number, (ODU); Gokwe, M. G. Bingham, 1178 (MO); Pungue R., Dist. Inyanga, N. Lelehase, 3673; 3674 (MO).

12- *Striga forbesii* Benth. in Hooker's Comp. Bot. Mag. 1: 364 (1836); Skan in Fl. Trop. Afr. 4, 2: 410 (1906); Broun & Massey, Fl. Sudan: 330 (1929); Andrews, Flow. Pl. Sudan 3: 146 (1956); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963); Musselman & Hepper, Kew Bull. 41 (1): 213-214 (1986).

Plants annual, stiffly erect, 37-72 cm tall. Stem 4-angled, grooved, simple, or sparsely branched usually from the base, scabrid-hispid, sparsely covered with short, divergent, or slightly retrorse hairs. Lower leaves reduced, ascending, lanceolate, margins entire, tips obtuse, 2-10 mm long, 2-6 mm wide; upper leaves opposite, lanceolate, sessile, ascending, tips acute, scabrid-hispid, coarsely toothed, (3-5)-nerved, 15-40(90) mm long, 3-12 mm wide. Internodes 2-5(7) cm, leaves usually shorter than internodes. Inflorescence 12(20) cm, usually shorter than the rest of the stem, flowers opposite, shortly pedicellate in open raceme. Lower bracts 3-nerved, lanceolate to narrowly-elliptic, spreading, or ascending, coarsely toothed, longer than calyx, 20-50(90) mm long, 3-12 mm wide; upper ones linear to lanceolate, margins entire, ciliate, shorter than calyx, 4-15 mm long, 1-2 mm wide. Bracteoles linear to lanceolate, 4-12 mm long, 0.5-2 mm wide. Calyx 10-15 ribbed, at least one terminating each calyx lobe, ribs hispid, calyx tubular, 9-14(20) × 3-5 mm; calyx tube 4-6 mm long; teeth 5 equal, broadly-lanceolate, as long as, or longer than tube, recurved, ciliate, 5-9(14) mm long. Corolla salmon-pink, densely glandular-pubescent; corolla tube very narrow, 20-25 mm long, 1 mm wide, bent at its top; lobes of lower lip spreading, obovate, 6-9 mm long, 3-6 mm wide, upper lip bifid, wider than long, 3-6 mm long, 6-9 mm wide. Capsule ovate to subovate, 5-7 mm long, 4-5 mm wide; seeds brown, 450 × 254 microns; style long persistent; stigma sticky, covered with fine hairs, pollen mass noticed on the stigma.

Striga forbesii is one of the most widely distributed species. It is common in the Sudanian domain savannas, from Senegal in West Africa to Somalia and extends south in East Africa reaching its southern limits in Transvaal, the Republic of South Africa (Fig. 8). Within these areas, it might be confined to the relatively wet savannas.

Because of its wide distribution in Africa, together with the fact that it has the potential to attack agricultural crops especially maize, sorghum and sugar cane, *S. forbesii* should be considered as an important economic species, similar to *S. hermonthica*, and special attention should be directed to its biology and reproduction. Preventive measures should be taken to limit its spread.

Striga forbesii resembles *S. latericea* and both share a number of characters: leaf-like bracts especially the lower floral bracts, large calyx teeth which are longer than calyx tube, and the salmon-pink corolla. *Striga forbesii* differs from *S. latericea* in that it possesses stiff hairs which give the plant a harsh texture, its coarsely toothed leaves which are generally broader than the leaves of *S. latericea* and the corolla of *S. forbesii* is consistently shorter with smaller lobes compared to that of *S. latericea.*

Botswana: near Pandamentenga, Chobe Reg., L. J. Musselman, C. R. Riches, & D. M. Ralston, 4/9/86 (ODU). Cameroon: near Guider, northern prov., L. J. Musselman, 10/13/88 (ODU). Malawi: Kyimbila, Nyasa, A. Stolz, 213 (GH); 2 miles N. Mzambazi, northern prov., J. Pawek, 13954 (MO); Nyasa Hochland-Stat. Kyimbila, A. Stolz, 213 (US). Somalia: Mareeri, Middle Juba Region, L. J. Musselman, 7086 (ODU). South Africa: Cultis Inanda, J. M. Wood, 7500 (US); Dist. Waterberg, Transvaal, Gaepin, 1709 (US). Swaziland: Swaziland Irrigation Scheme, Tshaneni, C. Parker, 1066 (ODU). Tanzania: IARI, near Kilosa, C. Parker, 2210 (ODU). Uganda: Omukatooma, Dist. W. Ankole, Rwaburindore, 1813 (US); Rhino Camp, Bahr El Jebel, E. Mearns, 2885 (GH). Zaire: Olru-Uele, J. Lebrun, 3557 (GH). Zimbabwe: Kwe Kwe, Midland Region, L. J. Musselman, 4/10/86 (ODU).

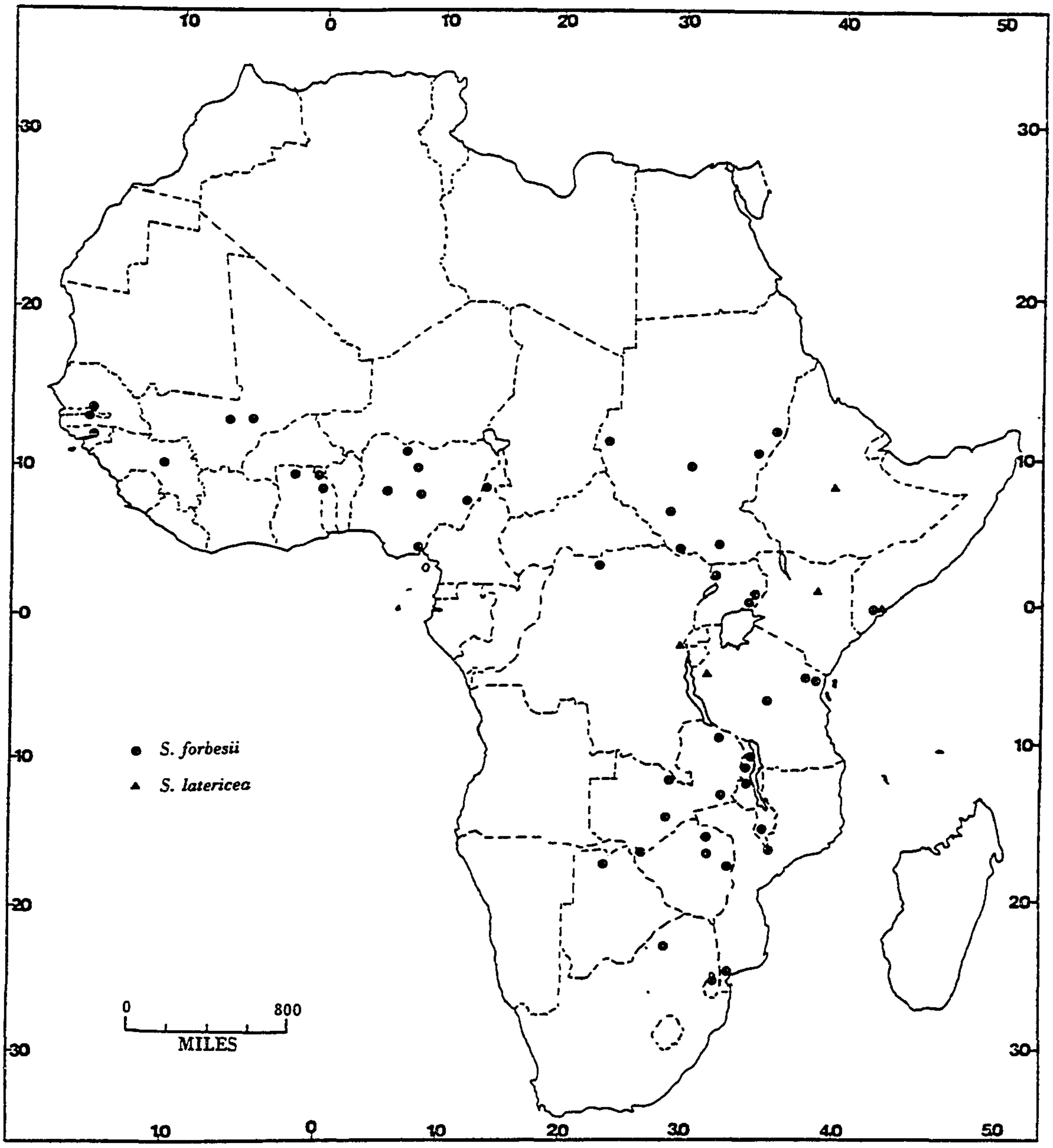

Fig. 8: Distribution of *Striga forbesii* and *S. latericea*.

13- *Striga fulgens* (Engl.) Hepper in Kew Bull. 38: 598 (1984).

Buchnera fulgens Eng., Bot. Jahrb. 28: 478 (1900) Skan in Fl. Trop. Afr. 4, 2: 392 (1906).

Perennial herb, up to 50 cm tall. Stem slender, densely branched. Lower leaves opposite, upper leaves subopposite, linear, 8-21 mm long, 1-2 mm broad. Inflorescence lax, flowers alternate. Bracts broadly lanceolate. Calyx 10-ribbed, tubular, 6-9 mm long. Flowers bright scarlet or orange-red, corolla tube cylindrical, 10-12 mm long, nearly glabrous outside.

Known only from the type specimen, Tanzania.

14- *Striga gastonii* A. Raynal, Bull. Mus. natn. Hist. nat. Paris, Sect. B, Adansonia, 3: 225-227 (1987).

Perennial, entirely glabrous, cespitose, 5 cm tall. Leaves and bracts scale-like, about 3.5 mm long. Spike dense, nearly extending from the base of plant. Calyx 5-ribbed; teeth 5 acuminate. Corolla purple; tube narrow, sparsely glandular pubescent, bent and expanded at top, 9 mm long; lower lobes acute, 4 mm long, upper lip bilobed.

Known only from the type specimen. Endemic to the lateritic plains in southern Tchad.

15- *Striga gesnerioides* (Willd.) Vatke in Oesterr. Bot. Zeitschr. 25: 15 (1875); Crowfoot, Fl. Pl. N. & C. Sudan: Fig. 136(1) (1928); Andrews Fl. Pl. Sudan 3: 144, Fig. 37 (1956); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 373 (1963); Musselman & Hepper, Kew Bull. 41 (1): 213-214 (1986).

Buchnera gesnerioides Willd., Sp. Pl. 338 (1801).

B. orobanchoides R. Br. in Endl., Bot. Zeit. 2: 388, t. 2 (1832).

Striga orobanchoides (R. Br.) Benth. in Hooker's Comp. Bot. Mag. 1: 361 (1836); Skan in Fl. Trop. Afr. 4, 2: 402 (1906); Broun & Massey, Fl. Sudan: 329 (1929); Crowfoot, Illus. Fl. Sudan, Fig. 136 (1928).

S. orchidea Hochst. in Fl. XXIV. 43 (1841).

Plants annual, or occasionally perennial, cespitose succulent, 5-30 cm tall. Stem simple or usually branched from the base, square and grooved, sparsely to densely hispid or densely pubescent, with appressed, ascending, or divergent hairs, drying black or brown. Plants with copious adventitious roots arising from subterranean scales. Leaves generally scale-like, opposite to subopposite, whorled or even rosette, appressed, scabrous-pubescent or scabrous-hispid; lower leaves lanceolate to broadly lanceolate, 3-6 mm long, 1-4 mm wide; upper leaves lanceolate to narrowly lanceolate, 4-10 mm long, 1-3 mm wide. Flowers opposite to subopposite, shortly pedicellate in simple raceme, or sessile in simple spike, dense, occupying much of the stem, or sparse 3-8 per inflorescence. Bracts lanceolate, as long as or shorter than calyx, scabrous, hispid along margins, 2.5-6 mm long, 2-3 mm wide. Bracteoles subulate, margin hispid, 2-4 mm long, .5-1 mm wide. Calyx 5-ribbed, pubescent or hispid at least on ribs; calyx tube 3-6 mm long, 2-3 mm wide; teeth short, acuminate, pilose or hispid along margins, 1-2 mm long. Corolla blue to dark purple or sometimes white or creamy-white, hairy-pubescent, or with very few hairs corolla tube 8-14 mm long, bent at its top, 1 mm or less wide; lobes of the lower lip ovate, spreading, 2-6 mm long, 1.5-3 mm wide, upper lip bifid, usually wider than long, 1-2 mm long, 2-2.5 mm wide. Capsule ovate to subovate, flat, 4-7 mm long, 2-4 mm wide; style short or very long, hairy or glabrous, persistent with pollen mass attached to the sticky stigma.

Striga gesnerioides is the most widely distributed of all *Striga* species in Africa. It can be found anywhere south of the Sahara with the strains specific to *Euphorbia* species occupying the relatively drier regions (Fig. 9). It is the only species present in Morocco (Raynal-Roques 1991). This wide distribution could be attributed to the development of host-specificity, which allow the species to occupy a variety of habitats. *Striga hermonthica*, *S. asiatica* and *S. gesnerioides* are the only three species found north of the Sahara.

We can safely assume that *S. gesnerioides* only parasitizes broad-leaved plants. This feature, plus the succulence and the cespitose growth habit, the reduction of leaves, and the masking of the chlorophyll with other pigments identify *S. gesnerioides* and its close relatives from other members of the genus. *Striga gesnerioides* is closely related to and probably arose from an ancestor common to *S. lepidagathidis*, *S. gastonii*, and *S. chrysantha*.

The species is regarded among the most variable taxa within the genus. It has evolved a number of host-specific strains each of which is adapted to a narrow host-range. However, the morphological differences among the strains do not justify splitting the taxon into different species or even subspecies (see comments under variation in *S. gesnerioides*). I have chosen to consider - in some detail - the morphology of each strain separately not only to show the differences but also the similarities between the strains.

Angola: Catete, Sd, 9200 (US). Botswana: 88 km S. Gomare on Rd. to Kokame, L. J. Musselman, C. R. Riches and D. M. Ralston, 4/8/86 (ODU); 100 miles W. Lobatse on Malopo Rd., P. J. Mott, 1091 (MO); Cape Verde St., Jago, Wilkes, 1838-1842 (US); margins of small pan, L. J. Musselman, 7012; 7013 (ODU). Congo: Faradje-Olru, L. Lebrun, 3535 (MO). Ethiopia: Abyssiniae, Barbey, 1051 (US); Erer River area, 60km W. Dawa on Hwy to Addis Ababa, Burger, 914 (US); Harar prov., Burger, 2846 (US). Ghana: Sandema, UER, Shannon, 88-44 (US). Kenya: near Hunter's lodge on Nairobi-Mombasa Rd., Machakos Dist., Faden, 77/309 (US). Malawi: Sd, Buchanan, 1141 (US).

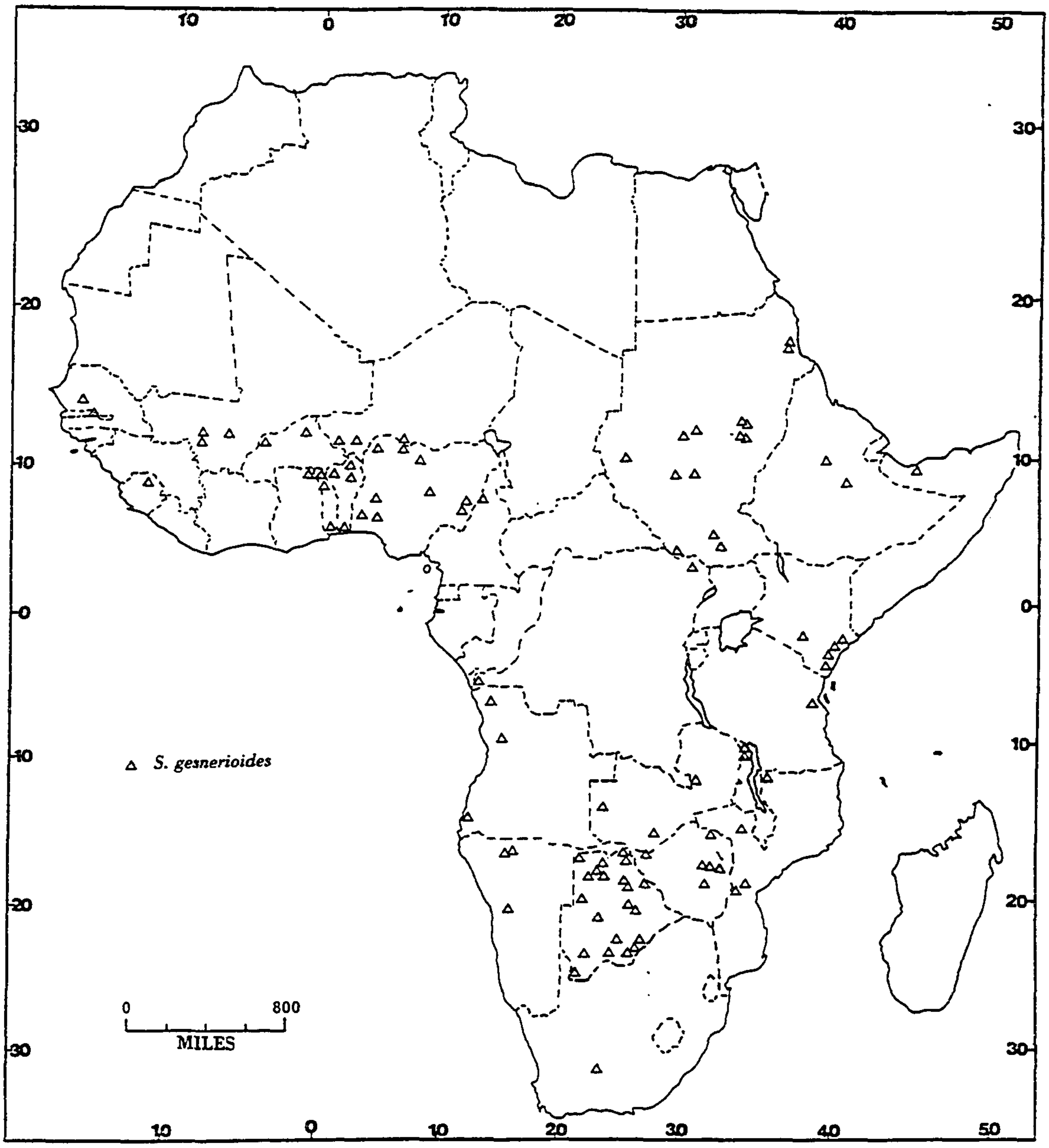

Fig. 9: Distribution of *Striga gesnerioides*.

Namibia: along Rd. to Ethosha Pans Nat. Park, L. J. Musselman & J. H. Visser, 4/2/86 (ODU); Karibib, Reg. Otisondu, Seydel, 4491 (US). Sudan: near Telo, South Kordofan prov., L. J. Musselman, 6174 (ODU).

Euphorbia Strain:

Stiffly erect perennial plant, 9-25 cm tall. Stem purple when fresh, simple, or sparsely branched from the base, terete, thick, covered with fine dense mainly retrorse, rarely divergent hairs, drying brown. Lower leaves appressed, opposite or whorl, reduced, broadly-lanceolate, 4-6 mm long, 3-5 mm wide; upper leaves reduced, lanceolate, opposite or whorled (3/node), appressed, scabrous-pubescent, 5-8 mm long, 2-3 mm wide. Internodes 0.5-3.5 cm. Inflorescence 6-17 cm, very much longer than the rest of stem, flowers opposite to subopposite in dense spike, 2-6 flowers open per inflorescence branch. Lower and upper bracts similar, lanceolate, ciliate, incurved, shorter than calyx, 4-9 mm long, 2-3 mm wide. Bracteoles subulate, 4 mm long, 1 mm wide. Calyx entirely pubescent, 5-ribbed, calyx 7-9 × 3 mm; calyx tube 5-6 mm long; teeth 5 unequal, ciliate, lanceolate, half the tube length, 2-3 mm long. Corolla mauve to pale mauve, sparsely hairy, corolla tube 10-12 mm long, 1 mm wide, bent at top; lobes of lower lip obovate, longer than wide, 3 mm long, 2 mm wide, upper lip indistinctly bilobed, wide-obovate, wider than long, 2 mm long, 3 mm wide. Capsule ovate to subovate, 7 mm long, 3-4 mm wide; seeds brown, 385 × 234 microns; style short, hairy, persistent, pollen mass still attached to the sticky stigma.

Ethiopia: 1 km NE Desse near Borkenna R., Wello prov., J. Sutherland, 381 (MO). Namibia: Great Karas Mountains, Great Namaqualand, Van Ortendahl, 487 (UPS). Sudan: Jebel Mawnja, Red Sea prov., L. J. Musselman, 6180 (ODU). South Africa: Bank of Kareiga R., Bathurst Dist., R. D. A. Bayliss, 5212 (GH); Douglas Heights, Albany Dist., R. D. Bayliss, 3158 (GH).

Indigofera Strain:

Plants annual, up to 18 cm tall. Stem erect, sparsely branched mainly from base, obtusely square, furrowed, densely covered with soft, divergent hairs, drying black. Lower and upper leaves similar, opposite, appressed, lanceolate, reduced, 2-6 mm long, 1-2 mm wide. Internodes short, does not exceed 1 cm long. Inflorescence up to 14 cm, longer than the rest of stem, flowers opposite to subopposite in loose spike, 2-6 flowers open per inflorescence branch. Lower and upper bracts similar, lanceolate, ciliate, shorter than calyx, 3-4(6) mm long, 1-2 mm wide. Bracteoles linear, 3-4 mm long, 0.5 mm wide. Calyx tubular, ribs hispid, transparent between ribs, 5-7 × 1-2 mm; calyx tube 3-4 mm long; teeth 5 equal, or almost so, narrowly-lanceolate, ciliate, about the same length as tube, 2-3 mm long. corolla sparsely hairy, 7-10 mm long, 1 mm wide bent just above calyx; lobes of lower lip obovate, obtuse, usually longitudinally rolled inside when dry. longer than wide, 4-5 mm long, 2 mm wide, upper lip bifid, obtuse, obovate, 2-3 mm long, 2.5-3 mm wide. Capsule obovate, about 4 × 2 mm; seeds brown, 319 × 206 microns; style persistent, expanded at top, pollen mass noticed on stigma.

Sudan: Jebel Obeid, Abu Naama, K. I. Mohamed, 10/25/88 (ODU).

