

**SPECIES DIVERSITY AND ADVANCEMENT  
OF SWERTIA (GENTIANACEAE):  
ECOLOGICAL AND MORPHOLOGICAL CORRELATES**

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*Swertia* L. with about 150 species worldwide is one of the most divers genera of the Gentianaceae. Based on previous work for morphological phylogeny of the family, *Swertia* can be considered as a primitive genus of the temperate subtribe Gentianinae Gilg. To explain diversity in *Swertia*, species number per 100,000 sq. km were calculated and mapped for important parts of the generic range, evolutionary advancement indices (AI) for 118 species were determined (based on morphological traits) and a correlation analysis, with ecological and phenotypical variables, was undertaken. Diversity centres are East Himalaja plus Chinese provinces of Yunnan and Sichuan (with diversity maximum of 16.3 in Nepal) and the East African Rift Valley Region (with highest diversity in Malawi, 6.8). Advancement indices of species range from 0.12 to 0.78 within 0 and 1, theoretically possible. The nine most primitive species (AI<0.25) are distributed in Asia and Africa, above an altitude of at least 2,500 m while in North America most species are highly advanced (AI>0.65). Correlation analysis with ecological factors such as latitude, altitude, habitat type suggests that the genus originated in the moist montane