Ipomoea Strain:

Plants annual, 15-32 cm tall. Stem erect, obtusely square, grooved, simple or usually branched from the base, scabrous, very sparsely hispid, with divergent, soft, short hairs, drying black. Lower and upper leaves similar, reduced, opposite, appressed, lower broadly lanceolate, 2-3 mm long, 2 mm wide, upper narrowly-lanceolate, 4-12 mm long, 1-2 mm wide. Internodes long, 1-4 cm. Inflorescence up to 20 cm, as long, or longer than the rest of stem, flowers opposite in open spike, 2-4 flowers open per inflorescence. Lower and upper bracts similar, lanceolate, tips slightly incurved, shorter than calyx, 3-6 mm long, 1-2 mm wide. Bracteoles 3-4 mm long, 0.5 mm wide. Calyx 5-ribbed, ribs hispid, 5-7 × 2 mm; calyx tube 3-5 mm long; teeth 5 unequal, acuminate, or triangulate, ciliate, shorter than tube, 2-3 mm long. Corolla blue, with very few hairs, almost glabrous, corolla tube 9-13 mm long, 1 mm wide, angled at top; lobes of lower lip spreading, oval, 3-5 mm long, 2-3 mm wide, upper lip bifid, wide-obovate, 2-3 mm long, 2-4 mm wide. Capsule subovate, flattened, 4 mm long, 2 mm wide; seeds dark-brown, 298 × 204 microns; style very long, persistent; stigma with persistent pollen.

Mali: 14 km N. Koulokani, L. J. Musselman & K. I. Mohamed, 10/6/88 (ODU). Senegal: 10 km N. Dakar, L. J. Musselman et al, 7066 (ODU); Kheur Serigne Sarr, 16 km E. Diourbel, prov. Central, L. J. Musselman et al., 7064 (ODU). Sudan: Balangya, South Kordofan prov., L. J. Musselman, 8/23/86 (ODU).

Jaquemontia Strain:

Plants annual, up to 30 cm tall. Stem erect, simple, or sparsely branched at base, obtusely square, furrowed, sparsely to densely pilose with divergent hairs, drying black. lower and upper leaves similar, reduced, opposite, appressed; lower leaves broadly-lanceolate, 2-3 mm long, 2 mm wide; upper leaves lanceolate, 4-10 mm long, 1-2 mm wide. Internodes 2-4 cm long. Inflorescence up to 18 cm, very much longer than the rest of stem, flowers opposite in open spike, 2-4 flowers open per inflorescence branch. Lower and upper bracts similar, lanceolate to broadly-lanceolate, incurved, ciliate, shorter than calyx, 3-8 mm long, 2 mm wide. Bracteoles linear, 2-4 mm long, 0.5-1 mm wide. Calyx 5-ribbed, ribs hispid, 5-8 × 2 mm, tubular/obovate; calyx tube 4-6 mm long; teeth 5 unequal, acuminate, much shorter than tube, 1-2(3) mm long. Corolla pale blue, or mauve, with very few hairs, 8-11 mm long, 1 mm wide, bent at top; lobes of lower lip obovate, 3-4 mm long, 2-2.5 mm wide, upper lip widely obovate, indistinctly bifid, 2 mm long, 3 mm wide. Capsule oval to subobovate, 5-6 × 2 mm; seeds dark-brown, 314 × 202 microns; style persistent, long, laterally flattened, densely hairy at apex, pollen mass evident on the sticky stigma.

Niger: Kane, 224 km from Niamey on Maradi Rd., C. Parker, 2312 (ODU); Maradi, C. Parker, 2031 (ODU). Nigeria: Jos-Shendam Rd., D. A. Knepper 8/26/89 (ODU). South Africa: Sd, L. J. Musselman, 6269 (ODU).

Merremia Strain:

Plants annual, up to 18 cm tall. Stem succulent when fresh, cespitose, stiffly erect, obtusely square, furrowed, sparsely to densely pilose, hairs divergent, drying black. Lower and upper leaves similar, reduced, opposite, appressed; lower leaves broadly-lanceolate, 2-4 mm long, 2-3 mm wide; upper leaves lanceolate, 4-8 mm long, 1-2 mm wide. Internodes short, 2 cm long. Inflorescence very long, up to 14 cm, longer than the rest of stem, flowers imbricate forming somewhat dense spike, 2-8 flowers open per inflorescence branch. Lower and upper bracts similar, broadly-lanceolate, ciliate, incurved, shorter than calyx, 4-8 mm long, 1-3 mm wide. Bracteoles lanceolate, 3-4 mm long, 1 mm wide. Calyx 5-ribbed, ribs hispid, obovate, 5-6 × 2 mm; calyx tube 3-4 mm; teeth 5 unequal, acuminate, shorter than tube, about 2 mm long. Corolla very sparsely pubescent, 8-10 mm long, 1 mm wide, bent at top, lobes of lower lip obovate, usually longitudinally rolled inside when dry, 3-5 mm long, 1-2 mm wide, upper lip bifid, 2 mm long, 2.5-3 mm wide. Capsule oval to subovate, 4-5 × 2 mm; seeds brown, 302 × 184 microns; stigma persistent, long, hairy especially at apex, expanded at top, pollen mass noticed on stigma.

Sudan: Tozi, southern part of the Blue Nile prov., K. I. Mohamed, 10/26/88 (ODU).

Nicotiana Strain:

Plants annual, 5-22 cm tall. Stem simple, slender, obtusely square, furrowed, covered with dense, short, soft, divergent hairs, drying brown. Leaves opposite, reduced, appressed; lower leaves broadly-lanceolate, 1-4 mm long, 1-2 mm wide; upper leaves narrowly-lanceolate, scabrous-hispid, 4-12 mm long, 1-2 mm wide. Internodes 1-3 cm long. Inflorescence up to 11 cm, usually shorter than the rest of stem, flowers sparse, opposite in lax spike, 2-3 flowers open per inflorescence branch. Bracts lanceolate, incurved, ciliate; lower bracts as long, or longer than calyx, 7-9 mm long, 2-2.5 mm wide; upper bracts shorter than calyx, 3-6 mm long, 1-2 mm wide. Bracteoles linear, 3-4 mm long, 1 mm or less wide. Calyx 5-ribbed, ribs hispid, tubular, 4-7 × 2-3 mm; calyx tube 3-4 mm long; teeth 5 unequal, acuminate, ciliate, shorter than calyx, 1-2 (rarely 3) mm long. Corolla pink/mauve, with very few hairs or glandular-hairs; corolla tube 8-10 mm long, less than 1 mm wide bent at its top; lobes of lower lip obovate, 2-3 mm long, 1-2 mm wide, upper lip bifid, 2 mm long, 2.5 mm wide. Capsule obovate, 4 mm long, 2-3 mm wide; seeds light-brown, 306 × 200 microns; style long, persistent; stigma sticky with some pollen attached to its surface.

Niger: near the Weed Research Organization Station, C. Parker, 1316; 2265 (ODU).

Tephrosia Strain:

Plants annual up to 23 cm tall. Stem slender, simple, or sparsely branched from base or below middle, obtusely square, furrowed, stem with very few hairs, almost entirely glabrous, drying brown. Lower and upper leaves similar, reduced, opposite, appressed, lanceolate, 2-8 mm long, 1-2 mm wide. Internodes up to 2.5 cm long. Inflorescence up to 14 cm, very much longer than the rest of stem, flowers opposite to subopposite in open spike, 2-4 flowers open per inflorescence branch. Lower and upper bracts similar, broadly-lanceolate, ciliate, shorter than calyx, 3-6 mm long, 1.5-2 mm wide. Bracteoles 3-4 mm long, 0.5-1 mm wide. Calyx mostly obovate, ribs hispid, 5-6.5 × 2 mm; calyx tube 4-4.5 mm long; teeth 5 unequal, acuminate, ciliate, very short, 1-2 mm long. Corolla blue very sparsely pubescent, 8-10 mm long, 1 mm wide, bent at top; lobes of lower lip oval, 2-4 mm long, 1-2 mm wide, upper lip bifid, 2 mm long, 2.5-3 mm wide. Capsule oval to subobovate, 4-5 × 2 mm; seeds black, 313 × 200 microns; style long, persistent, hairy, expanded at top, pollen mass persistent on the stigma.

Burkina Faso: 5 km north Tenkodogo, S. B. Safa & L. J. Musselman, 10/9/87 (ODU). Cameroon: 29 km S. Garoua, L. J. Musselman & others, 10/16/88 (ODU). Nigeria: Mokwa, Niger State, D. A. Knepper, 9/19/89 (ODU).

Vigna Strain:

Plants annual, 8-26 mm tall. Stem stiffly erect, cespitose, obtusely square, grooved, sparsely hispid with somewhat soft, divergent hairs, drying black. Lower and upper leaves similar, opposite, appressed, scabrous-hispid, lower leaves broadly-lanceolate, 2-4 mm long, 2 mm wide; upper ones lanceolate, up to 11 mm long, 1-2 mm wide. Internodes 1-3 cm long. Inflorescence up to 10 cm, as long, usually shorter than the rest of stem, flowers opposite forming somewhat dense spike, 2-6 open per inflorescence branch. Bracts lanceolate, hispid along margins and midribs, incurved; lower bracts as long, or longer than calyx, 6-9 mm long, 2-2.5 mm wide; upper bracts, shorter than calyx, 3-6 mm long, 2 mm wide. Bracteoles linear, ciliate, 2-3 mm long, 0.5 mm wide. Calyx 5-ribbed, ribs hispid, slightly obovate, 5-6 × 2 mm; calyx tube 3-4 mm long; teeth 5 unequal, acuminate, ciliate, 1.5-2 mm long. Corolla purple, with very few soft hairs, appearing glabrous, corolla tube 8-10 mm long, 1 mm wide, bent at top; lobes of lower lip spreading, obovate, slightly inrolled, 2-3 mm long, 1-2 mm wide, upper lip bifid, wider than long, 1-2 mm long, 2 mm wide. Capsule ovate to subovate, 4 mm long, 2 mm wide; seeds dark-brown, 304 × 198 microns; style long, persistent, pollen mass still present on the stigma.

Burkina Faso: 5 km S. Gourcy, S. B. Safa & L. J. Musselman, 10/10/87 (ODU). Mali: Sotuba near Bamako, L. J. Musselman & K. I. Mohamed, 10/1/88 (ODU). Niger: near WRO Station, C. Parker, 2264 (ODU). Nigeria: Near Kano airport, Kano State, D. A. Knepper, 8/24/89; 8/22/89 (ODU).

16- *Striga hallaei* A. Raynal, Bull. Jard. Bot. Natn. Belg. 39: 374 (1969).

Annual, stiffly erect, unbranched, up to 60 cm tall. Leaves lanceolate, shortly petiolated, coarsely toothed, 3-nerved, up to 70 mm long, 30 mm wide. Bracts leaf-like, longer than calyx. Calyx 5-ribbed, glandular-pubescent; teeth 5 equal, twice as long as the tube. Corolla salmon pink; tube slender, bent at top, 22-25 mm long; lower lobes three, broadly rounded, upper lip bifid.

The only known species within the genus that inhabits openings within the rain forest. Known from Gabon and Zaire.

17- *Striga hermonthica* (Del.) Benth. in Hooker's Comp. Bot. Mag. 1: 365 (1836); Skan in Fl. Trop. Afr. 4, 2: 407 (1906); Crowfoot, Fl. Pl. N. & C. Sudan: Fig. 136(2) (1928); Broun & Massey, Fl. Sudan: 330 (1929); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 372 (1963). Musselman & Hepper, Kew Bull., 41 (1): 216-218 (1986).

Buchnera hermonthica Del., Fl. Egypte: 245, t.34 Fig. 3 (1813).
Striga senegalensis Benth. in DC. Prodr. 10: 502 (1846).

Plants annual up to 90 cm tall. Stem square, furrowed, with few to many dichotomous branches from the middle, scabrous, sparsely to densely hispid, hairs divergent at the base of the stem, ascending above. Plants rarely albino. Lower leaves reduced, opposite, appressed, broadly-lanceolate, 2-8 mm long, 1-3 mm wide; upper leaves linear to narrowly-elliptic, opposite, spreading or ascending, 15-110 mm long, 2-8(17) mm wide. Internodes 2-5 cm, leaves longer than internodes. Inflorescence 4-25(40) cm, usually much shorter than the rest of the stem, flowers opposite in simple spike, spike lax at its base, dense above, usually many flowers (>10) open per inflorescence branch. Lower bracts linear to narrowly-elliptic, spreading or ascending, ciliate, longer than calyx, 12-50(95) mm long, 2-5(10) mm wide; upper bracts lanceolate, ascending, ciliate, as long, or just shorter than calyx, 5-12 mm long, 1-2 mm wide. Bracteoles linear, 4-15 mm long, 0.5 mm wide. Calyx 5-ribbed, ribs hispid, ovate, 7-12 × 2-3 mm; calyx tube 5-10 mm; teeth 5 unequal (adaxial reduced to 1 mm or less); teeth very short, acuminate, ciliate, 2-4 mm long. Corolla pink or mauve, rarely white, sparsely hairy, rarely glandular-pubescent; corolla tube (13)16-20 mm long, 1-2 mm wide, bent and expanded immediately above calyx or at its middle; lobes of lower lip obovate, 7-15 mm long, 3-6(10) mm wide, upper lip obovate, bifid, longer than wide, 4-9 mm long, 4-7 mm wide. Capsule ovate, 3-6 mm long, 1.5-3 mm wide; seeds light-brown, 366 × 201 microns; style persistent, long, exceeding calyx; stigma bilobed, with few stiff hairs on its surface.

Striga hermonthica is considered one of the most serious pest of food crops (sorghum, maize, millet) especially in the Sahelian and the Sudanian domains in Africa. It is also an environmental pollutant since it is one of the main reasons behind the use of chemicals, shifting agriculture, abandonment of lands, emigration and starvation. Its range extends from Senegal to Ethiopia and it reaches its southern limits in Zaire and Malawi; also known from a few collections from Angola, Namibia, and the Nile Delta, Egypt (Fig. 5). However, the species is abundant and frequently common on cultivated cereals in the Sahel and the Sudanian savannas. In this region, the species develops two host-specific strains. The first is common further north in the sub-Sahara of Africa and attacks millet, the main crop in this region while the second is common further south hosted by sorghum, the main food crop. Here, it is not found in native grasslands except in the Nuba Mountains of the Sudan Republic (Musselman and Hepper 1986) where it may be a native.

Striga hermonthica resembles S. *aspera* (see comments under the latter for the key characters of both species). The morphological description above is based on specimens collected from north of the equator and they did not differ from the type S. *hermonthica*. However, S. *hermonthica* from south of the equator shows some deviations. The specimens number 1304 and 1330 from Malawi, and specimen number 2108 collected from Tanzania have the main features of S. *hermonthica* ; a spike that is laxed-flowered at its base, and dense at its top; a corolla that is never glandular-pubescent but hairy on its outside; a corolla that bent just above calyx; a triangulate, acuminate, and shorter calyx teeth, with the adaxial one being reduced to less than one mm, as well as differ in that they possess a slender, unbranched stem; narrower, erect leaves which are linear-elliptic or subobovoid; their upper bracts are abruptly different from the lower bracts; corolla tube is short with smaller lobes; and the calyces are much smaller compared to those of S. *hermonthica* from north of the equator.

Angola: Catete, Sd, 9199 (US). Burkina Faso: Lai, C. Parker, 2306 (ODU); 60 km E. Ouagadougou, S. B. Safa & L. J. Musselman, 10/9/87 (ODU). Egypt: on the River Nile, near Cairo, J. T. Moggridge, 1868 (US); Rodah, near Cairo, G. Schweinfurth, 1880 (US); Sd, Radjil, 594 (GH). Ethiopia: N. of Addis Ababa, Shoa prov., J. G. Meyer, 7594 (US); Waldia, prov. Yedjo, Abyssinia, H. V. Harlan, 1029870 (US); W. Gojjam, C. Parker, 4075 (ODU). Ghana: Navrongo, Upper Region, O. Ryding, 120 (UPS); Winkogo to Togo Rd., Hossain and Agyakwah, GC37957 (US). Malawi: Dedza Mt. forest, Dedza, A. J. Salubeni, 1330 (MO); Kyimbila, A. Stolz, 1304 (MO). Mali: Kangounmani, Nr Masantola, C. Parker, 1994 (ODU); Sotuba, Bamako, L. J. Musselman & K. I. Mohamed, 10/1/88 (ODU). Niger: 2 km W. Maradi (Niamey Road), C. Parker, 2316; 2317 (ODU); Collected on the Niger, W. B. Baikie, 1865 (GH); Vogel Mountains, F. Niger, 495 (UPS); Sd, C. Barter, 136; 1821 (GH). Nigeria: Anguna-Malami, Zaria, D. A. Knepper, 9/24/89 (ODU); 6 km E. Azare, Bauchi State, D. A. Knepper, 9/22/89 (ODU); Damari R. Basin 15 km up River from jct. at Tubo River, T. B. Croat, 53417 (MBGU); Jos-Shendam Rd., D. A. Knepper, 8/26/89 (ODU); Koriga, Kaduna State, D. A. Knepper, 9/20/89 (ODU); Mokwa, L. J. Musselman & R. A. Mansfield, 5535 (ODU); Sakaru-Zaria, 30 km E. Zaria, Kaduna State, D. A. Knepper, 9/23/89 (ODU); IRA at Samaru, L. J. Musselman & R. A. Mansfield, 5527 (ODU); 28 km. N. Zaria on Kano Road, C. Parker, 2321 (ODU). Senegal: Sd, Rogers, 1821 (GH). Sudan: Abu Naama, Blue Nile prov., K. I. Mohamed, 10/27/88 (ODU); Barakat, Gezira, L. J. Musselman, 6139 (ODU); S. of Doka, Kassala, L. J. Musselman, 6279 (ODU); S. of El Obeid, North Kordofan prov., L. J. Musselman, 6155 (ODU); Hag Abdulla, Gezira, L. J. Musselman, 6140 (ODU); Jebel Abal, Abu Naama, Blue Nile prov., K. I. Mohamed, 10/25/88 (ODU); Jebel Obied, Abu Naama, Blue Nile prov., K. I. Mohamed, 10/25/88 (ODU); Jebel Randwat, Abu Naama, Blue Nile prov., K. I. Mohamed, 10/25/88 (ODU); Kenana, Blue Nile, L. J. Musselman, 6143; 6144; 6145 (ODU); C. Parker, 2332 (ODU); Khartaget, N. Kordofan, L. J. Musselman, 6162 (ODU); Nuba Mountains, South Kordofan prov., E. Boicher, 1841 (GH); Rigaba, Abu Naama, Blue Nile prov., K. I. Mohamed, 10/25/88 (ODU); Tozi, Abu Naama, Blue Nile prov., K. I. Mohamed, 10/26/88 (ODU); Um Shagera, Kassala, L. J. Musselman, 6152 (ODU). Tanzania: Mahenge, Schieben, 2108 (S); Mwanza, Lake prov., Davis, no. 2 (US); Greenway, 7392 (US). Uganda: along Bahr El Jebel, between Nimule and Gondokoro, E. A. Mearns, 3005 (GH). Zaire: Faradje-thuri, J. Lebrun, 3374 (GH); Ithwa, Reeda, 1370 (US); Libenge, J. Lebrun, 1759 (GH); Moba-Katungu, Mitte, 314 (US); Niabembe, Steyagi, no. MF (US); Rutshuru, Ghesquiere, 3724 (GH).

18- *Striga hirsuta* (Benth.) K. I. Mohamed *comb. nov.*

Striga hirsuta Benth. in DC., Prodr. 10: 502 (1846).

Plants very small 2-6(20) cm tall. Stem slender, simple, or sparsely branched from middle, sparsely to densely hispid, hairs ascending. Lower leaves opposite, appressed, linear, 0.5-3 mm long, 0.5 mm or less wide; upper leaves reduced, subopposite/ alternate, incurved, ascending, linear to narrowly-lanceolate, 3-15 mm long, 0.5-1 mm wide. Internodes less than 1 cm long, leaves as long, usually shorter than internodes. Inflorescence up to 14 cm long, very much longer than the rest of stem, flowers alternate in open raceme, 1-2 flowers open per inflorescence branch. Lower bracts narrowly-lanceolate, recurved, hispid along margins and midribs, longer than calyx, 6-15 mm long, 1 mm wide; upper bracts lanceolate, as long, or slightly shorter than calyx, 2-5 mm long, 0.5-1 mm wide. Bracteoles linear, 3-5 mm long, 0.5 mm wide. Calyx tubular, hispid along ribs, 4-5.5 × 2 mm; calyx tube 2-3 mm long; teeth 5 equal, tapering at apex, as long, or slightly shorter than tube, 1.5-2.5 mm long. Corolla red with yellow throat, sparsely glandular-pubescent, 8-10(12) mm long, 0.5-1 mm wide, bent at top; lobes of lower lip 2-3(5) mm long, 1-2(3) mm wide, upper lip bifid, 1-2 mm long, 2-4 mm wide; seeds brown, 301 × 163 microns.

Striga hirsuta is common in the Sudanian savanna. Its range extends from Senegal to Ethiopia and south into Kenya, Tanzania, Malawi and Angola (Fig. 4). West Africa is probably the center of origin of S. *hirsuta* because it is abundant in native grasslands and as far as is known it does not attack crops in adjacent fields.

Striga hirsuta is typically a small plant. It emerges, flowers, and matures in a fairly short time yet not reaching up to two inches in height. Most of the above-ground stem is occupied by the inflorescence.

Striga hirsuta has simple or sparsely branched stems (below the middle), with ascending hairs; linear, reduced, opposite or subopposite, ascending leaves; internodes less than 1 cm, leaves as long or shorter than internodes; the lax raceme with alternate flowers; calyx teeth 5 equal, as long or slightly shorter than tube; corollas small with small lobes.

Burkina Faso: Fada-N'Gourma, S. B. Safa & L. J. Musselman, 10/25/87 (ODU). Cameroon: near Guider, northern prov., L. J. Musselman & others, 10/13/88 (ODU). Eritrea: Abyssiniae Reg. Gafata, Sd., 1842 (US). Ethiopia: Defo, near Gelemso, Harar prov., C. Parker, 4041 (ODU). Mali: Baguineda, 22 km E. Bamako, L. J. Musselman & K. I. Mohamed, 10/8/88 (ODU); Bakma, S. Bamako, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); Dialakoro, 32 km S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88 (ODU); Kamesoba, between Bamako-Siby, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); Mafia, 11 km N. Koulikoro, L. J. Musselman & K. I. Mohamed, 10/1/88 (ODU); between Siby and Kongula, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU). Liberia: Harper, Maryland Co., J. T. Baldwin Jr., 5988 (US). Niger: Gafata, prov. Tigre, Sd., 1842 (GH); Sd, C. Barter, 530 (ODU). Nigeria: Jos-Plateau State, D. A. Knepper, 8/25/89 (ODU). Seychelles Isl.: Vallee de Mai, E. R. Belle, 196 (GH). Sudan: near Balangya, South Kordofan prov., L. J. Musselman, 8/23/86 (ODU). Tanzania: Biharamulo, on Nyamirembe Rd., H. Balslev, 447 (MO). Zaire: Ombane, C. R. Aschemeier, 11 (US).

19- *Striga junodii* Schinz. in Mem. Herb. Boiss 10: 62 (1896-1900).

Perennial, stiffly erect plants, 30-60 cm tall. Stem simple, or mainly branched from base, 4-angled, ridged, scabrid-hispid, stem hairs short, stiff, curved upward. Lower leaves opposite, scale-like, appressed, narrowly-elliptic, tips acute, 2-4 mm long, 1 mm wide; upper leaves linear, ascending, opposite below, alternate above, margin entire, tips acute, scabrous, hispid along margins and midrib, 10-30 mm long, 1-2 mm wide. Internodes 1-4.5 cm, leaves shorter than internodes. Inflorescence up to 12 cm, much shorter than the rest of the stem, flowers 5-10 per inflorescence, shortly pedicellate, alternate in open raceme, 1-2 flowers open per inflorescence branch. Lower and upper bracts similar, linear, shorter than calyx, 2-12 (usually 3-5) mm long, 1 mm wide. Bracteoles minute, 2 mm long, less than 0.5 mm wide. Calyx 15-18-ribbed, three terminating each calyx tooth, ribs conspicuous, hispid, calyx tubular, 11-15 × 2-4 mm; calyx tube 7-9 mm long; teeth 5 equal, narrowly-lanceolate, ciliate, as long, or slightly shorter than tube, 4-7 mm long. Corolla purplish; corolla tube narrow, 20-22 mm long, 1 mm wide, densely pubescent, bent and inflated at apex; lobes of lower lip spreading, bifid, obovate, longer than wide, 8-11 mm long, 4-5 mm wide, upper lip bifid, wider than long, 5-8 mm long, 8-11 mm wide. Capsule 8-10 mm long, 4 mm wide; seeds brown, 477 × 263 microns; style persistent, with some pollen mass attached to the stigma.

Striga junodii is known from only a few collections. It is found in the southern part of Mozambique and the northeastern region of the Republic of South Africa, and as far as known, it does not extend north where a closely related species S. *pubiflora* reaches its northern limits in Kenya (Fig. 10). Thus the two species do not overlap in their geographical distribution i.e they may have different ecological requirements.

Striga junodii is distinguished by its short stiff ascending hairs; similar lower and upper floral bracts which are shorter than the calyces; purple corollas which are consistently shorter and smaller than corollas of S. *pubiflora*, and is the only species among the genus with a bifid or slightly notched lower corolla lobes, a character that might be insignificant but important in identifying the species.

Mozambique: Inhambane, Sd., 12092 (MO; S; UPS); Rikatla, Dist. Lourenco Marques, H. A. Junod, 276 (BRE). South Africa: Nelspruit, province Transvaal, L. L. Britton, 4778 (BRE); Prosser 1784 (BRE).

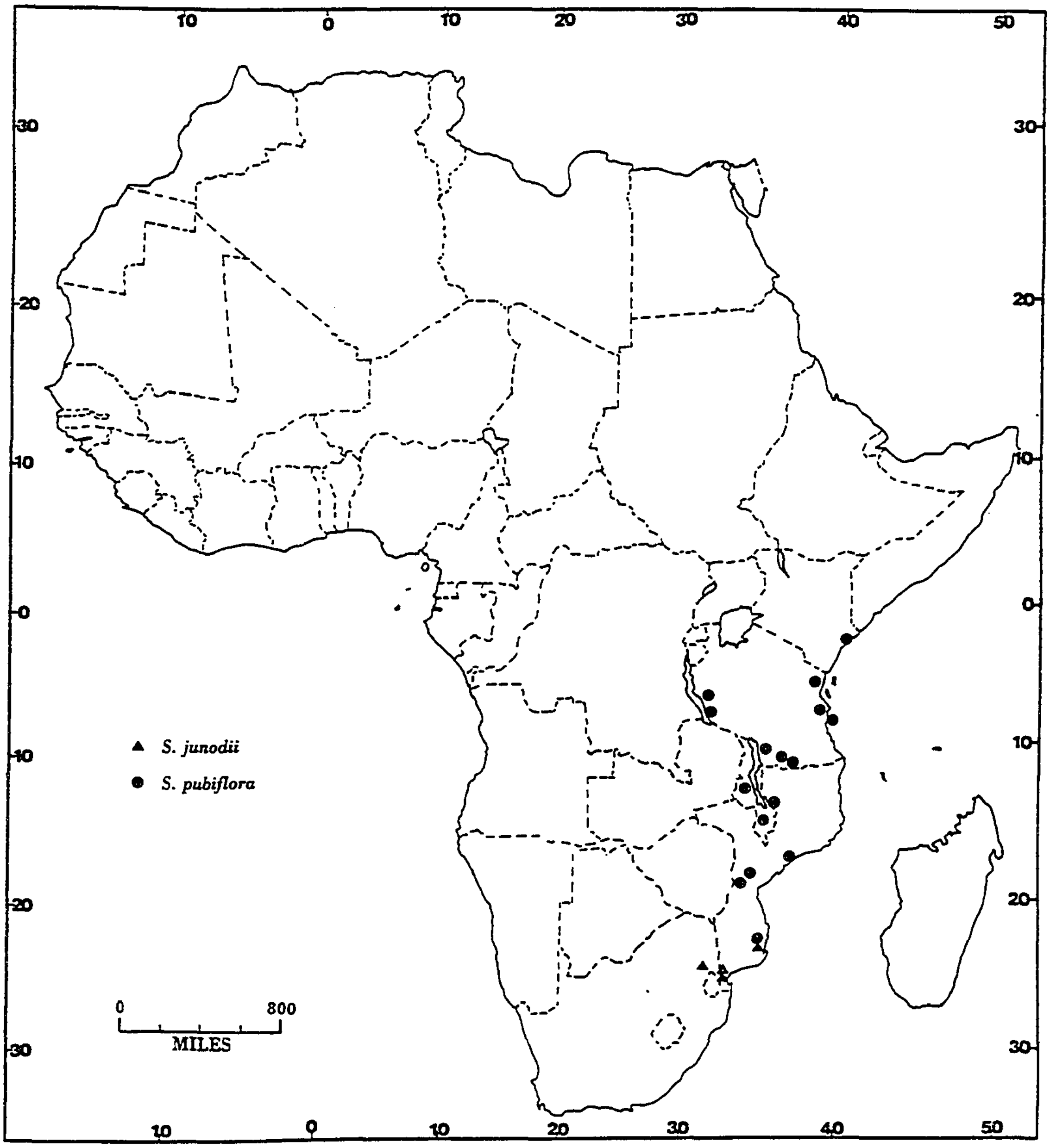

Fig. 10: Distribution of *Striga junodii* and *S. pubiflora*.

20- *Striga klingii* (Engl.) Skan. in Fl. Trop. Afr. 4, 2: 413 (1906).

Buchnera klingii Engl. Bot. Jahrb. 18: 69 (1893).

Plants annual, up to 86 cm tall. Stem stiffly erect, simple, or sparsely dichotomously branched from above the middle, obtusely square, rough, glandular-scabrid, covered with dense, hispid, ascending hairs. Lower leaves reduced, opposite, spreading, ovate, or narrowly-elliptic, margin entire, apex obtuse, 2-15 mm long, 3-5 mm wide; upper leaves 3-nerved, opposite, ascending, narrowly-elliptic, glandular-scabrid, margin coarsely toothed, leaf apex obtuse, 20-40(70) mm long, 3-7(12) mm wide. Internodes 2-6 cm, leaves as long, usually shorter than internodes. Inflorescence 3-11 cm, shorter than the rest of the stem, flowers imbricate, in very dense spike, 2-3 open per inflorescence branch. Lower bracts narrowly-elliptic, margin entire, tips acute, entirely glandular hispid, longer than calyx, 10-22 mm long, 2-4 mm wide; upper bracts lanceolate, ascending, enclosing calyces, as long, or just shorter than calyces, 7-12 mm long, 2-3 mm wide. Bracteoles linear, 6-8 mm long, less than 0.5 mm wide. Calyx 12-15 -ribbed, 3 ribs terminating each calyx tooth, ovate, hispid, 8-10 × 2-3 mm; calyx tube 5-6 mm long; teeth linear, 4 equal, or 5 unequal, entirely hispid, as long or slightly shorter than tube, 3-5 mm long. Corolla pink, hairy or usually glandular-pubescent; corolla tube linear, 10-13 mm long, 1 mm wide, angled and inflated just above calyx; lobes of lower lip spreading, oval, 4-7 mm long, 2-4 mm wide, upper lip wider than long, obovate, 2-3 mm long, 3-4 mm wide. Capsule oblong, 5-6 mm long, 2-3 mm wide; seeds dark-brown to black, 605 × 361 microns; style persistent with some pollen attached to stigma surface.

Striga klingii is confined to the wet savannas in West and Central Africa. It extends from Senegal to Guinea Bissau, Guinea, Sierra Leone, Ghana, Togo, Cameroon, Nigeria, Niger, Central African Republic, and southern Sudan (Fig. 11).

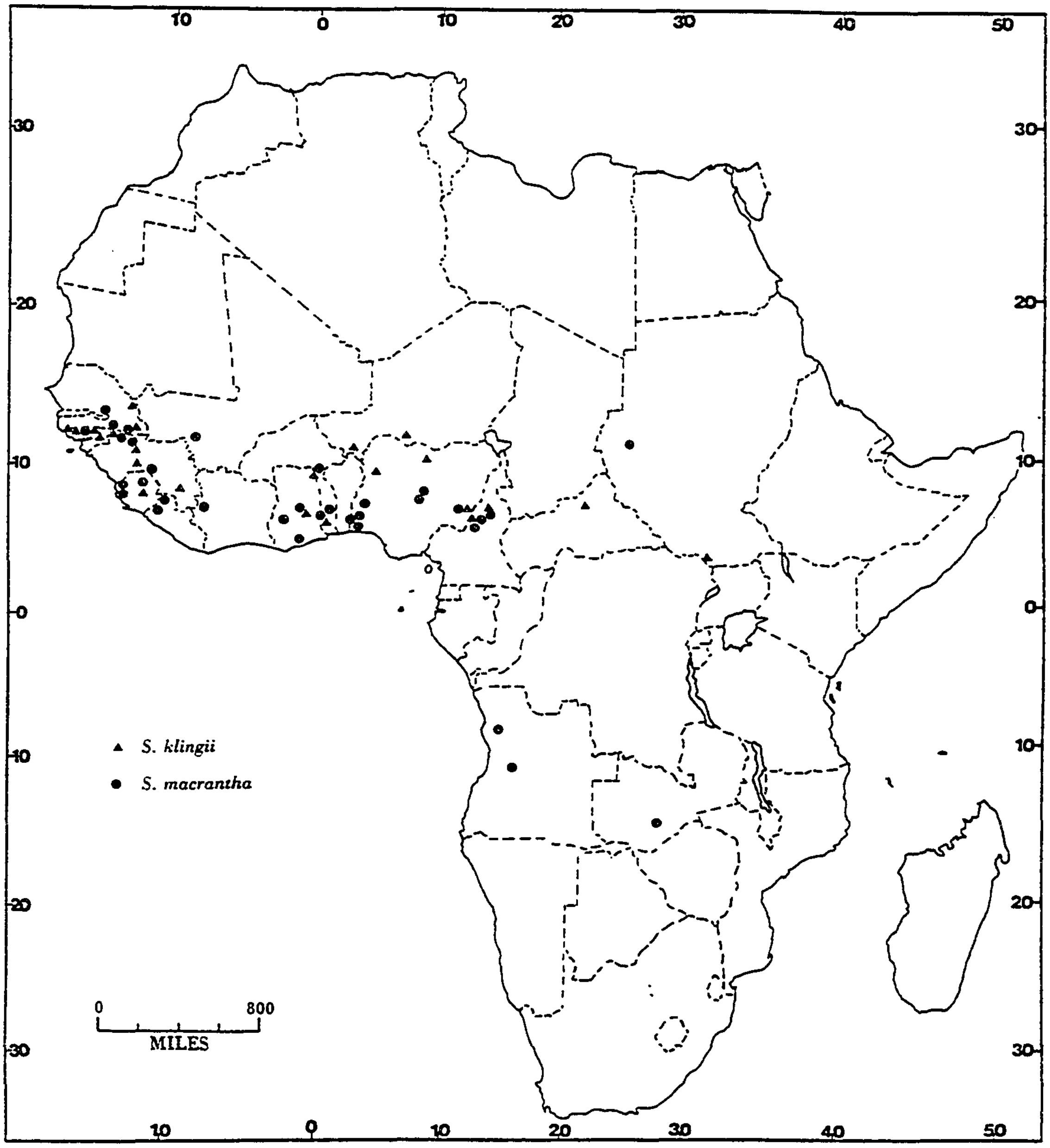

Fig. 11: Distribution of *Striga klingii* and *S. macrantha*.

Although it is not difficult to distinguish *Striga klingii* form the closely related species *S. macrantha* in the field, where they occupy a similar habitat, the two look alike when dry. *Striga klingii* can be identified by its pink flowers, small and short corollas that bend just above calyx, leaves longer than the internodes, with obtuse leaf-apex, and calyx teeth almost equaling the tube length.

Cameroon: at Ngaouyanga, 29 km N. Dogba, northern prov., L. J. Musselman, 10/16/88 (ODU). Central African Republic: Camp Koumbala, J. M. Fay, 6021 (MO). Guinea: Sambailo, Youkounkoun, J. G. Adam, 13884 (MO). Guinea Bissau: entre Bafata e Bambadinea, E. Santo, 3808 (MO); entre Sao Domingos e Suzana, E. Santo, 3668 (MO); Farim entre Canjambarim e Farim, E. Santo, 3622 (MO). Niger: Sd, C. Barter, 158 (GH). Nigeria: near Mokwa, L. J. Musselman & R. A. Mansfield 5533 (ODU). Senegal: Kedougou, J. G. Adam, 26881 (MO). Sierra Leone: Sekurela, Kabala, J. G. Adam, 21995 (GH; MO). Sudan: Ibikes 40 miles NW Yei, Equatoria prov., J. G. Meyers, 7867 (GH).

21- *Striga latericea* Vatke. in Linnaea 43: 311 (1882); Skan in Fl. Trop. Afr. 4, 2:411 (1906).

Plants perennial, up to 60 cm tall. stem stiffly erect, square, furrowed, simple, or little branched from base, scabrous, covered with somewhat soft, dense hairs, hairs divergent at stem base, retrorse above. Lower leaves ascending, lanceolate, margins entire, tips obtuse, 2-10 mm long, 2-6 mm wide; upper leaves opposite, ascending, lanceolate, or narrowly-elliptic, 3-nerved, margins inconspicuously toothed, tips acute, 20-35 mm long, 3-6 mm wide. Internodes up to 8 cm, leaves shorter than internodes. Inflorescence up to 15 cm, very much shorter than the rest of the stem, flowers opposite, shortly pedicellate, in a simple raceme, raceme lax at its base, dense above, 2-3 flowers open per inflorescence branch. Lower bracts narrowly-lanceolate, entirely hispid, longer than calyx, 20-33 mm long, 2-6 mm wide, or usually, shorter than calyx, 8-14 mm long, 2 mm wide; upper bracts lanceolate, shorter than calyx, 3-7 mm long, 1-2 mm wide. Bracteoles linear, 2-10 mm long, less than 1 mm wide. Calyx at least 15-ribbed, 3 ribs terminating each calyx tooth, entirely hispid, 10-24 × 2 mm, broader at teeth; calyx tube 5-10 mm long; teeth 5 unequal, broadly-lanceolate, entirely hispid, usually longer than tube, 5-15 mm long, teeth of lower calyces are exceptionally large, 3-nerved. Corolla salmon-pink, densely glandular-pubescent, 22-30 mm long, 1 mm wide, arched at top; lobes of lower lip obovate, 10-15(20) mm long, 7-9 mm wide, upper lip bifid, wide-obovate, 7-13 mm long, 13-14 mm wide.

The work of Parker (1986, 1988) has shown that S. *latericea* is a perennial plant that produces aerial shoots from adventitious buds developing from the roots. The aerial parts also have a perennial habit with new shoots arising from the lower nodes after much of the stem matures and dies off.

Unlike *Striga forbesii*, a species of wide distribution in West, East and southern Africa, S. *latericea* (its closest relative) is limited to East Africa, in few localities in Somalia, Ethiopia, Kenya and Tanzania (Fig. 8). Here the two species might occur sympatrically. Beside its presence in natural grassland savannas, S. *latericea* is a problem of sugar cane in Somalia and Ethiopia.

Striga latericea can be distinguished from S. *forbesii* by its dense, soft hairs; relatively smaller and narrower leaves which are inconspicuously toothed; the 3-toothed and large lobes of the basal calyces; and by its larger corollas.

Ethiopia: Metahara Sugar Estate, Awash valley, C. Parker 4034 (ODU). Kenya: Majiyachumki, J. Adanson, 615 (S); Mwea Irrigation Scheme, C. Parker 2984 (ODU). Somalia: Juba Sugar Proj., C. Parker, 3384 (ODU).

22- *Striga lepidagathidis* A. Raynal, Bull. Mus. natn. Hist. nat. Paris, Sect. B, Adansonia, 224-225 (1987).

Plants succulent, cespitose entirely glandular pubescent, short, up to 12 cm tall. Leaves and bracts lanceolate, reduced. Spike dense, longer than the stem. Calyx 5-ribbed; teeth 5, about half the tube length. Corolla purple, pink, or white; tube up to 12 mm long; lower lobes 3 spreading, tips acute, 4-5 mm long, 2 mm wide, upper lip emarginate, 2-3 mm long.

Known only from the type specimen.

23- *Striga lutea* (Lour.) K. I. Mohamed *comb. nov.*

Striga lutea Lour., Fl. Cochinch.: 22 (1790); Skan in Fl. Trop. Afr. 4, 2: 409 (1906); Broun & Massey, Fl. Sudan: 331 (1929); Saldanha in Bull. Bot. Surv. India 5(1): 67-70 (1963); Hepper, Rhodora 76: 45-47 (1974).

Plants appearing leafless, 7-40 cm tall. Stem slender, simple, or sparsely branched from middle, densely hispid, hairs divergent at the base of the stem, ascending above. Lower and upper leaves similar, reduced, appressed, lanceolate; lower leaves opposite, 1-2 mm long, 0.5 mm wide; upper leaves alternate, 3-7 mm long, 1 mm or less wide. Internodes 1-2.5 cm, leaves shorter than internodes. Inflorescence 5-20 cm, usually shorter than rest of stem, flowers sparse, alternate in an open raceme, 1-2 flowers open per inflorescence branch. Lower and upper bracts similar, lanceolate, hispid along midribs and margins, shorter than calyx, 1-4 mm long, 0.5-1 mm wide. Bracteoles linear, 1-3 mm long, less than 0.5 mm wide. Calyx tubular, hispid along ribs, 4-6 × 1-2 mm; calyx tube 3-4 mm long; teeth 5 equal, linear, very short, about 1/2 the tube length, 1-2 mm long. Corolla yellow, or red, sparsely to densely glandular-pubescent, corolla tube 10-11 mm long, 0.5 mm wide, bent at top; lobes of lower lip obovate/oval, 2-3(5) mm long, 1-2 mm wide, upper lip 1-2 mm long, 2-3 mm wide; seeds light-brown, 338 × 183 microns.

Striga lutea has the same geographical range as *S. hirsuta* (Fig. 4) and the two are sympatric though, *S. lutea* is less frequent. Also, the plants are easily overlooked in the field because they possess a slender unbranched stem and reduced leaves.

This species has simple, slender stem, with divergent hairs; alternate, reduced, linear-lanceolate, appressed leaves; long internodes (1-3 cm); a loose inflorescence, with alternate flowers, shorter than the rest of the stem below it; calyx subulate, 5 equal, about half the tube length; corolla sizes are intermediate between *S. asiatica* and *S. hirsuta.*

There is an intermediate "form" between *S. lutea* and *S. hirsuta*, [specimens number 10/13/87 (ODU) and 4 (GH)] that has an erect, little branched stem and more developed leaves, with pink flowers.

Congo: Albertville, Lake Tanganykia, D. H. Linder, 1927 (GH). Mali: Dialakoro, 32 km S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88 (ODU); Just N. Bamako, C. Parker, 4001 (ODU); Kamesoba, between Bamako-Siby, L. J. Musselman & K. I. Mohamed, 10/2/88 (ODU); Zantiebougou, S. Baguineda, L. J. Musselman & K. I. Mohamed, 10/5/88 (ODU). Niger: 5 km S. Banfora, S. B. Safa & L. J. Musselman, 10/13/87 (ODU); Niangokolo Agronomic Res. Station, S. B. Safa & L. J. Musselman, 10/25/87 (ODU); collected on Niger R., W. B. Baikie 1865 (GH). Nigeria: National Grain Corporation, Bida/Mokwa Junction, R. A. Mansfield, 9/4/78 (ODU); V. Parkinson, 9/18/85(ODU). Uganda: Bugoye, Dummer, 2629 (US). Zanzibar Isl.: Sd. A. G. Curtis, 4 (GH).

24- *Striga macrantha* (Benth.) Benth. in DC. Prodr. 10: 503 (1846); Skan in Fl. Trop. Afr. 4, 2: 413 (1906); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963); Musselman & Hepper, Kew Bull. 41 (1): 218-219 (1986).

Buchnera macrantha Benth. in Hooker's Comp. Bot. Mag. 1: 366 (1836).

B. buettneri Engl. in Chev. Bot. 475 (1894).

Course, stiffly erect, annual herb, up to 2 m tall. Stem simple, or sparsely dichotomously branched (1-2 pairs), 4-angled, grooved, densely hispid, hairs short, stiff, ascending. Lower leaves opposite, reduced, broadly lanceolate, ascending, margin entire, or finely toothed above middle, 8-20 mm long, 4-5 mm wide; upper leaves opposite, 3-nerved, linear to narrowly-elliptic, ascending, or rarely spreading, margin coarsely toothed, tips acute, 5-12(16) cm long, 4-15(20) mm wide. Internodes 3-9 cm, leaves longer than internodes. Inflorescence 2-6(12) cm, very much shorter than the rest of stem, usually branching with one terminal, two lateral branches, flowers imbricate, shortly pedicellate in compact spike, 2-3 flowers open per inflorescence branch. Lower bracts lanceolate, recurved, exceeding calyx, 10-20 mm long, 2-5 mm wide; upper bracts broadly-lanceolate, ascending, enclosing calyx, as long, or longer than calyx, 7-8 mm long, 3-6 mm wide, bracts entirely hispid, tips acute. Bracteoles lanceolate, 2-7 mm long, 0.5-2 mm wide. Calyx 10-ribbed, entirely densely hairy, ovate, 7-10 × 3-5 mm; calyx tube 4-7 mm long; teeth 5 unequal, lanceolate, tips acute, recurved, about half the tube length, 2-4 mm long. Corolla white, densely pubescent, corolla tube narrow, 17-24 mm long, less than 2 mm wide, bent and inflated at top; lobes of lower lip obovate, spreading, 7-10 mm long, 2-8 mm wide, upper lip bifid, wider than long, 3-7 mm long, 4-10 mm wide. Capsule ovate, 7 mm long, 4 mm wide; seeds dark-brown, 500 × 246 micron; style very long, persistent with some pollen attached to stigma surface.

Striga macrantha is restricted to the wet savannas in West and Central Africa. It ranges from Senegal east into Guinea Bissau, Sierra Leone, Liberia, Ivory Coast, Mali, Ghana, Togo, Cameroon, Nigeria, Niger, Central African Republic, and southern Sudan, also locally present in Angola and Zambia in southern Africa (Fig. 11).

Striga macrantha can be distinguished from *S. klingii* by its white flowers; long and consistently larger corollas that bend at the top; short calyx teeth that are about half the tube length; and by leaves that are shorter than the internodes, with acute tips.

Cameroon: 29 km N. Dogba at Ngaouyanga, L. J. Musselman & others, 10/16/88 (ODU); 3 Km W. of Ngaoundere, W. de. Wilde, 4585 (MO). Guinea: Sambailo, Youkounkoun, J. G. Adam, 13885 (MO). Guinea Bissau: Bafata, Saltinho, E. Santo, 3824 (MO); Farim, Bijene, E. Santo, 3643 (MO). Liberia: Fanfield, Yekeba, J. G. Adam, 24394 (MO); Village Grassfield, Yekeba, J. G. Adam, 29806 (US); Inpaka, near Kolahun Summit, J. C. Bequaert, 35 (GH); Yekeba, Yekeba, J. G. Adam, 25117 (MO). Mali: Manduingues, Bamako, J. G. Adam, 11339 (MO); Sotuba, Bamako, J. G. Adam, 11248 (MO). Niger: Sd, C. Barter, 985 (GH). Nigeria: Abeokuta, J. T. Baldwin Jr., 13639 (MO); (US); North Nigeria, H. V. L., P785 (MO); Olokemeji, Abeokuta, D. P. M. Guile, 1662 (MO); Univ. of IFE Camp., Oyo, M. M. Suabad, 6994 (MO); southern Guinea savanna, L. J. Musselman & R. A. Mansfield, 5522 (ODU). Senegal: Kedougou, J. G. Adam, 20029 (MO). Sierra Leone: Kusubuula, Kabala, J. G. Adam, 21957 (MO); 2 miles W. of Waterloo, F. A. Melville & T. Hooker, 287a (MO).

25- *Striga passargei* Engl. Bot. Jahrb. 23: 515, t. 12 Figs. M, N (1897); Skan in Fl. Trop. Afr. 4, 2: 403, note under *S. aspera*, (1906); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 372 (1963). Musselman & Hepper, Kew Bull. 41 (1): 219-220 (1986).

Plants annual, up to 46 cm tall. Stem erect, usually sparsely to densely branched from middle, obtusely square, furrowed, scabrous, sparsely to densely hispid, hairs divergent, or ascending. Lower leaves broadly lanceolate, opposite, reduced, appressed, 1-3 mm long, 1-1.5 mm wide; upper leaves opposite to subopposite, linear, or narrowly-elliptic, spreading, scabrous-hispid, tips acute, 7-45 mm long, 1-3 mm wide. Internodes 1-3 cm, leaves longer than internodes. Inflorescence up to 26 cm, as long, or usually longer than the rest of the stem, flowers alternate (rarely opposite) in open spike, 2-3 flowers open per inflorescence branch. Lower bracts linear to narrowly-elliptic, spreading, exceeding calyx, 12-60 mm long, 1-3 mm wide; upper bracts linear to lanceolate, usually as long, or longer than calyx, 4-12 mm long, 1 mm wide. Lower bracteoles linear, exceeding calyx, 12-20 mm long, 0.5-2 mm wide; upper bracteoles usually shorter than calyx 4-6 mm long, 0.5-1 mm wide. Calyx 5-ribbed, ribs hispid, ovate, 8-12 × 2-3 mm; calyx tube 3-8 mm long; teeth 5 equal, lanceolate, recurved, ciliate, usually about 1/2 tube length, rarely as long, or longer than tube, 3-8 mm long. Corolla cream-white, or pink, glandular-pubescent, 6-8 mm long, 1 mm wide, angled just above calyx, or 10-17 mm long, bent and inflated at top; lobes of lower lip slightly rounded, longer than wide, 2-6 mm long, 2-4 mm wide, upper lip bifid, obtuse, wider than long, 1-3 mm long, 2-5 wide. Capsule small 5 mm long, 3 mm wide; seeds dark-brown to black, 347 × 201 mm; style persistent.

Striga passargei is restricted to the low-land areas within the Sudanian domain in Africa. Known from Senegal, Mali, Burkina Faso, Ghana, Togo, Nigeria, Niger, and Sudan, and few collections from Tanzania, Zambia, and Namibia (Fig. 12).

Although *Striga passargei* is a variable species, it is not specifically difficult to identify. It has long floral bracts which might even be longer than leaves; a long, loose, open inflorescence with alternate flowers; and the five-equal calyx teeth are of about the same length as the tube. It is closely related to S. *aspera* and S. *brachycalyx.*

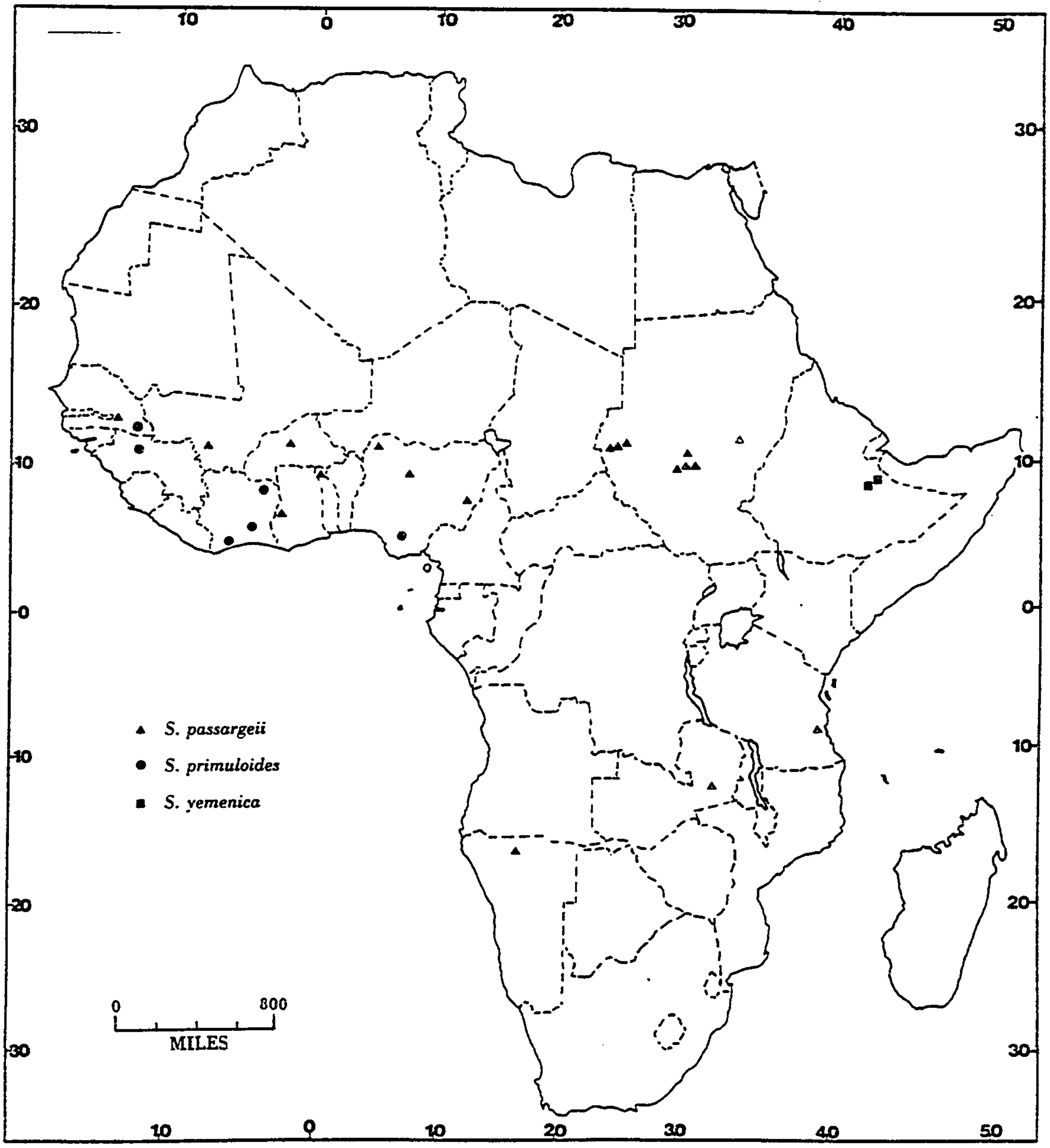

Fig. 12: Distribution of *Striga passargei*, *S. primuloides*, and *S. yemenica*

Burkina Faso: 5 km S. Ouada, S. B. Safa & L. J. Musselman, 10/9/87 (ODU); 55 km N. Ouagadougou, S. B. Safa & L. J. Musselman, 10/19/87 (ODU). Ghana: Bin National Park, near Black Volta, Hall and Swaine GC46220 (US). Mali: Dialakoro, 32 km S. Bamako, L. J. Musselman & K. I. Mohamed, 10/4/88 (ODU). Namibia: Ondangua, Ovamboland, L. E. Kers, 1399 (S). Nigeria: IITA, Borno State, V. Parkinson, 1985 (ODU). Senegal: Dialakoto, Region Oriental, L. J. Musselman et al., 7063 (ODU); Sd, L. J. Musselman, 7061 (ODU). Sudan: Jebel Tozi, Abu Naama, J. D. Lea, 58 (ODU); Kadugli, South Kordofan prov., L. J. Musselman, 8/23/86 (ODU). Tanzania: T8 Kingupira Forest, K. Vollesen, 3311 (UPS).

26- *Striga pinnatifida* Getachew Aweke. Kew Bull. 47(2) 293-294 (1992)

Plants annual, sparsely branched erect herb up to 45 cm tall. Leaves alternate, pinnatifid with linear segments, 1.5-3 cm long. Flowers alternate, axillary, solitary. Lower bracts like leaves. Calyx 10-ribbed, 10-15 mm long, teeth 5. Corolla tube 20 mm long, lower lobes 6 mm long. Stigma linear, obtuse, capsule oblong-ovoid.

Known only from the type, Ethiopia.

27- *Striga primuloides* A. Chev. in Bull. Soc. Bot. Fr. 58, Mem. 8: 185, (1912); Chev. Bot. 478 (1936); Hepper in Fl. W. Trop. Afr. ed. 2, 2: 371 (1963).

Plants perennial, 30-70 cm tall. Stem erect, usually simple, appearing leafless, obtusely square, grooved, pilose, hairs divergent. Lower and upper leaves similar, lanceolate, appressed, alternate, scale-like, 2-5 mm long, 1-2 mm wide. Internodes 1-5 cm, leaves shorter than internodes. Inflorescence 2-5(15) cm, much shorter than the rest of the stem, flowers sparse, alternate in lax spike, 4-8 flowers open per inflorescence branch. Lower and upper bracts similar, hispid, lanceolate, shorter than calyx, 4-7 mm long, 1-2 mm wide. Bracteoles minute 2-3 mm long, less than 0.5 mm wide. Calyx approximately 15-ribbed, at least one terminating each calyx tooth, calyx 8-9 × 1 mm; calyx tube 5 mm long; teeth 5 unequal, lanceolate, slightly shorter than tube, 3-4 mm long. Corolla white to yellowish, densely glandular-pubescent; corolla tube slender, 22-30 mm long, 1 mm wide, angled at top; lobes of lower lip obovate, spreading, 9-10 mm long, 8-9 mm wide, upper lip broadly obovate, 5 mm long, 10 mm wide. Capsule tubular about 4 mm long 1 mm wide; style persistent.

Striga primuloides is restricted to the southern Guinea savannas. It is known from Senegal, Guinea, Ivory Coast and Nigeria but it might occur elsewhere in this part of Africa (Fig. 12).

Striga primuloides can be identified by its extremely reduced, alternate leaves; its approximately 15-ribbed calyx; the yellowish-white flowers; and the large corollas.

Ivory Coast: along road from Gawi to Seye, in gallery forest of Iringou River, G. J. H. Amshoff, 193 (MO).

28- *Striga pubiflora* Klotzsch. in Peters, Reise Mossamb. Bot.: 227 (1861); Skan in Fl. Trop. Afr. 4, 2: 412 (1906).

S. zanzibarensis Vatke in Linnaea 43: 310 (1882).

Plants perennial, 35-75 cm tall. Stem stiffly erect, simple, or little branched from the base, obtusely square, grooved, densely hispid with divergent hairs, hairs somewhat soft. Lower leaves, reduced, opposite, appressed, narrowly-elliptic, tips obtuse, 3-10 mm long, 2 mm wide; upper leaves linear to narrowly-elliptic, opposite on the lower part of the stem, alternate above, ascending, margins entire, rarely toothed, scabrid-hispid, entirely covered with dense ascending hairs, 10 -50 mm long, 1-2(4) mm wide. Internodes 2-5 cm, leaves usually shorter than internodes. Inflorescence up to 30 cm, shorter than the rest of the stem, flowers shortly pedicellate, alternate in open raceme, 1-3 flowers open per inflorescence branch. Lower bracts linear, longer than calyx, 22-27 mm long, 2 mm wide; upper shorter than calyx, 5-17 mm long, 1-2 mm wide, Bracteoles 2-5(10) mm long, 0.5 mm wide. Calyx tubular, 15-ribbed, densely hispid along ribs, ribs prominent, three terminating each calyx tooth, calyx 13-21 × 2-3; calyx tube 8-12 mm long; teeth lanceolate, 5, equal, as long, or usually shorter than tube, 4-12 mm long. Corolla white, densely pubescent, hairs spreading or retrorse; corolla tube narrow, 27-35 mm long, *rarely shorter than 27 mm,* 1 *mm wide, bent and expanded at top;* lobes of lower lip three, spreading, longer than wide, obovate, 14-20 mm long, 10-17 mm wide, upper lip wider than long, widely obovate, only slightly bifid, 9-12 mm long, 10-20 mm wide. Capsule tubular, flattened, 10 mm long, 3.5 mm wide; seeds dark-brown, 516 × 278 microns; style long, persistent, with some pollen persistent on stigma.

Common to the seasonally flooded savannas of southeastern Africa. Its range extends from Kenya south into Tanzania, Zanzibar, Malawi and Mozambique (Fig. 10).

Striga pubiflora can be separated from *S. junodii* by its soft, dense, divergent hairs; its long lower floral bracts usually exceed the calyx length; and by the large white corolla lobes. It also resembles *S. angustifolia* but is consistently larger.

Malawi: Kasungu National Park, Central prov., J. Pawek, 12015 (MO); Zomba Mt., Chivunde valley road, South Region, I. F. La Croix, 2735 (MO). Mozambique: Inhambane, Sd., 12092 (US); 25 mile S. Muda, District Manica and Sofala, L. C. Leach, 11232 (MO). Tanzania: N. Bush, Kibaha, B. Harris, 786 (S); S. Honga road (64 Km from Songea on Njombe Rd), Songea District, also collected at 120 Km from Songea on Lindi Rd., J. B. Gillett, 17889 (MO); 100 km NW. Lindi, H. J. Schlieben, 6021 (S); Mafia Isl. G. B. Wallace, (713); Mahenge-Plateau, H. J. Schieben, 2281 (S); Mlimba, C. F. Paget-Wilkes, 700 (MO); Mogo Forest Reserve, Kisarawe Dist. eastern prov., S. Paulo, 105 (MO); Pande Forest Reserve, B. J. Harris & A. McCusker, BJH2568 (MO); Songea-Tunduru Rd., Songea District, J. Kew, 19911 (MO). Zanzibar Isl.: Fessland bec Lamu J. M. Hildebrandt, 1907 (UPS).

29- *Striga yemenica* Musselman & Hepper Notes from Royal Bot. Gard. Edin. 45(1): 43-50, (1988).

Plants annual, 18-22 cm tall. Stem of medium thickness, square, furrowed, simple or very sparsely branched below middle, indumentum of dense, retrorse, stiff hairs. Lower leaves reduced, opposite, lanceolate, appressed, 1-5 mm long, 1 mm wide; upper leaves opposite, lanceolate ascending, 10-22 mm long, 1-2 mm wide. Internodes 0.8-2 cm, leaves usually shorter than internodes. Inflorescence open spike, up to 11 cm, slightly longer than the rest of stem, flowers sessile, opposite. Lower bracts lanceolate, ciliate, longer than calyx; upper bracts lanceolate, as long, usually shorter than calyx. Bracteoles linear, 2-5 mm long, 0.5 mm wide. Calyx 5-ribbed, hispid, tubular, 5-7 × 2 mm; tube 4-5 mm long; teeth 5 unequal, acuminate, very short, 1 rarely 2 mm long. Corolla red or mauve, tube narrow, 7 mm long, 0.5 mm wide, densely retrorsely pubescent, bent at top; lobes of lower lip rounded, about 0.5-1 mm long, upper lip 0.5 mm long. Capsule slightly obovate, 3-4 × 1 mm; style persistent.

The type specimen is from the Yemen Arab Republic; it has also been collected in Harar province, Ethiopia (De Wilde 5486 & 7223 MO). The present description is based on the specimen number 10316 collected from the same region (Fig. 12).

Striga yemenica is a small plant with dense retrorse hairs; the stem below the inflorescence is short with a maximum of six pairs of leaves; and the calyx and the corolla lobes are small.

Ethiopia: 1 km west Abu Yonis, 30 km NW Jejega, Harar prov., L. Boulos, 10316 (MO).

SUMMARY:

A total number of 29 species and 6 subspecies occur in Africa, 25 are restricted to Africa. Species diversity varies by region. The subtropical zone has 74% (25) of the taxa including 41% (14) endemics. Here, the West African part (from Senegal to eastern Nigeria) has 62% (21) of the total taxa including 24% (8) endemics. South of the equator the number of taxa represents 56% (19) of the total with 21% (7) endemics, a proportion slightly less than that shown for West Africa alone. The higher species diversity and endemics strongly suggest the subtropical zone, particularly West Africa as centers of distribution of *Striga*. It appears that the number of taxa and the rate of endemism in Africa decreases from west to east and also north to south. The decrease eastwards continues across the Red Sea and the Indian Ocean to the Arab Peninsula and southeast Asia.

CHAPTER THREE

VARIATION IN THE GENUS STRIGA.

INTRODUCTION

One of the problems inherent in the taxonomy of witchweeds is the difficulty encountered in separating the species complexes. The polymorphic species like *S. gesnerioides*, *S. hermonthica* and *S. asiatica* that developed host-specific "strains" also present taxonomic difficulty. The status and nomenclature as well as the affinities of these groups has not been sufficiently addressed. The objective of this chapter is to study *Striga* taxonomy and compare the different species groups and host-specific strain. Using multivariate statistics as a tool, the intra- and interspecific variability of the various taxa was emphasized and then related to either the spatial distribution or host.

MATERIALS AND METHODS

Definitions:

Within the genus *Striga* there is geographical and host-induced variation. The two types of variation can be expressed within (intraspecific) or among (interspecific) species. The geographical variation is the difference among species, host-specific strains, or demes of the same taxon parasitizing the same host but growing at different geographical locations. On the other hand, the host-induced variation is the difference among species, host-specific strains, or demes of the same species gathered from a single locality or at the same latitude but parasitizing different hosts. There is a third type of variation, that established by the species since its divergence from its ancestor and during its evolutionary history. I refer to this as the species induced variation which is a result of the combined effect of shifting to new host and new habitat. It represents the statistically significant difference in the measured variables between two or more species under similar conditions, i.e parasitizing the same host and growing at the same locality. Analysis of each kind of variation was based on randomly chosen plants that represent the range and/or the various hosts that can be parasitized by the species or host-specific strains.

Characters used to identify and classify *Striga* species (Hepper 1963, 1984, Ramaiah *et al.* 1983, Raynal-Roques 1987, Musselman 1987) are either of quantitative or qualitative nature. The quantitative characters include height, length, and width, and the qualitative include corolla color, host, duration, need for germination stimulant, leaf position and all the ecological features that cannot be quantified and therefore irrelevant for statistical analysis. The quantitative characters were further divided into two categories: the vegetative characters include stem height, number of branches, leaves and bracts length, leaves width, and internodes length. These characters tend to vary with changes in the physical environment and hosts (Hepper 1960); and should be given less weight although they are easy to notice and helpful in constructing keys. The second category include the floral characters which are more important because they are associated with reproduction and constitute the features by which species with reduced vegetative growth can be identified and classified.

Six vegetative and seven floral (reproductive) characters were quantified for statistical analysis. These were A=Stem height (cm); B=Number of branches; C=Leaf length (mm); D=Leaf width (mm); E=Internode length (mm); F=Inflorescence length (cm); G=Number of flowers open/inflorescence; H=Lower bract length (mm); L=Calyx tube length (mm); M=Calyx teeth length (mm); N=Corolla tube length (mm); O=Lower corolla lobe length (mm); and P=Upper corolla lobe length (mm).

This analysis was based on herbarium specimens we collected from Sudan, Mali, Nigeria, Burkina Faso, Botswana, South Africa, and Cameroon, between 1987-89, and also on the herbarium specimens cited in chapter 2. Each gathering was considered a population. The number of plants used to assess each type of variation differed from species to species; however, a total of seven measurements were taken for each character per individual plant. Plants and measured variables were randomly selected except characters A, B, F, G, and H for which, all available variables were measured because either there was a limited number of them or the analysis was dependent on the total numbers present in each plant.

The procedure of multivariate statistics (multiple analysis of variance) was used to compare the effect of the groups (species, geographical locations, hosts) on the measured variables and to determine the correlated responses of the dependent variables. The analysis requires and must be performed on normally distributed data; hence, transformations were made whenever necessary. Since thirteen measured variables were to be assessed, the biological alpha level was adjusted to 0.004 (0.05/13).

Upon the completion of the analysis, a matrix was designed so that comparing any two groups was possible. Results were plotted on the matrix and two of its axes were similarly labeled with the species, subspecies, host specific-strain, or the geographical locality in question. Latitudes were plotted in ascending or descending order to detect and associate the overall changes (if any) in the number of measured variables with latitudes. However, no attempt was made to trace and correlate the changes in individual variables with changes in latitude which was not the subject of this study. In these matrices only the significant variables are shown.

RESULTS AND DISCUSSION

Geographical variation in *Striga elegans*

Herbarium specimens of *S. elegans* gathered from six localities between latitudes 01° 20' S and 33° 10' S were analyzed for evidence of geographical variation. Results suggest that *Striga elegans* was fairly homogeneous over its range, and only four of the thirteen measured variables were significantly different ($P < 0.003$), with an average of only 1.2 variables varying between any two localities (Table 1). There was no clear correlation between variability and latitude i.e. the significant difference between populations obtained from remote sites was not higher than adjacent sites (Table 1).

General variation in *Striga asiatica*

Twelve populations of *Striga asiatica* collected at different geographical locations (between latitudes 30° 40' S and 13° 00' N) and from two different hosts were compared to assess the overall differences between them (Table 2). The South African (site 1) population was gathered from sorghum-infested fields, whereas the Botswana (site 2) population was gathered from sorghum and wild grass hosts. The remaining ten populations were collected from wild grass hosts.

Like *S. elegans*, *S. asiatica* showed no clear pattern of increasing or decreasing variation from the equator north or south following the moisture gradient but populations sampled from adjacent sites were less different than those from remote sites. The populations gathered from South Africa (site 1), Botswana (site 2), and Kenya (site 6) displayed the highest number of significant variables.

Although the Botswana (site 2) and the South African populations (site 1) were not significantly different from each other, they showed highly significant differences from

Table 1: Floral and vegetative features showing significant geographical variation in *Striga elegans*.

Site	1	2	3	4	5	6
Lat.	01°20'S	09°50'S	18°08'S	25°30'S	28°50'S	33°10'S
Long.	36°48'E	34°50'E	23°11'E	311°5E'	29°44E'	26°25'E
1		D	D		E	
2				A E	A E	A E
3				A E	A E N	A E
4					N	D
5						
6						

Letters in matrix represent the significant variables ($P < 0.003$); A=Stem height (cm), D=Leaf width (mm), E=Internode length (mm), N=Corolla tube length (mm),

site 1- in Kenya, 2- Tanzania, 3- Botswana, 4-6 South Africa.

Table 2: Vegetative and floral features showing significant variation among populations of *Striga asiatica* parasitizing various hosts and obtained from different geographical locations.

	1 30°40'S 29°00'E	2 18°09'S 24°24'E	3 05°55'S 29°08'E	4 05°00'S 56°00'E	5 02°39'S 31°23'E	6 01°10'S 35°55'E	7 09°50'N 08°40'E	8 10°00'N 13°45'E	9 10°30'N 29°48'E	10 11°39'N 07°26'W	11 12°23'N 08°16'W	12 13°00'N 07°40'W
1			A C EFGH LMN P	AB EFG LMNO	ABC EFGH MN P	AB E G MN	A EFG LMN P	ABCE FGHL MNOP	A C EFGH L OP	C FGHL MNOP	A C EFGL MNOP	ABCE FGHL MNOP
2			ABCD EFGH MN	ABCD EFGH MN	ABC EFGH MN	AB D E G MN	ABC EFGH L N	ABCD EFGH LMNOP	ABCD EFGH L NOP	A C FGH MNOP	ABCD EFGH MN	ABCD EFGH LMNOP
3						C FGO	G	P	G	A P	F	BC L P
4						A C FMO	A	C P	AB M	ABC EFGP	ABC FG	C P
5						C FG	GL	C L P	B GL	AB P	AB F	C L OP
6							C FLO	ACFG LMOP	CF HLOP	ACFG HNOP	CFG MNOP	ABCFG HLMOP
7								C GMP	C	A C GP	C FGM	ABC GMOP
8									ABC GMP	ABC P	ABC FP	
9										B G	FGM	ABC GMP
10											B P	ABC FLP
11												ABC FLP
12												

Letters in matrix represent the significant variables ($P < 0.0001$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- collected from South Africa, 2- Botswana, 3- Congo, 4- Seychelles, 5- Tanzania, 6- Kenya, 7- Nigeria, 8- Cameroon, 9- Sudan, 10-12 Mali.

the remaining populations in 6 to 13 variables (P=0.0001). The high floral and vegetative variability among these two populations on one hand and the remaining populations on the other hand strongly suggested that the combined effect of host and geographical location was greater than their individual effect or their sum when the two were measured independently. To express the effect each might have on variation, the effect of geographical location (Table 3) was assessed independent of the host effect (Table 4).

Geographical variation in *Striga asiatica*

The two populations of S. *asiatica* parasitizing sorghum from South Africa (site 1) and Botswana (site 2), were removed from Table 2 and then the analysis was performed on the remaining populations, all of which were collected from wild grass hosts. Table 3 shows the possible geographical variation among the populations of *Striga asiatica*. Compared to the results obtained from Table 2, removal of the populations parasitizing sorghum (site 1 and part of site 2) reduced the number of significant variables between the population gathered from Botswana (site 1) and the remaining sites by a maximum of four (average 2.1 variables per site), and between Kenya (site 1) and other sites by one variable. All other populations showed an increase in the number of significant variables suggesting that populations in Table 3 were more homogeneous than in Table 2. There were also slight changes in the significant variables themselves (Table 2 and 3). This variation was partly vegetative and partly floral (reproductive). Nevertheless, the Botswana population (site 1) showed the highest number of significant variables. Since this site was separated from the other sites by at least 12 degrees, the differences between them might be attributed to their geographical locations.

Table 3: Vegetative and floral features showing significant geographical variation in *Striga asiatica.*

Site	1	2	3	4	5	6	7	8	9	10	11
Lat.	18°09'S	05°55'S	05°00'S	02°39'S	01°10'S	09°50'N	10°00'N	10°30'N	11°39'N	12°23'N	13°00'N
Long.	24°24'E	29°08'E	56°00'E	31°23'E	35°55'E	08°40'E	13°45'E	29°48'E	07°26'W	08°16'W	07°40'W
1		A C EFGH LM	A CD EFG LM	A C EFGH LM	A C EF	ABC E M	A CD EFGH LMP	A C EFG LMP	A CD E GH LMP	A CD EFGH LM	A CD EFGH LMNOP
2			A C		C LM O	BC L	L P	CD	A F P	A M	A E L NOP
3					A D LM O	AB D	L P	A D E	ACEF HLM P	A CE HLM	L N P
4					C LM	BC N	D L NOP	CE NO	A E NOP	A E M	D L NOP
5						MNO	CD LMNOP	LMNOP	A CH LM OP	CDH LM O	A CDE LMNOP
6							BCD EL P	B L	A C HL P	BCD H L	ABCD EL OP
7								ACDE L P	A E P	A EH M P	
8									CD H	CD H M	A CD HL P
9										P	A E N P
10											A EH MNOP
11											

Letters in matrix represent the significant variables ($P < 0.0001$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- in Botswana, 2- Congo, 3- Seychelles, 4- Tanzania, 5- Kenya, 6- Nigeria, 7- Cameroon, 8- Sudan, 9-11 Mali.

Table 4: Vegetative and floral features showing significant variation among populations of *Striga asiatica* parasitizing sorghum and grasses.

Variables	host=sorghum (means)	host=grass (means)	alpha
Number of branches	13.00	1.80	0.0001
Leaf width (mm)	1.66	1.08	0.0005
Internode length (mm)	18.41	26.80	0.0005
Lower bract length (mm)	36.88	15.20	0.0001
Lower corolla lobe length (mm)	4.00	3.17	0.003

Host induced variation in *Striga asiatica*

Two populations of *Striga asiatica* parasitizing wild grasses and sorghum, collected from a single locality in Botswana at latitude 18° 09' S were compared to assess the possible host induced variation. They varied significantly in only five variables four of which were vegetative characters (Table 4), suggesting that the variation attributed to host was generally vegetative and less pronounced than that attributed to latitude (Table 3 and 4).

To further investigate the pattern of high variability shown by the population samples from South Africa (site 1) and Botswana (site 2) in Table 2, and Botswana (site 1) in Table 3, the species was divided into three aggregates based on geography, morphology, and host, and referred to as "strains".

1. The South African strain (asiatica). This is a large, profusely branched plant with usually bright red or yellow corollas. It grows on sorghum as its main host. It resembles the South and North Carolina *Striga asiatica* and possibly reached the United States from southern Africa or from the Islands (such as Comoros) in the Indian Ocean in the vicinity of southern Africa.
2. The West African strain (hirsuta). This is a very small plant, on average 6 cm. in height, with usually red or yellow flowers. It is confined entirely to native grasslands, parasitizing only native grasses, and it was never seen on cultivated crops even in fields where S. *asiatica* was parasitizing grasses on the field's edges. This specific strain is very common in West Africa with intermediate forms known from Central and East Africa. It probably bridges the morphological gap between lutea and asiatica strains as well as the closely related species *Striga elegans.*
3. The yellow strain (lutea). This is erect, tall, less branched, with reduced leaves, and usually yellow flowered; but unlike the first two it has a wider distribution in Africa. Strain lutea is less frequent than hirsuta and asiatica. Its hosts are wild grasses.

Intra- and interspecific variability in the species complex of *Striga asiatica*[1] and *S. elegans*

Striga elegans superficially resembles *S. asiatica* and the two overlap in their distribution in South and East Africa. Inclusion of both species in the analysis might lead to a better understanding of the intra- and interspecific variablity within the species complex and clarify their relationships. Tables 5a and 5b compare the differences between *S. elegans* and the three strains of *S. asiatica* in thirteen floral and vegetative features. There were highly significant differences between the four strains, with the South African (asiatica) and the West African (hirsuta) strains being significantly different in all thirteen variables ($P < 0.0001$). When compared, the West African (hirsuta) and the yellow strain (lutea) showed the lowest number of significant variables (6 variables). If the difference between these two strains was excluded then, the interspecific variation between *S. elegans* on the one hand and any strain of *S. asiatica* on the other hand was smaller than the intraspecific variation within *S. asiatica*, suggesting that *S. elegans* is closely related to *S. asiatica*. Results also showed that *S. asiatica* is a highly variable taxon (Table 5a and 5b).

The intraspecific variability in morphology among the populations of *Striga asiatica* was noted earlier by Musselman and Hepper (1986), Musselman (1987) and Ralston *et al.* (1987). In addition to the variation in the thirteen measured variables mentioned above, there were differences in parasitic behavior, habitat, phenology, host, corolla color, pubescence of the stem, leaves, and corollas, the number of calyx ribs, and inflorescence density. The number of significantly different variables among the strains of *S. asiatica* and *S. elegans* shown in Table 5a and 5b are summerized in Fig. 13.

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[1] In this discussion *Striga asiatica* includes the strains asiatica, lutea, and hirsuta

Table 5a: Vegetative and floral features showing significant variation among strains of *Striga asiatica* and *S. elegans*.

Strain/sp.	asiatica	hirsuta	lutea	S. elegans
asiatica		ABCD EFGH LMNOP	ABCD FGH LMNOP	ABC FGH LMNOP
hirsuta			A C E H MNO	A CD E G LMNOP
lutea				CD GH LMNOP
elegans				

Letters in matrix represent the significant variables ($P < 0.0001$); A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

Table 5b: Vegetative and floral features showing significant variation among strains of *Striga asiatica* and *S. elegans*.

Variables	asiatica	hirsuta	lutea	elegans
Stem height	35.00	12.63	21.86	23.77
Number of branches	6.53	1.37	2.07	1.82
Leaf length(mm)	28.99	7.91	4.40	16.59
Leaf width(mm)	1.46	0.70	0.71	1.81
Internode length(mm)	20.82	8.96	14.70	19.51
Inflorescence length(cm)	17.53	6.40	8.43	7.52
Flowers open/inflorescence	1.94	1.08	1.07	3.95
Lower bract length(mm)	29.13	8.36	3.66	10.08
Calyx tube length(mm)	5.43	3.52	3.73	6.71
Calyx teeth length(mm)	2.83	1.93	1.47	3.85
Corolla tube length(mm)	11.93	9.48	10.36	15.88
Lower corolla lobe length(mm)	3.83	2.31	2.79	7.97
Upper corolla lobe length(mm)	2.46	1.43	1.79	4.62

Means significantly different at ($P < 0.0001$)

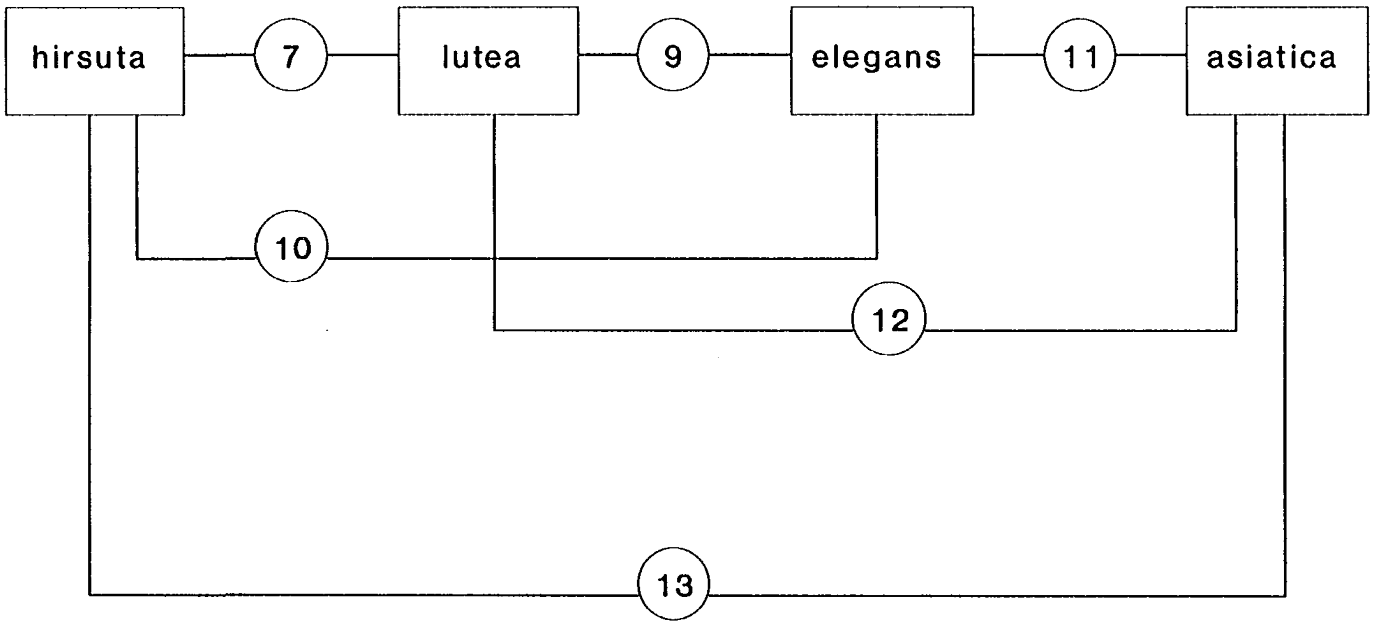


Fig. 13: Summary of the variation (in 13 floral and vegetative features) between "strains" asiatica, hirsuta, lutea, and elegans (from Table 5a and 5b).

There is a good relationship between variability among the four strains (which increased from left to right in Fig 13) and their spatial distribution. Strains hirsuta and lutea are common in the grassland savanna north of the equator especially in West Africa, then they gradually decrease in abundance and frequency south of the equator. Their range also extends to southeast Asia. *Striga elegans* is restricted to southern and eastern Africa; while, the strain asiatica occurs in South Africa and unlike the other strains, is reported to occur in almost all sorghum-growing semi-arid regions of Asia as a serious problem on sorghum and pearl millet in India and Pakistan, maize in Thailand, sugar cane in Australia, rice in Burma, Indonesia and Thailand (Rao 1984), sorghum and millet in Yemen and Saudia Arabia (Musselman and Hepper 1988) and maize and sorghum in the United States of America. In Africa, except in Botswana and the Republic of South Africa (Ralston *et al.* 1987) and until recently in Togo (Agbobli and Huguenin 1987, Agbobli 1991), strain asiatica was not known as a problem on crops. I have checked collections of S. *asiatica* from different parts of the world (southeast Asia, Australia, Seychelles, Comoros, Zanzibar, Madagascar, U.S.A) and found that strain asiatica morphologically matches the population found in southern Africa. The natural question then is: are we dealing with a variable taxon that has many infraspecific forms or different species, and what is the relationship between the spatial distribution, morphology and parasitic behavior, and the phylogeny of these "taxa" ?

The genetic diversity of S. *asiatica* has not been thoroughly investigated and the few studies done have focused on racial differences among the agronomically important strains. Werth *et al.* (1984) suggested that the morphological and physiological differences between strains of S. *asiatica* could be attributed to genetic differences. Musselman and Hepper (1986) note that S. *asiatica* in the South Kordofan area is not reported as an agronomic pest because of its phenology. After the commencement of rains it flowers sooner than does the most damaging species, S. *hermonthica*. The center of distribution of S. *asiatica* is not known and Raynal-Roques (1987) excluded it from the taxa native to Africa. Harlan and Stanler (1976) demonstrated that sorghum have originated in the Sudano-Ethiopian region and spread to other parts of the world. Rao and Musselman (1987) proposed *Striga* has originated in the same region as sorghum and moved along the routes of introduction of its host (sorghum), and only the self-fertilized taxa like S. *asiatica* survived. They suggest this is how the red-flowered S. *asiatica* "complex" was introduced to India (the second center of origin of sorghum) and South Africa. India and South Africa are among the two regions where S. *asiatica* does most of its damage to crops. This parasite is never reported as a problem on sorghum in the Sudano-Ethiopian region but it is conceivable that seeds could have been moved along with its host as contaminants. We can assume that the strain asiatica developed its new morphology, ability to attack crops, phenology and genetics after it has moved to India or South Africa.

It is more likely that strain asiatica evolved either outside Africa (e.g. India) or in South Africa. The first assumption is based on the fact that India is the second center of origin of sorghum and one of the major areas where strain asiatica causes its damage. If this hypothesis is true then strain asiatica reinvaded South Africa. The second assumption is backed by the presence of the closely related species S. *elegans* only in South and East Africa which could be a suitable ancestor of the strain asiatica (Chapter 4). Although strains hirsuta and lutea are present outside Africa but they are more common in the native grasslands of the Sudano-Ethiopian region and may be native to this region. They were most likely the ones originally introduced to Asia and South Africa. This was quite possible since S. *asiatica* is an inbreeder (Nickrent and Musselman 1979) and in isolation, inbreeders have a higher chance of initiating a new population than outbreeders (Rao and Musselman 1987). Invasion of the new habitat accompanied by a shift to new host (e.g. strain asiatica) probably facilitated all the morphological and behavioural transformations that took place in the species complex.

This analysis suggests that S. *elegans* is an intermediate form between lutea and asiatica strains. If these strains are to be considered variants of the same species, S. *elegans* might also be considered as an intraspecific variant of the same species complex, which is not consistent with the high variablity in the species complex showed in this study (Table 5a, 5b and Fig. 13) and with the current treatment of S. *elegans.* In fact, the intraspecific variability among this species complex exceeds that shown in any of the species in this study, including that of the S. *bilabiata* complex. On the other hand, if S. *elegans* is treated as a separate species, all strains of S. *asiatica* should be given the same taxonomic rank supported by differences in their morphology, ecology, geography, and parasitic behavior.

The long lasting dispute over the correct name and the identity of the taxon currently known as S. *asiatica* and the presence of relatively large number of synonyms, indicate the variability, and the need for revision of its taxonomy. Based on the results of this analysis and on chapter 4, S. *asiatica* is divided into three species while S. *elegans* is maintained. The diagnostic characters for the proposed species is shown in Table 6.

1- *Striga asiatica* occurs mainly in southern Africa. The cladistic analysis (Chapter 4) suggests that it is the most derived of the four species and evolved from a species similar to S. *elegans*. It is a large, leafy, profusely branched, scabrid-hispid, with linear-elliptic, ascending leaves and bracts, large calyces and flowers, and densely pubescent corolla. Its hosts are mainly agronomic crops. The characteristics of this species fits the original description of the type specimens of S. *asiatica* given by Linnaeus (1753) and discussed in Hepper (1974).

2- *Striga hirsuta* occurs in West and Central Africa. Its frequency and presence in large populations (large demes) in native grasslands in West Africa suggest that it is native to this region. Plants are little branched, small, densely hirsute, with linear

Table 6: Diagnostic characters of S. *asiatica*, S. *hirsuta* and S. *lutea*.

Character	S. *asiatica*	S. *hirsuta*	S. *lutea*
Distribution	southern Africa	Sudano-Ethiopian region	Sudano-Ethiopian region
Host	agronomic crops, wild grasses	native wild grasses	native wild grasses
Stem	leafy, branched, tall, up to 40 cm, scabrid-hispid	less leafy, little branched, short, 2-6 cm, hispid	slender, looking leafless, up to 40 cm, hispid
Leaf shape	linear-elliptic spreading	linear, ascending	lanceolate, appressed
Bracts	linear, longer than calyx	narrowly-lanceolate longer than calyx	lanceolate, shorter than calyx
Calyx lobe length	less than half tube length	equaling tube length	half tube length
Corolla: pubescence	densely pubescent	sparsely pubescent	sparsely pubescent
Tube length	11-14 mm	8-10 mm	10-11 mm
Lower lobe length	3-5 × 2-3 mm	2-3 × 1-2	2-3 × 1-2

ascending leaves, small calyces, relatively long calyx lobes (=tube length), and small sparsely pubescent corollas.

3- *Striga lutea* is found in the Sudano-Ethiopian region, it is locally infrequent in occurrence; being the least derived (Chapter 4). It has tall, slender, leafless stem, leaves are reduced to small scales, lanceolate, appressed, short calyx teeth, and small sparsely pubescent corolla.

The corolla color bears no significance in this treatment since any of the three species could have a red, yellow, and white corolla in the same population; however, S. *asiatica* usually has red flowers, S. *lutea* yellow, and S. *hirsuta* has both red and yellow.

Variation in *Striga hermonthica*

Herbarium specimens of *Striga hermonthica* parasitizing sorghum, millet, and grasses from eight sites located between latitudes 09° 28' N and 13° 30 N' were examined to assess the overall variation among them (Table 7). Of the thirteen measured variables, ten were significantly different ($P < 0.0012$), six of which were vegetative features that might vary relative to the nutritional status of the host/parasite interface; specifically with a host like sorghum that received additional irrigation or special treatment (terrace) which made water more available. A vigorous host might escape parasitism but if *Striga* attachment takes place it will probably result in a healthy large parasite. This is evident since the largest and tallest *Striga hermonthica* plants were those collected from irrigated fields. Populations sampled from Obied (site 2) and Abu Naama (site 3) Sudan, were grown in areas where terrace cultivation is a common practice. Although not significantly different from each other, populations from sites 2 and 3 exhibited the highest number of significant variables when compared to the remaining populations. This may suggest these two areas as centers of distribution of S. *hermonthica*.

Table 7: Vegetative and floral features showing significant variation among populations of *Striga hermonthica* parasitizing various hosts and obtained from different geographical locations.

Site	1	2	3	4	5	6	7	8
Lat.	13°32'N	13°28'N	12°49'N	12°47'N	11°05'N	10°37'N	09°50'N	09°28'N
Long.	07°04'E	30°31'E	33°40'E	07°59'W	12°50'E	07°30'E	09°25'E	05°11'E
1		B H O	B D H O		A	A D N	F	B
2				B H OP	AC EF H O	ABC EF H P	ABC EF H	E
3				B H O	AC F H	ABC F H P	ABC F H	
4					E NO	A D E NO	EF P	B E
5						P		A F
6							P	AB N
7								AB F
8								

Letters in matrix represent the significant variables ($P < 0.0012$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), H=Lower bract length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- in Niger, 2-3 Sudan, 4- Mali, 5-8 Nigeria.

Geographical variation in *Striga hermonthica*

Geographical variation in *Striga hermonthica* was assessed in five populations parasitizing sorghum (Table 8a) and three parasitizing millet (Table 8b). Eight vegetative and only two floral features were significantly different ($P < 0.004$), with the populations gathered from sorghum infested fields showing the highest number of significant variables (Table 8a and 8b). The sorghum-strigas displayed a pattern of increasing variability along a moisture gradient which increases from north to south with the populations collected from adjacent sites showing the least differences. Its intraspecific variability ranged from two to eight variables per site, most of which were vegetative. The millet-strigas, because they were common to the relatively drier zones without supplementary irrigation, were fairly homogeneous confirming that the variabilities in the sorghum-strigas were due the moisture availability through irrigation and terraces.

Host induced variation in *Striga hermonthica*

Herbarium specimens of *Striga hermonthica* parasitizing sorghum and millet similarly gathered from three different latitudes were compared for a possible host effect. They differed significantly in only four variables (Table 9), three of which were floral characters [corolla tube length (N), lower corolla lobe length (O), and the upper corolla lobe length (P)]. It has been documented that *Striga hermonthica*, an out-crosser (Safa *et al.* 1984), has developed host-specificity to sorghum and millet hosts (Wilson-Jones 1955, Parker and Reid 1979, Musselman and Hepper 1986). In the Sub-Sahara of Africa, where millet is the main grain crop because it does well under relatively low moisture, it developed host-specificity to millet, while further south where sorghum is more

Table 8a: Vegetative and floral features showing significant geographical variation in *Striga hermonthica* (host: sorghum).

Site	1	2	3	4	5
Lat.	13°28'N	12°49'N	11°05'N	10°37'N	09°50'N
Long.	30°31'E	33°40'E	12°50'E	07°30'E	09°25'E
1		A D	ABC F H	ABC EF H P	ABC EF H
2			A C	ABC EFGH P	ABC EF H
3				A E G	A E G
4					D P
5					

Letters in matrix represent the significant variables ($P < 0.004$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), O=Lower corolla lobe (mm), and P=Upper corolla lobe length (mm). Site 1 and 2 in Sudan, 3-5 Nigeria.

Table 8b: Vegetative and floral features showing significant geographical variation in *Striga hermonthica* (host: millet). (See Table 8a for variables).

Site	Niger	Nigeria	Nigeria
Lat.	13°32'N	12°47'N	09°28'N
Long.	07°04'E	07°59'W	05°11'E
Niger			B E
Nigeria			B E O
Nigeria			

Table 9: Vegetative and floral features significantly different among populations of *S. hermonthica* parasitizing sorghum and millet.

variables	host sorghum (means)	host millet (means)	alpha
Lower bract length (mm)	25.88	36.05	0.0001
Corolla tube length (mm)	17.22	15.60	0.001
Lower corolla lobe length (mm)	9.54	7.44	0.0001
Upper corolla lobe length (mm)	5.99	4.88	0.0001

common than millet, *Striga* developed host-specificity to sorghum. If host-specificity has to be maintained under sympatry, and because *S. hermonthica* is an outbreeder, the two strains should express differences that reduce the chances of interbreeding (character displacement). The differences between the sorghum and the millet strains were mainly floral (Table 9). This kind of variation is expected to reduce the chances of cross pollination under sympatry, and if established, could lead to genetic isolation. Although host-specificity reduces the host range of the parasite it may lead to successful attachment and better adaptability to a specific host under specific conditions. If we consider a host like sorghum which developed resistance to the parasite, host-specificity and virulence in the parasite are then of great selective advantage. In areas where sorghum and millet were grown in the same or adjacent fields, host-specificity broke down (Ramaiah 1984, Rao and Musselman 1987), showing that different forms of *S. hermonthica* have not became fixed due to cross pollination and exchange of genes between the two populations (Ramaiah 1984).

The interacting effects of host and geographical location on variation among populations of *Striga hermonthica*

The possible effects of host, geographical location, and their combined effects of (host/geographical location) were compared using herbarium specimens of *Striga hermonthica* gathered at three latitudes and from two hosts (sorghum and millet). The three types of variations are shown here and in Table 10:

1) Possible host effects were obtained when populations of *Striga hermonthica* gathered from sorghum-infested fields were compared to those from millet at a given geographical locality. On average the two populations differed significantly in 3.67 variables per locality.

Table 10: Vegetative and floral features showing significant variation due to host [sorghum (s) and millet (m)], geographical, and host/geographical effects in *S. hermonthica*.

Site	1 (s)	1 (m)	2 (s)	2 (m)	3 (s)	3 (m)
Lat.	13°18'N	13°32'N	12°49'N	12°47'N	09°50'N	09°28'N
Long.	30°31'E	07°04'E	33°40'E	07°59'W	09°25'E	05°11'E
1 (s)		BC1) H OP	2)	ABC3) H OP	ABC2) F H	C3) H P
1 (m)			D3) H O	2)	A3) F	B2)
2 (s)				D1) OP	A D2) F H	3)
2 (m)					A3) F OP	B2) O
3 (s)						AB1) F
3 (m)						

1) = Host variation
2) = geographical variation
3) = (host/geographical) variation

Letters in matrix represent the significant variables ($P < 0.003$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), F=Inflorescence length (cm), H=Lower bract length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm). Site 1 and 2 in Sudan and 3- Nigeria.

2) Possible geographical variation at the host-specific strain level (sorghum and millet strains) were obtained when S. *hermonthica* plants collected from the same host were compared at different geographical localities. These populations exhibited an average difference of two variables per site, suggesting that S. *hermonthica*, regardless of its host, is fairly homogeneous over its range.

3) Effects of interaction between host and geographical location on variation was obtained when S. *hermonthica* plants parasitizing sorghum and millet were compared at different geographical localities. Here the number of significant variables averaged three per site which was slightly less than that attributed to host induced variation at a given locality. It follows that the intraspecific variability in S. *hermonthica* was higher than the interspecific variability (variation among host-specific strains is higher under sympatry than under allopatry) confirming results obtained from Table 9. This is consistent with the findings of Musselman *et al.* (1991) who studied differences among populations of S. *hermonthica* and concluded that they exhibit considerable intrapopulational variation in contrast to S. *asiatica* and S. *gesnerioides* (both inbreeders) which are relatively uniform within a given population.

Overall, S. *hermonthica* showed a high number of significant variables but for any two sites or host-specific strains compared the number of significant variables was relatively low (Table 7-10) suggesting that it was homogeneous over its range as is expected for an outbreeder.

It seems that most of the variability within S. *hermonthica*, although low, was caused by geographical effects rather than host-specificity. Bharathalakshmi *et al.* (1990) attributed most of the genetic variablity in S. *hermonthica* to geographical separation rather than to host specialization. Even what could be interpreted as host effect (Table 9) was in fact a variation induced by climate before the parasite was successful in invading the host i.e. the variation was established first, then the host was attacked.

Geographical variation in *Striga aspera*

Herbarium specimens of *Striga aspera* parasitizing various native grasses gathered from seven localities between latitude 07° 10' and 13° 55' N were examined to show the possible geographical effect on variation. In general, 10 variables exhibited significant differences ($P < 0.0012$), 60% of which were vegetative (Table 11). Also, when any two sites were compared, the number of significantly different vegetative variables was more than double the floral ones, suggesting that variation in *S. aspera* was primarily vegetative. There was evidence of an increase in the number of significant variables with changes in latitude.

Like *S. hermonthica*, *S. aspera* is an outbreeder (Musselman *et al.* 1991). Among populations gene-flow is expected to maintain a certain level of homogeneity across the species range. This is consistent with the results obtained.

Variation in the species complex of *Striga hermonthica* and *S. aspera*

A total of 385 and 315 measures for each variable were taken from populations of *S. hermonthica* and *S. aspera* respectively, and analyzed to estimate their overall differences (Table 12). The plants were gathered from different hosts and fairly represent the geographical range of the two species (between latitude 3° 00' and 14° 00' N). Of the thirteen variables, ten were significantly different ($P=0.0001$), with no significant differences in the number of branches (B), inflorescence length (F), and the calyx teeth length (M).

Table 11: Vegetative and floral features showing geographical variation in *Striga aspera.*

Site	1	2	3	4	5	6	7
Lat.	07°10'N	09°30'N	10°36'N	11°39'N	12°19'N	12°35'N	13°55'N
Long.	28°00'E	08°40'W	04°44'W	07°26'W	08°30'W	07°46'W	08°25'W
1		E	AB E	A CD E H	A CD E H NO	A CD E H	E N
2			B	A C E GH	C GH NOP	C E H	N
3				BCD E GH	BCD GH N	BCD E H	BC N
4					NOP	GH	A CD GH N
5						G N	C GH P
6							H N
7							

Letters in matrix represent the significant variables ($P < 0.0012$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- in Sudan 2- Nigeria, 3- Burkina Faso, 4-7 Mali.

Table 12: Vegetative and floral features showing significant variation among *Striga hermonthica* and *S. aspera.*

Variable	hermonthica (means)	aspera (means)	alpha
Stem height (cm)	43.48	28.31	0.0001
Leaf length (mm)	54.70	23.66	0.0001
Leaf width (mm)	3.98	1.02	0.0001
Internode length (mm)	26.65	16.63	0.0001
Flowers open/inflorescence	8.00	3.09	0.0001
Lower bract length (mm)	31.51	15.57	0.0001
Calyx tube length (mm)	6.63	4.20	0.0001
Corolla tube length (mm)	16.85	14.56	0.0001
Lower corolla lobe length (mm)	8.57	6.34	0.0001
Upper corolla lobe length (mm)	5.32	4.23	0.0001

a. Host induced variation:

It is difficult to assess the magnitude of the variation due to hosts in S. *hermonthica* and S. *aspera*, because the former commonly parasitizes cereal crops while the latter parasitizes wild grasses, i.e., the two species do not occur on a single host at the same site. In the few instances where this data was obtained, it was insufficient for a multivariate statistics and the results might be misleading. However, in a preliminary analysis the host was found to have some effects. When the two species were compared on similar hosts they showed less differences than when compared on different hosts.

b. Species induced variation:

Striga hermonthica and S. *aspera* were similarly sampled from herbarium specimens collected at four geographical localities and then the data was assessed to quantify the variation between the two species under similar environmental conditions. Differences already established between the two species (species induced variation) were similar to those reported in (Table 12) with only slight changes in the means of the ten significant variables.

c. Geographical variation:

Geographical variation in S. *hermonthica* and S. *aspera* were expressed in eight significant variables ($P < 0.0025$), five of which were vegetative (Table 13).

This study suggests that the differences already established between S. *hermonthica* and S. *aspera*, are quantitative and greater than those attributed to host and geographical location.

d. Variation due to Species, geographical location, and the combined effects of (species/geographical location)

Table 13: Vegetative and floral features showing significant geographical variation in *Striga hermonthica* and *S. aspera*.

Site	1	2	3	4
Lat.	13°28'N	11°40'N	10°37'N	09°28'N
Long.	30°31'E	08°50'E	05°30'E	07°11'E
1		D G	ABCD E N	C E M
2			ABCD E G M	CD E G
3				ABCD M
4				

Letters in matrix represent the significant variables ($P < 0.0025$): A=Stem height (cm), B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), G=Number of flowers open/inflorescence, M=Calyx teeth length (mm), and N=Corolla tube length (mm).

site 1- in Sudan, 2-4 from Nigeria.

Herbarium specimens of *Striga hermonthica* and *S. aspera* gathered at four latitudes were analyzed to quantify the possible effects of the above three factors on variation. Results summarized in Table 14 were:

1) Variation attributed to species effect under similar geographical conditions i.e. when *S. hermonthica* and *S. aspera* were compared at the same latitude. The magnitude of this variation averaged 7.5 significant variables at each site.
2) Variation attributed to geographical separation at the species level were obtained when populations within the same species were compared at different geographical locations. This variation averaged 3 and 3.83 variables per site for *S. hermonthica* and *S. aspera* respectively, suggesting that they are both homogeneous over their range.
3) The combined effects of latitude and species induced variation were obtained when *S. hermonthica* and *S. aspera* were compared at different latitudes. The average variation here was 7.75 significant variables per site, which was only slightly higher than that attributed to species effect (1) at the same latitude. It seems that the two species expressed the same magnitude of variation when they occur sympatrically and allopatrically (7.5 and 7.75 significant variables respectively). They are outbreeders and among their significantly different variables were those associated with the corolla tube length (N), the lower (O), and upper (P) corolla lobes. Under sympatry, the corolla tube length is significantly different among them in three out of four sites [not significant at site 4 (h) and (a)]. The lower corolla lobe length is significant in all four cases while the upper lobe is significant in only one case [site 1 (h) and (a)]. Differences associated with the corolla dimensions probably reduces the chances of interbreeding under sympatry. In cases where there was no significant difference in corolla dimensions the two species might interbreed; In fact the work of Musselman *et al.* (1991) produced the first hybrid in the genus *Striga*

Table 14: Species, latitude, and (species/latitude) induced variation in *Striga hermonthica* (h) and *S. aspera* (a).

Site	1 (h)	1 (a)	2 (h)	2 (a)	3 (h)	3 (a)	4 (h)	4 (a)
Lat.	13°28'N	13°55'N	11°40'N	11°39'N	10°37'N	10°36'N	09°28'N	09°30'N
Long.	30°31'E	30°25'E	07°15'E	08°26'E	06°30'E	06°44'E	09°11'E	09°15'E
1 (h)		CD1) G L NOP	A C2) F H O	A CD3) E GH L NOP	A C2) EF H P	D3) GH L OP	2) E H OP	CD3) G L OP
1 (a)			A CD3) H L NOP	A CD2) FGH	A CD3) E GH L NO	C2) N	CD3) E GH L NOP	2) N
2 (h)				A CD1) EFGH L NO	2) G	A CD3) L NO	2)	A CD3) H L N
2 (a)					A CD3) EFGH L NO	A CD2) E GH	A CD3) E GH L O	A C2) EFGH
3 (h)						A CD1) E G L NO	A2) N	A CD3) E GH L NO
3 (a)							CD3) E G L O	D2) G
4 (h)								CD1) E L O
4 (a)								

1) = Differences due to species
2) = Differences due to latitude at the species level
3) = Differences due (species/latitude) interaction

Letters in matrix represent the significant variables ($P < 0.0001$): A=Stem height (cm), C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- in Sudan, 2-4 from Nigeria.

between S. *hermonthica* and S. *aspera* with viable seeds. They also noted where the species occur sympatrically some plant forms seems to have intermediate characters between the two species and can be identified as either of them and to that natural hybridization between them seems almost certain since S. *aspera* is visited by butterflies, moths and bees similar to S. *hermonthica* visitors reported in Musselman *et al.* (1983). In Burkina Faso S. *aspera* is known to cause damage to maize and sugar cane similar to that of S. *hermonthica* on millet and sorghum. Could this change in S. *aspera* parasitic behavior be attributed to a possible gene exchange between the two species that provide a larger gene pool which could enable S. *aspera* as well as S. *hermonthica* to attack a wider range of host crop species?

In conclusion, the higher significant differences between the two species (Table 12 and 14) compared to their low within species variation (Table 7, 11, and 14) support the current taxonomic treatment of recognizing two species. It is likely that S. *hermonthica* diverged from its ancestor (possibly S. *aspera)* and with the domestication of cereal crops it was able to evolve strains that parasitized crops. The ability to invade new habitats and hence new hosts led to the development of different morphologies and strains. The necessary genetic changes were made possible through isolation of small demes and finally one of them may have evolved into the taxon now known as S. *hermonthica.* The presence of natural hybrids suggests that the reproductive isolation was not yet perfected and the divergence was recent.

Variation in *Striga brachycalyx*

Herbarium specimens of S. *brachycalyx*, collected from four localities between latitudes 09° 08' and 13° 08' N, were examined to assess intraspecific variability (Table 15). *Striga brachycalyx* was homogeneous over its range being significantly different in only five variables ($P < 0.002$), three of which were vegetative. The number of significant variables showed a slight increase with latitude especially for sites three and four.

Table 15: Vegetative and floral features showing significant geographical variation in *Striga brachycalyx*.

Site	1	2	3	4
Lat.	13°12'N	12°00'N	10°37'N	09°08'N
Long.	03°22'W	00°19'W	04°44'W	05°40'E
1		OP	AB D OP	B D OP
2			AB D	B D
3				A
4				

Letters in matrix represent the significant variables ($P < 0.002$): A=Stem height (cm), B=Number of branches, D=Leaf width (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1-3 in Burkina Faso and site 4- from Nigeria.

The closely related species S. *aspera* (chapter 4) resembles S. *brachycalyx* in its overall appearance. They are sympatric in their distribution, frequently in large demes, and occupying relatively drier savannas. Unlike S. *aspera* which occasionally invades the agroecosystem, *Striga brachycalyx* is not known to attack food crops although is very common in natural grassland.

Intraspecific variability in *Striga gesnerioides*

Striga gesnerioides has developed well known host-specific strains, each parasitizing restricted hosts. Table 16a expresses the overall differences in thirteen variables among seven host-specific strains. The sources of this variation could be due to host plants and/ or differences in climatic conditions since the species occupies a wide geographical range.

Generally, strains of S. *gesnerioides* differed significantly in four vegetative and five floral characters ($P < 0.0024$), with the differences between any two strains being less than six variables and averaging two (Table 16a). The Strain specific to *Euphorbia* species showed the highest number of significant variables from the remaining strains. It is consistently different from them in its broader leaves (D) and longer corollas (N). The remaining strains showed significant differences in only one or two variables. When compared to each other, strains specific to hosts within the same family (Fabaceae or Convolvulaceae) showed the least number of significant variables. The difference between strains parasitizing Fabaceae was a maximum of 2 with an average of 1 variable, while it was 3 and 1.33 for strains within Convolvulaceae (Table 16a).

Host induced variation in S. *gesnerioides*

Not all of the host-specific strains included in Table 16a were analyzed with regard to host effects because they were not available from a single site or at least the same

Table 16a: Vegetative and floral features showing significant variation among strains of *Striga gesnerioides*.

Strain	JACM	COWP	IPOM	EUPH	MERM	TEPH	INDO
JACM			D	D N		H	C L
COWP			B D G O	B D L NOP	OP	B	OP
IPOM				D	BC G		L
EUPH					B D G N	D H L N	CD L N
MERM						B H	C L
TEPH							
INDO							

Letters in matrix represent the significant variables ($P < 0.0024$): B=Number of branches, C=Leaf length (mm), D=Leaf width (mm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

Strains were collected from the following host plant: JACM= *Jacquemontia*, COWP= *Vigna*, IPOM= *Ipomoea*, EUPH= *Euphorbia*, MERM= *Merremia*, TEPH= *Tephrosia*, and INDO= *Indigofera* latitude and their inclusion would be misleading. Variation attributed to host was thus investigated in four strains of S. *gesnerioides* gathered at the same latitude (Table 16b). They differ significantly in only three variables ($P < 0.002$), with the strain specific to *Merremia* and *Jacquemontia* species showing no significant differences.

Hosts of S. *gesnerioides* include *Jacquemontia, Merremia,* and *Ipomoea* in the family Convolvulaceae, *Nicotiana* (Solanaceae), *Euphorbia* (Euphorbiaceae), *Vigna, Indigofera* and *Tephrosia* (Fabaceae) with at least four host-specific strains one each of *Euphorbia, Vigna, Nicotiana* and Convolvulaceae (Musselman 1984, Musselman and Parker 1981). The *Vigna*-strain is much branched, with a green stem, and bluish flowers causing its most damage in the drier regions. The *Euphorbia*-strain has a large single primary haustorium, dark red stem, dark-purple flowers, and is restricted to the drier regions. In Africa the *Nicotiana*-strain is restricted to South Africa and Zimbabwe. It is less branched but otherwise resembles the cowpea-strain. The strain specific to Convolvulaceae has a slender red and less branched stem with pinkish flowers. The mechanism of host-specificity is not fully understood. Wild (1948) attributed it to germination stimulants; while Parker and Reid (1979) provided experimental evidence that the small flower (*Jacquemontia tamnifolia*) morning glory strain could be germinated by the cowpea root exudate, but not be parasitized. Musselman and Parker (1981) suggest that an incompatibility factor must be responsible for some of the observed specificity. Host specificity has developed under various habitats where the survival strategy is to invade the hosts available in that area, i.e., attacking new hosts in the absence of the conventional hosts. This gave S. *gesnerioides* great flexibility in invading new habitats and contributed to its successful spread and abundance throughout almost all Africa, parts of the Arab Peninsula, Asia and the United States of America. Although S. *gesnerioides* has evolved a strong host-specificity among its populations these "morphs" do not have significant morphological and genetic differences and hence they should be treated as host-specific "strains" of the same species.

Table 16b: Vegetative and floral features showing significant host variation in *S. gesnerioides*.

Strain	JACM	MERM	COWP	INDO
JACM			H L P	H L
MERM			H P	H L
COWP				P
INDO				

Letters in matrix represent the significant variables ($P < 0.0024$): H=Lower bract length (mm), L=Calyx tube length (mm), and P=Upper corolla lobe length (mm).

Strains were collected from the following host plant: JACM= *Jacquemontia*, COWP= *Vigna*, IPOM= *Ipomoea*, EUPH= *Euphorbia*, MERM= *Merremia*, TEPH= *Tephrosia*, and INDO= *Indigofera*

Relationships among the subspecies of *Striga bilabiata*

Herbarium specimens identified as *Striga bilabiata* subspecies *bilabiata*, *rowlandii*, *barteri*, and *ledermannii* obtained from four different gatherings were assessed to infer their relationship. Of the thirteen variables a minimum of six and a maximum of ten variables exhibited significant differences among the four subspecies (Table 17a and 17b). The subspecies *bilabiata* and *ledermannii* showed the lowest number of significant variables while *ledermannii* and *barteri* showed the highest, occupying the two extremes. However, there was a character gradient between them and they overlapped at their minima or maxima with one or more of the other subspecies (Table 17b).

Striga bilabiata subspecies *jaegeri* was not included in this study because of inadequate sample size. In a preliminary analysis it was found that this subspecies, which is relatively larger in its overall size than the remaining subspecies of *S. bilabiata*, was not significantly different from them in four to nine variables, being more similar to the subspecies *ledermannii* and different from *barteri*. Also the inclusion of subspecies *jaegeri* tended to slightly reduce the number of significant variables between the four subspecies shown in Table 17a.

Striga linearifolia and *S. bilabiata*

Among other features, members of the genus *Striga* are delimited by the shape and size of the corollas. All the subspecies of *S. bilabiata* share a two-lipped corolla which might be the single dependable feature that unites them. The possession of the bilabiate corolla and the other features that *S. linearifolia* shares in common with the subspecies of *S. bilabiata* may place it as an infraspecific form of the species complex. To see how well this species fits in the complex, seven populations of *S. linearifolia* obtained from

Table 17a: Vegetative and floral features showing significant variation among subspecies of *Striga bilabiata.* (see Table 17b for variables).

Subsp.	rowlandii	bilabiata	barteri	ledermannii
rowlandii		A C E H LM P	A C D EF H M	CD E H LMNOP
bilabiata			CD F H LM OP	A D L NOP
barteri				A D EF H LMNOP
ledermannii				

Table 17b: Vegetative and floral features showing significant variation among subspecies of *Striga bilabiata.* (subspecies names as in Table 17a).

variable	S.rowl	S.bila	S.bart	S.ledr	alpha
A	29.58	18.90	17.18	29.00	0.0001
C	28.08	13.42	20.17	16.41	0.0001
D	1.46	1.59	1.03	2.16	0.0001
E	20.18	10.14	7.60	10.29	0.0001
F	8.13	5.92	11.23	6.28	0.0001
H	5.60	9.03	17.18	10.58	0.0001
L	4.75	3.76	5.34	2.94	0.0001
M	1.21	2.18	4.10	2.06	0.0001
N	12.02	11.54	12.05	10.67	0.0001
O	2.54	3.00	2.06	1.51	0.0001
P	2.94	3.94	2.70	1.98	0.0001

Letters in matrix and table 16a-b represent the significant variables ($P < 0.0001$): A=Stem height (cm), C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

different localities were analyzed together with the populations of S. *bilabiata* used in Table 17a and 17b. Results are shown in Table 18a and 18b.

Inclusion of S. *linearifolia* slightly affected the number of the significant variables among the subspecies of S. *bilabiata* as shown in Table 17a. When S. *linearifolia* was included, the inflorescence length (F) and the corolla tube length (N) were not significantly different among the subspecies *rowlandii* and *barteri*, and *bilabiata* and *ledermannii* respectively; and the internode length (E) was not significantly different between the subspecies *barteri* and *ledermannii* (compare Tables 17a and 18a). This implied that the inclusion of S. *linearifolia*, as with S. *ledermannii*, resulted in the reduction of the number of significant variables between the subspecies of S. *bilabiata*.

This analysis shows that S. *linearifolia* fits very well in the species complex of S. *bilabiata*. All together, the five subspecies and the subspecies *jaegeri* form a natural group with characters imperceptibly grading into one another. The removal of any subspecies from the complex will result in a morphological gap which can be misinterpreted. For example inclusion of S. *linearifolia* and subspecies *ledermannii* reduced the number of significant variables among the species complex. Among the five subspecies, *bilabiata* showed the lowest number of significantly different variables while *ledermannii* expressed the highest number. On average the former differed significantly in 6.75 variables and the latter in 8.0. Similar values were 7.25, 7.75 and 7.75 for *rowlandii*, *barteri*, and *linearifolia* respectively. *Striga linearifolia* showed a consistently significant difference from the remaining subspecies in its long stem (A) and reduced leaves (C) nevertheless, it remains in an intermediate position, i.e., it is not the most different.

In his publication "The S. *bilabiata* complex in Africa" Hepper (1960), analyzed some of the features of the species previously known as S. *rowlandii*, S. *barteri*, S. *ledermannii*, S. *welwitschii*, S. *glandiflora*, and S. *bilabiata*. He proposed the reduction of S.

Table 18a: Vegetative and floral features showing significant variation among the subspecies of *Striga bilabiata* and *S. linearifolia*.

Taxa	rowlandii	bilabiata	barteri	ledermannii	linearifolia
rowlandii		A C E H LM P	A CD E H M	CD E H LMNOP	A C H LMNO
	bilabiata		CD FH LM OP	A D L OP	A C EFG OP
		barteri		A D F H LMNOP	A C E GH LMN
			ledermannii		A CD EFGH L P
				linearifolia	

Table 18b: Vegetative and floral showing significant variation among the subspecies of *Striga bilabiata* and *S. linearifolia*. (Taxa as in Table 18a).

variable	S.rowl	S.bila	S.bart	S.ledr	S.linr	alpha
A	29.58	18.90	17.18	29.00	39.68	0.0001
C	28.08	13.42	20.17	16.41	6.39	0.0001
D	1.46	1.59	1.03	2.16	1.33	0.0001
E	20.18	10.14	7.60	10.29	20.79	0.0001
F	8.13	5.92	11.23	6.28	10.32	0.0001
G	2.95	3.67	4.10	4.11	4.44	0.0001
H	5.60	9.03	17.18	10.58	7.53	0.0001
L	4.75	3.76	5.34	2.94	3.50	0.0001
M	1.21	2.18	4.10	2.06	2.02	0.0001
N	12.02	11.54	12.05	10.67	10.88	0.0001
O	2.54	3.00	2.06	1.51	1.97	0.0001
P	2.94	3.94	2.70	1.98	3.04	0.0001

Letters in the matrix and table represent the significant variables ($P < 0.0001$): A=Stem height (cm), C=Leaf length (mm), D=Leaf width (mm), E=Internode length (mm), F=Inflorescence length (cm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

barteri, *S. rowlandii*, and *S. ledermannii*, to the rank of subspecies; then, using the earliest name available [*S. bilabiata* (Thunb.) Kuntze] he treated them as subspecies. He also described the new subspecies *jaegeri* (=*S. welwitschii* Engl.). Hepper's treatment is widely accepted except that some taxonomists (Musselman 1987, Raynal-Roques 1987, 1991) still refer to *S. ledermannii*, others confuse *S. linearifolia* with *S. bilabiata*. In the same publication Hepper also proposed the name *S. linearifolia* as the correct valid name based on *Buchnera linearifolia* Schumach. and Thonn. because this latter name is what was then known as *S. strictissima* Skan a synonym of *S. canescens* Engl. This study confirms Hepper treatment of *S. ledermannii* as a subspecies of *S. bilabiata* and suggests that *S. linearifolia* also be considered as a subspecies of *S. bilabiata*.

Geographical variation in *Striga bilabiata* subsp. *linearifolia*

Herbarium specimens of *S. linearifolia* gathered from different localities between latitudes 10° 40' S and 12° 00' N were compared to assess the geographical variation (Table 19). They differed significantly in four vegetative and six floral characters ($P < 0.003$). The population sampled from Rumpi, Malawi (site 1) showed the highest number of significant variables, being different from the other in the size of calyx (M), corolla lobes (O, P), and the number of flowers open per inflorescence branch (G). The high morphological variability showed by site 1 could be due to the fact that it represents the extreme of the geographical range of the subspecies. The other five populations were fairy homogeneous when compared to each other (Table 19).

Table 19: Vegetative and floral features showing significant geographical variation in subspecies *linearifolia.*

Site	1	2	3	4	5	6	7
Lat.	10°40'S	00°15'N	06°03'N	08°31'N	09°31'N	10°42'N	12°00'N
Long.	33°54'E	32°28'E	37°35'E	21°13'E	07°38'W	04°50'W	01°30'W
1		E G M O	A C E GH LM O	E G M OP	C E G LM OP	E LM OP	E G M OP
2			E LM	P	LM P	E G L P	MN P
3				A P	A P	A OP	A C GH L P
4						G	P
5						G	L N P
6							G N
7							

Letters in matrix represent the significant variables ($P < 0.0008$): A=Stem height (cm), C=Leaf length (mm), E=Internode length (mm), G=Number of flowers open/inflorescence, H=Lower bract length (mm), L=Calyx tube length (mm), M=Calyx teeth length (mm), N=Corolla tube length (mm), O=Lower corolla lobe length (mm), and P=Upper corolla lobe length (mm).

site 1- in Malawi, 2- Uganda, 3- Ethiopia, 4- Burkina Faso, 5- Ivory Coast, and 6 and 7 Burkina Faso.

CHAPTER FOUR

PHYLOGENY OF STRIGA

INTRODUCTION

The application of cladistics to taxonomic problems is increasingly popular among botanists but it is still in its infancy. As Humphries and Funk (1984) have pointed out, not only is the method demanding, but also, for many botanists it is quite unacceptable because of its apparent failure to accommodate reticulate evolution or hybridization.

The word "relationship" has many valid uses in systematics. It is often employed to indicate overall resemblance but Hennig (1966) and his school have used it to mean the genealogical relationship, that is relative recency of common ancestry. Within a group, two or more taxa are regarded as being more closely related to each other than to other members of the group if they share a common ancestor that is not shared with the group. The phylogeny of a recent group is essentially the result of a series of historical events each consisting of a single species (a common ancestor) dividing into two or more descendant (daughter) species which, in turn, may also split to produce daughter species.

The Cladistic Analysis Method is advocated by Hennig and his school. According to this method, the group to be analyzed must consist of all the descendants of one common ancestor, that is be monophyletic. Analysis is limited to derived (apomorphic) features. Cladists argue that, if two or more species share a derived feature not found elsewhere in the group, this is provisional evidence of joint evolutionary experience in the form of a common ancestor not shared by species that lack the feature. If enough of such shared, derived features (synapomorphies) are available with different distributions it is possible to build a hypothesis of relationship for the whole group. In cladistic practice common ancestors are always treated as having divided into only two daughter stocks (sister groups) and so that all apparent polychotomies are really an unresolved series of dichotomies.

Generally, there are three steps in cladistic study: the choice of taxa and sampling of characters, the determination of synapomorphies, and the search for the most parsimonious cladogram incorporating the least number of assumptions. However, all three steps have had various problems ascribed to them, such as how to determine homologies, problems of parallel and convergent evolution, and cladogram construction. In this study I attempted to use the cladistic method to estimate the genealogical relationships among *Striga* species.

MATERIALS AND METHODS

The Program Phylogenetic Analysis using Parsimony (PAUP) IBM version 2.4 was used to infer the phylogeny of *Striga*. PAUP has different options that can be used for various data sets to estimate the shortest tree. The Lundberg (1972) Rooting was used and favored over the Outgroup Rooting Procedure because it has the advantage of minimizing additional homoplasy introduced by the inclusion of the outgroups. It seeks the shortest unrooted tree for the ingroup taxa, which is then rooted at the position where a hypothesized ancestor would join the tree.

Many methods for assessing the evolutionary polarity of characters have been proposed, including the Outgroup Analysis, the Ingroup Analysis and the Ontogenetic Methods. Among these methods the outgroup analysis is usually the most widely accepted because it finds the simplest hypothesis of ancestral state based on simple parsimony. Thus, it requires fewer ad hoc hypotheses of character state change and allows examining the outgroups, which helps to ensure that the ingroup cladograms obtained are parsimonious. Therefore, in this study characters were polarized and ordered prior to data entry using the Outgroup Algorithms of Maddison *et al.* (1984).

The direction of character polarity was determined using the outgroups *Buchnera, Cycnium, Rhamphicarpa, Melasma,* and *Thunbergianthus* from the Buchnereae and *Scoparia* from the Digitaleae. The latter taxon was included to provide a non-parasitic, distantly related taxon. *Buchnera* was chosen because it is presumably closely related to *Striga* (Musselman 1987, Minkin 1987) and probably its sister group. The others were used to provide features necessary to polarize characters within the group under study.

The outgroup algorithms finds and assigns the most parsimonious character state to the outgroup node which can then be used for the ingroup analysis. In general, assigning a character to a given node depends on the preceding node's label and the label of the terminal taxon of the node in question. The following is an explanation of how a label is assigned to the outgroup node which seems like a voting procedure. Terminal taxa among the outgroups (refer to Fig. 14) were labeled with their observed character states (a, b). Then proceeding from the outgroup terminal taxa towards the outgroup node, the nodes were labeled according to the following rule: a node is labeled 'a' if the two immediately-adjacent nodes that are further from the outgroup node are labeled 'a' and 'a' or 'a' and 'a, b'. A node is labeled 'b' if the two immediately-adjacent noded that are further from the outgroup node are labeled 'b' and 'b' or 'b' and 'a, b'. The

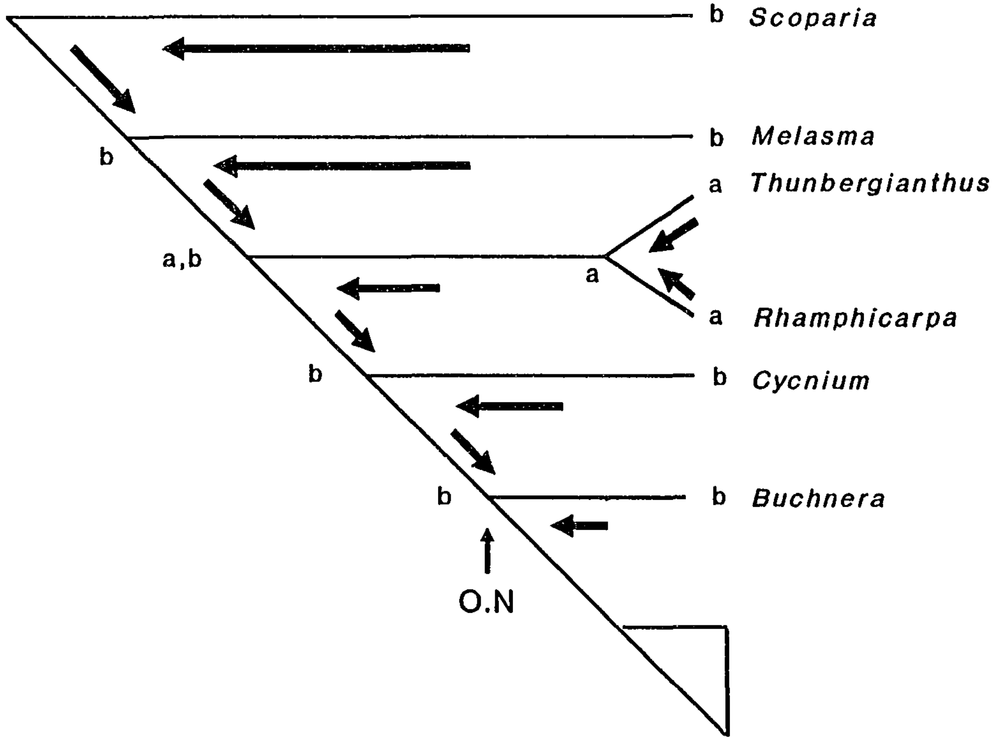


Fig. 14: Assignments of character state for the outgroup nodes. Nodes are labeled starting at the outgroup terminal taxa and proceeding towards the outgroup node (O.N.).

node was labeled 'a, b' if they are labeled 'a' and 'b' or 'a, b' and 'a, b'. In this case the character was considered "unresolved" and cannot be used. Labeling proceeded towards the outgroup node until finally a label was applied to the outgroup node (Fig. 14). The label assigned to the outgroup node was the plesiomorphic state and its alternative was the apomorphic as shown in (Table 20 and Table 21).

Because the genus *Striga* is fairly large and some of its members are rare species it was difficult to simultaneously obtain data on pollen exostructure, seed features, and cytological structures such as chromosome numbers from all taxa. Instead, an array of physiological, ecological, floral, and vegetative characters (Table 20) were admitted into the program. Two analyses were performed: in the first, all characters were weighted equally; in the second, germination stimulant (character 2), host specificity (char. 3), plant succulence (char. 5), haustoria size (char. 6), and plant color (char. 7) were assigned the weight of "two". Characters (2) and (3) were weighted because they were unusual in members of the genus and define only one species, S. *angustifolia*, the species that germinates without a host stimulant has a wide host range of as many as 36 species including both dicotyledon and monocotyledon plants (Rao *et al.* 1986). The other three characters were weighted because they uniquely define *Striga* species that only parasitize dicotyledon plants.

In the first few program runs, the analysis was performed on 44 characters which resulted in trees with inconsistent topography. Then 14 characters were deleted, most of which were vegetative characters associated with the stem and leaf structures. The deletion of those characters very much improved the consistency index and resulted in stable tree topographies. For each run on the remaining 30 characters a maximum of 50 trees were sought and the one closest to the consensus tree was chosen as the most parsimonious.

Table 20: Plesiomorphic and apomorphic character states used in phylogenetic analysis of *Striga*.

Character	Character state	
	Plesiomorphic(-)	Apomorphic(+)
General:		
1. Duration	0=perennial	1=annual
2. Germination stimulant	0=not needed	1=needed
3. Host specificity	0=none	1=monocot 2=dicot
4. Typical habitat	0=natural grassland	1=agroecosystem
5. Plant succulence	0=not succulent	1=succulent
6. Haustoria size	0= many small	1=few large
7. Plant color	0=chlorophyllous	1=achlorophyllous
Main stem:		
8. Height	0=stiffly erect	1=cespitose
9. Indumentum	0=glabrous/sparse	1=dense hair
Leaves:		
10. Position	0=alternate/subalt.	1=opposite
11. Size	0=long broad	1=long narrow 2=reduced
12. caulineness	0=acauline	1=cauline
13. Margins & nerving	0=serrate/nerved	1=entire/not nerved
14. Leaf shape	0=elliptic/ovate	1=linear/lanceolate
Inflorescence:		
15. length	0=short	1=long
16. Flowers pedicellated/sessile	0=shortly pedicellated	1=sessile
17. Flowers density	0=lax	1=dense
Bracts:		
18. Length to calyx	0=shorter than	1=longer than
19. Margins & nerving	0=entire/not nerved	1=serrate/nerved
Calyx:		
20. Number of ribs	0=10 or more	1=less than 10
21. Teeth number	0=five or more	1=four
22. Equality of teeth	0=equal	1=unequal
Corolla:		
23. color	0=purple/blue/ cream/yellow	1=red/pink
24. Tube length	0=short	1=long
25. Bent or straight	0=straight	1=bent
26. Zygomorphy	0=weakly zyg.	1=zygomorphic
27. Lobes fusion	0=free	1=fused
27. Lobe tip shape	0=round/obtuse	1=acute
29. Tube pubescence	0=glabrous/sparse	1=pubescent/gland.
30. Corolla bilabiate	0=no	1=yes

Table 21: Data matrix for phylogenetic analysis of the genus *Striga*. (Character numbers and scoring from Table 20).

Taxa	Characters																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
S. aequinoctialis	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1
S. asiatica	1	1	1	1	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0
S. hirsuta	1	1	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0
S. lutea	1	1	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
S. aspera	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	1	0
S. hermonthica	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	0	1	0	1	1	1	1	0	1	0
S. baumanii	0	1	1	0	0	0	0	0	0	1	2	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
S. bilabiata:																														
subsp. *barteri*	0	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1
subsp. *bilabiata*	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1
subsp. *rowlandii*	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1
subsp. *jaegeri*	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	9	1	1	1	1	0	1	1
subsp. *ledermannii*	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1
subsp. *linearifolia*	0	1	1	0	0	0	0	0	1	1	2	1	1	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1
S. angustifolia	1	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0
S. brachycalyx	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	1	0
S. elegans	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1	1	0	1	0
S. forbesii	1	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	0	1	0

Table 22- continued

Taxa	Characters																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
S. latericea	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0
S. junodii	1	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0
S. pubiflora	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0
S. dalzielii	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	1	0
S. klingii	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	0
S. macrantha	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	1	1	0	1	0
S. passargei	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	0	0	1	1	1	1	0	1	0
S. primuloides	0	1	1	0	0	0	0	0	1	0	2	0	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0
S. yemenica	1	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	1	1	0	1	0
S. gesnerioides	0	1	2	1	1	1	1	1	1	1	2	0	1	1	1	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0
S. hallaei	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	1	0
S. chrysantha	1	1	1	0	0	0	0	1	1	1	2	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0
S. lepidagathidis	0	1	2	0	1	0	1	1	0	1	2	0	1	1	1	1	1	0	0	1	0	1	0	1	1	1	1	1	0	0
S. gastonii	0	1	2	0	1	0	1	1	0	1	2	0	1	1	1	1	1	0	0	1	0	1	0	1	1	1	1	1	0	0
S. pinnatifida	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	9	1	1	1	1	0	1	0
S. curviflora	1	1	1	1	0	0	0	0	1	1	2	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	0	1	0
S. densiflora	1	1	1	1	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	0	1	0
S. masuria	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0
S. fulgens	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
S. angollii	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	0	1	0

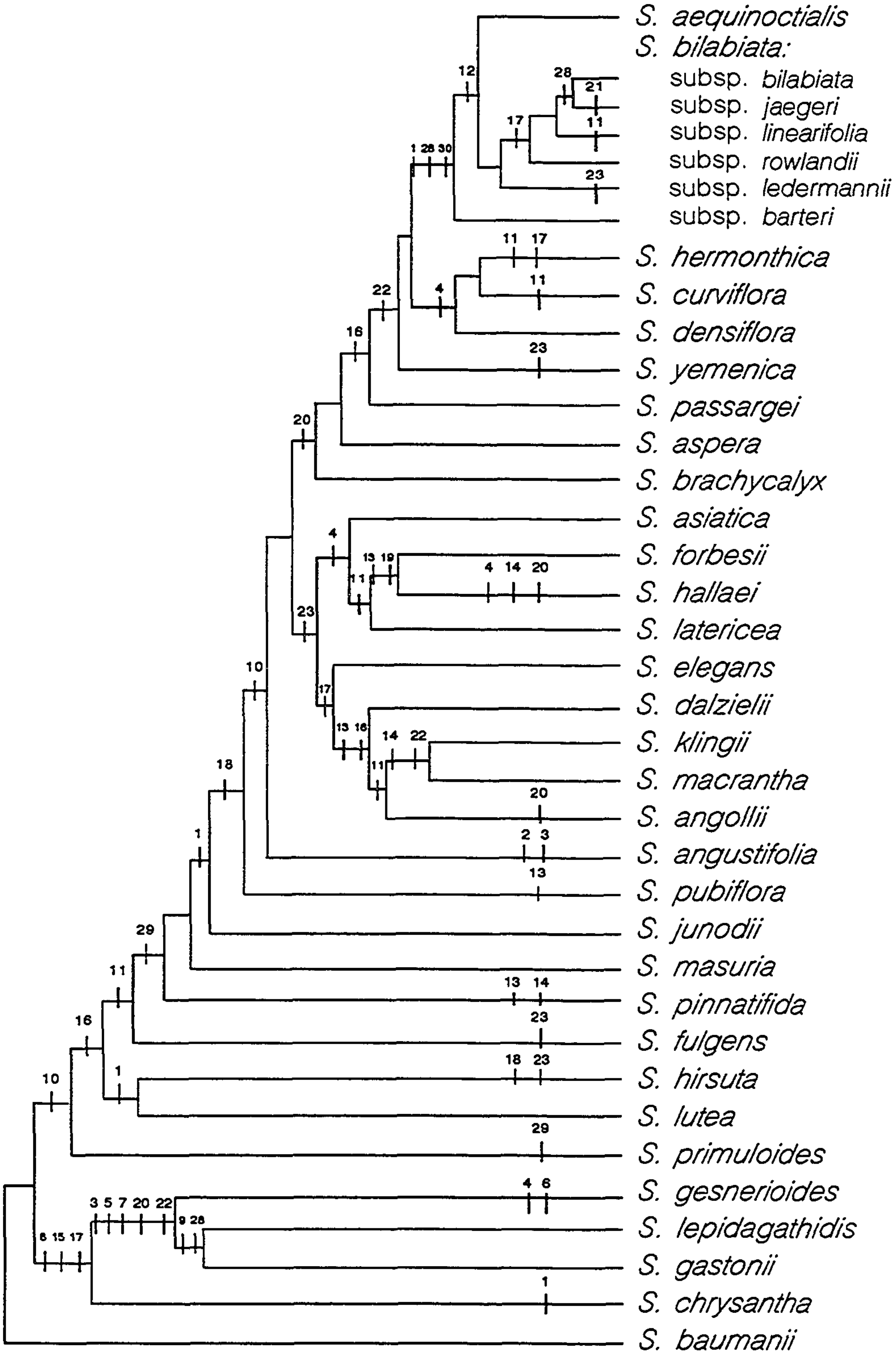
RESULTS

Weighing some of the characters, namely germination stimulant (char. 2), host specificity (char. 3), succulence (cha. 5), haustorium size (char. 6), and plant color (char. 7), did not change the tree topography obtained when all characters were assigned equal weight (Fig. 15). Even taxa like *S. angustifolia* that are uniquely defined by some of the aforementioned and *S. gesnerioides*, *S. lepidagathidis* and *S. gastonii* the only species defined by succulent stems, parasitizing dicotyledons, and appearing achlorophyllous, retained the same position on the cladogram with or without weight.

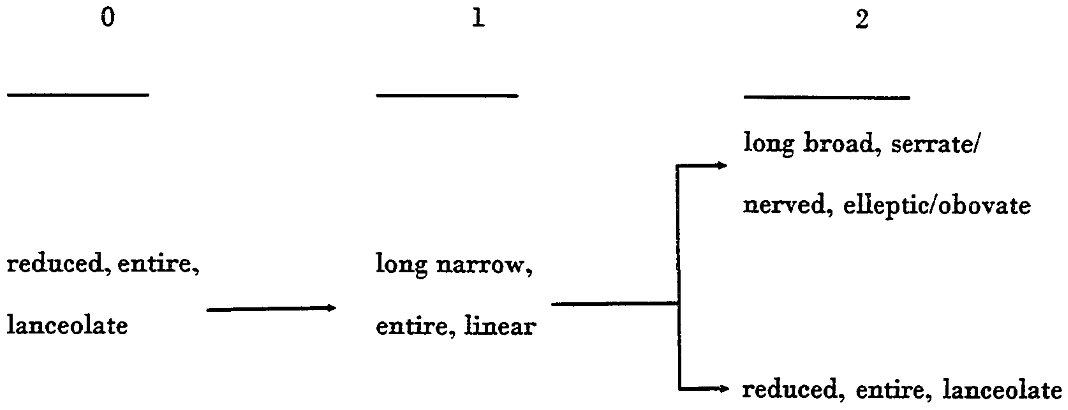
The ability of the parasite to invade different hosts in various habitats (wild hosts native to grasslands or crops in the agroecosystem) apparently evolved three times and proceeded in the same direction shown in Table 20, i.e., from parasitizing wild hosts in native grasslands and on to cultivated crops in the agroecosystem (char. 4). The first invasion was in *S. gesnerioides* the only taxon within *Striga* known to damage broad-leaf crops like cowpea *(Vigna)* and tobacco (*Nicotiana*). *Striga gesnerioides* probably evolved from within the species group of *S. lepidagathidis*, *S. gastonii* and *S. chrysantha* which are confined to natural grassland. The second invasion was evident in the Polypleurae in the species group of *S. latericea*, *S. forbesii*, and *S. asiatica* which were likely descended from a species similar to *S. elegans*, and the third was in the Pentapleurae by *S. densiflora*, *S. curviflora*, and *S. hermonthica* (Fig. 15).

Another character which showed homoplasy and reversal was duration (char. 1). It evolved from perennial to annual in *S. chrysantha*, *S. lutea* and *S. hirsuta*, and in all the species in the cladogram above *S. masuria* then was reversed at the node that gave rise to *S. bilabiata* and *S. aequinoctialis* (Fig. 15).

Fig. 15: Cladogram of *Striga*. Characters 1-30 as in Table 20. See text for discussion of character polarity, reversal and homoplasy.


S. aequinoctialis
S. bilabiata:
12
28
21
subsp. bilabiata
subsp. jaegeri
17
11
subsp. linearifolia
1 28 30
subsp. rowlandii
23
subsp. ledermannii
subsp. barteri
11 17
S. hermonthica
22
4
11
S. curviflora
16
S. densiflora
23
S. yemenica
S. passargei
20
S. aspera
S. brachycalyx
S. asiatica
4
13 19
S. forbesii
4 14 20
11
S. hallaei
23
S. latericea
10
S. elegans
17
S. dalzielii
13 16
14 22
S. klingii
18
11
S. macrantha
20
S. angollii
1
2 3
S. angustifolia
13
S. pubiflora
S. junodii
29
S. masuria
11
13 14
S. pinnatifida
16
23
S. fulgens
18 23
S. hirsuta
10
1
S. lutea
29
S. primuloides
4 6
S. gesnerioides
3 5 7 20 22
9 28
6 15 17
S. lepidagathidis
S. gastonii
1
S. chrysantha
S. baumanii

When the leaf size (char. 11), margin (char. 13), and shape (char. 14) were polarized using the Outgroup Methods the plesiomorphic character states were long and broad, serrate margins and 3-nerved, and elliptic or ovate leaves for the three characters respectively (Table 20). In the same order the apomorphic states were long and narrow or reduced leaves, entire margins, and linear or lanceolate leaves. Results suggested that the three features were reversed and the direction of character evolution was as follows: the reduced and lanceolate leaves with entire margins (associated with S. *baumanii* and the species group of S. *gesnerioides*, the ancestral species at the bottom of the tree) were transformed into long, narrow and linear leaves with entire margins in the remaining taxa. An exception was the species on the cladogram between S. *angollii* and S. *dalzielii*, and S. *latericea* and S. *forbesii* in which leaves were long and broad, elliptic or obovate, 3-nerved, and serrated margins. This was reversed in S. *linearifolia* with its reduced, lanceolate and entire margins. The following diagram explains character polarity for leaf size, margins and nerving, and shape as evident from the results.



In general, all taxa in the Pentapleurae section (defined by char. 20) except *S. hallaei*, *S. angollii*, and the species group of *S. gesnerioides*, shared a common recent ancestor and were clustered at the top of the cladogram between *S. brachycalyx* and *S. aequinoctialis*. *Striga angollii* and *S. hallaei* were unique among the Pentapleurae in having large, elliptic, 3-nerved leaves, with serrate margins. Other features that underwent homoplasy but followed the same path of character polarity as shown in Table 20 were the presence or absence of petioles (char. 16), inflorescence density (char. 17), equality of teeth (char. 22), corolla color (char. 23), and corolla tip shape (Char. 28).

In all the stages of the analysis using the Lundberg Rooting Procedure *S. baumanii* was fixed as a hypothetical ancestor (where the real outgroup would join the tree) strongly suggesting that *Striga* many have evolved from a similar taxon. Among the characters that changed from the plesiomorphic to apomorphic state between *S. baumanii* (the hypothetical outgroup node) and the ingroup node were the development of hairs (char. 9), the long, narrow (char. 24), and bent corolla tube (char. 25), strongly zygomorphic corolla (char. 26), and fused corolla lobes (char. 27).

It seems likely that *Striga gesnerioides*, *S. lepidagathidis*, and *S. gastonii* diverged immediately after the divergence of the early *Striga* species such as *S. baumanii* and *S. chrysantha* and followed a separate evolutionary line (Fig. 15). Results suggest that they share an immediate common ancestor (*S. chrysantha*) that was not shared by the other taxa (Fig. 15). They were defined by their ability to parasitize dicotyledons (char. 3), succulence (char. 5), and the purple or white stem (char. 7). *Striga lepidagathidis* and *S. gastonii* were defined by the lack of hairs (char. 9), including the glabrous corolla tube (char. 29) and *Striga gesnerioides* was separated from them by its ability to attack crops (char. 4) and its large haustoria (char. 6).

Striga lutea and *S. hirsuta* shared a single clade and diverged before, and separated from *S. elegans* and *S. asiatica* by at least ten taxa. *Striga lutea* and *S. hirsuta* were partly characterized by their reduced leaves (char. 11), sparsely pubescent corollas (char. 29), small bracts (char. 18) and inability to parasitize cultivated crops (char. 4).

The group of taxa between *S. angollii* and *S. asiatica* on the cladogram in Fig. 15 shared a recent common ancestor and subsequently diverged into the different species delimited by the features shown at each node. In general these features included leaf size (char. 11), margins and leaf nerving (char. 13), leaf shape (char. 14), pedicels (char. 16), spike density (char. 17), number of ribs (char. 20), and corolla color (char. 23).

The subspecies of *S. bilabiata* and *S. aequinoctialis* constituted the terminal taxa of all *Striga* species and descended from a recent common ancestor. They were characterized by the perennial habit (char. 1), acute corolla lobes (char. 28), strongly bilabiated corolla (char. 30), and cauline leaves (char. 12). The subspecies *barteri* seems to retain the most ancestral character and the remaining five subspecies of *S. bilabiata* and *S. aequinoctialis* were more likely evolved from a taxon similar to subspecies *barteri*. The subspecies *bilabiata* (the only taxon in this group found outside West and Central Africa) represented the most derived subspecies. Results suggest that the subspecies *linearifolia* (=*S. linearifolia*) was an intermediate taxon between *rowlandii* and *jaegeri* supporting its status as a subspecies of *S. bilabiata* and confirming the statistical analysis of results obtained in Chapter 3. Results also suggest a close relationship between the subspecies of *S. bilabiata* and *S. aequinoctialis*. The relationship between these taxa and their position on the cladogram remained constant throughout the entire stages of the program runs.

DISCUSSION

Among the features used to separate *Striga* from other closely related genera in the Scrophulariaceae is the long narrow corolla tube with a distinctive bend just below the limb and the bilabiate corolla (Musselman 1984, Musselman and Ayensu 1984). *Striga baumanii* has many features that are believed to be ancestral which made it a suitable hypothetical rooting for members of the genus *Striga*. Such features include the obscurely bent corolla tube that scarcely exceeds the calyx, and its five, similar and almost free corolla lobes. The large seeds of *S. baumanii* strongly suggest that it may germinate independent of a host (plesiomorphic). An unusual feature that is found only in this species is the indurate woody corolla; all other species have thin membranous corolla. Several authors (Atsatt 1977, Govier *et al.* 1968) have emphasized the importance of glandular hairs as excretory organs in hemiparasitic plants. These organs reduce the high levels of potentially toxic substances emanating from the host (Govier *et al.* 1968), or play a dual role in some parasitic plants, providing a toxin resistance mechanism and an herbivore repellent devise (Levin 1973). However, *S. baumanii* completely lacks glandular hairs except for few stiff non-glandular types along the leaf margins.

Perennial *Striga* species apparently have perennial hosts and annual species are associated mostly with annual hosts. Visser (1981) has asked whether an annual parasite induced to grow on a perennial host would assume the perennial habit and if a perennial parasite on an annual host might be able to complete its life cycle fast enough before the host dies off. According to my observations, *S. hermonthica*, parasitizing cultivated crops survives for weeks after the crop is harvested at the end of the growing season. Then if the crop is allowed to remain in place, or if it were perennial, or there was no seasonality of rains, there may be a good chance that the annual parasite could assume the perennial habit or at least the opportunity to co-exist with the host and in the long run, through natural selection, could evolve this habit if it is advantageous for its survival. Applying this equation to natural conditions in the grassland savannas of Africa where *Striga* co-exists with its hosts which are mostly perennial, we would therefore expect the perennial habit. However, with the natural global changes in climatic conditions towards less rains, and the destruction and disturbances of natural grassland savanna of Africa by man and his livestock, *Striga* species became ruderal and probably tend to favor the naturally disturbed habitats (r-selection) over the more stable habitats (k-selection). The development of annual forms from perennials is of great survival strategy to the parasite and its host and in *Striga* is evident in the short life cycle, with less energy allocated to vegetative growth, high production of tiny seeds which germinate only under conditions that guarantee the successful establishment of the parasite (e.g. stimulants).

Although many species of *Striga* are said to be perennials or occasional perennial (suggested by the result as plesiomorphic) the existence of true perennial forms in most of them is questionable except in S. *baumanii* (Raynal-Roques 1987, Musselman 1987), S. *latericea* Parker (1986, 1988), and the host-specific strain of S. *gesnerioides* that parasitize *Euphorbia* Musselman (1984). These exceptions are confined to tall perennial grasses where seasonality is less obvious or, in the case of S. *gesnerioides*, to the shrub *Euphorbia* in drier areas.

Results suggest that in the early stages of the diversification of *Striga* species two separate evolutionary lines emerged and diverged in different directions. The first evolutionary clade gave rise to S. *chrysantha*, S. *gastonii*, S. *lepidagathidis*, and terminated in S. *gesnerioides*, the most derived taxon in this group. *Striga gesnerioides* species complex (regardless of their evolutionary position among other species) are characterized by many features not common to other members of *Striga*. These include the cespitose growth habit, succulence, reduction of vegetative growth and tendency towards holoparasitism (Thalouarn *et al.* 1991), the lack of dense hairs or complete glabrosity, and dicotyledon as common hosts.

The second evolutionary line gave rise to the remaining *Striga* species. They are characterized by the stiffly erect growth habit, developed leaves, and hosts which are usually wild grasses or cultivated cereals. It is known that parasitic plants have a low photosynthetic efficiency compared to non-parasitic members within the same family. Shah *et al.* (1984) demonstrated that *S. hermonthica* has a low photosynthetic ability and has a high dependence on the host for assimilated carbon and nitrogen compounds. Thalouarn *et al.* (1991) provided similar evidence for *S. gesnerioides* but not *S. hermonthica*. To obtain adequate supply of sugars, the parasite causes an inhibition of the growth of the host shoot with an associated diversion of sugar to the root system. Moreover, according to Press *et al.* (1987) *Striga* species have high transpiration rates and the transpiration rate of the host is decreased as a result of *Striga* infestation even when soil moisture is not seriously limiting (Parker 1984). Therefore, *Striga* species with broad leaves are probably better equipped with larger transpiration surfaces which means they could withdraw more sugars and water from the host to compensate for their low photosynthetic ability. Conversely, plants with reduced leaves could be at a disadvantage or have slow growth rates. Those *Striga* species with extremely reduced leaves (*S. bilabiata* subsp. *linearifolia*, *S. aequinoctialis*, *S. primuloides*, *S. lutea*, *S. baumanii*, and *S. chrysantha*) and with poor chlorophyll content (Thalouarn *et al.* 1991) including *S. gesnerioides*, *S. lepidagathidis*, and *S. gastonii*, also tend towards holoparasitism (Visser 1981). Results showed that all these except the first two taxa have retained the most ancestral characters and were located on clades at the bottom of the cladogram i.e. not the most derived (Fig. 15). On the other hand, large, broad, nerved leaves were shown to associate with derived taxa.

Striga's invasion of the agroecosystem (char. 4) evolved three times: once in in *S. gesnerioides* and twice in the cereal-*Striga*. According to my results, *S. gesnerioides* and its species group (parasites of broad leaved-hosts) branched off in the early stages of the divergence of *Striga* from a taxon which parasitized cereals like *S. chrysantha* suggesting that parasitism of broad leaved hosts came second to that of cereals. It is conceivable that morphology and the behavior of the parasite can be influenced by the host and in the *S. gesnerioides* species group, the succulence, haustoria size, plant color, and the other features developed in this evolutionary line could be attributed to parasitizing broad leaved hosts. The two main differences between the dicot and monocot hosts which could have influenced the parasite were the number and size of roots and the shade cast on the parasite.

Within *Striga* there seems to be host specificity or preference to cultivated or wild host that is the most abundant in its habitat. Lewin (1932) was the first to observe the possible existence of "strains" in *Striga* and to explain its differential damage and distribution on wild and cultivated hosts. Parker and Reid (1979) by cross-inoculating the *Striga* collected from sorghum hosts in Nigeria and millet hosts in Niger confirmed the existence of host-specific strains to sorghum and millet in *S. hermonthica*. The evidence of host preference among the host-specific strains was provided by Hosmani and Parker (1980), who studied cross-induction of germination of *S. hermonthica* from sorghum and pearl millet, and *S. asiatica* from Tanzania and India, on maize, sorghum, and pearl millet varieties. They demonstrated that almost all maize varieties stimulated higher germination of *S. hermonthica* and *S. asiatica* seeds, and sorghum varieties germinated sorghum-*S. hermonthica* and not the millet-*S. hermonthica*. In Ethiopia where sorghum is the main food crop and ranks second in area coverage among the major cereals grown in the country (Mulatu and Kebebe 1991) *S. aspera* attacks millet but not sorghum, and *S. latericea* attacks sugar cane (Parker 1988). In Burkina Faso *S. aspera* is a pest to sugar cane and maize (Safa, personal communication). In West Africa maize is more susceptible to S. *hermonthica* than millet and sorghum (Kim 1991, Ramaiah 1987).

From this discussion it is obvious that *Striga* prefers certain hosts over others, and in most cases the sorghum-*Striga* can grow on other hosts while the pearl millet, maize, and sugar cane -*Strigas* will not grow on sorghum. This may explain the homoplasy mentioned earlier where crop parasitism (char. 4) evolved twice- once each in the species group of S. *hermonthica*, S. *curviflora* and S. *densiflora*, and the species group of S. *latericea*, S. *forbesii* and S. *asiatica*. The mechanism of host specificity is not fully understood. However, Wild (1948) suggested that it is related to germination stimulant, and Musselman and Parker (1981) attributed it to incompatibility factors. Perhaps a genetic factor may be involved.

The Pentapleurae *Striga* species evolved from within the Polypleurae and were clustered at the top of the tree (Fig. 15). An exception is the S. *gesnerioides* species group which diverged from the cereal-*Striga* in the Polypleurae but remained at the bottom of the tree as noted earlier. The second exception is S. *angollii* and S. *hallaei* the only species within the Pentapleurae, (like most Polypleurae) with large, elliptic, 3-nerved leaves, with serrate margins. The latter exception may be considered as intermediate between the Polypleurae and the Tetrosepalum or may resemble the early developed plants in the Pentapleurae. Discussion on the section Tetrosepalum is limited here because there is no clear distinction in the number of calyx ribs between members of the Polypleurae and the Tetrosepalum and there is a continuum in the number above ten ribs.

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While doing his dissertation research, he coauthored Musselman *et al.* " Recent research on the biology of *Striga asiatica*, *S. gesnerioides* and *S. aspera* " a paper presented for the International Workshops Organized by IITA, ICRISAT and IDRC, 22 - 24 August 1988, IITA, Ibadan, Nigeria and published in S. K. Kim (ed.) Combating *Striga* in Africa. In 1993 he presented Mohamed and Musselman " the genus *Striga* in Africa " for the 5th ASB Annual Meeting, Virginia Beach, Va, hosted by Old Dominion University and published in the ASB Bulletin 40 (2) as Abstract number 54.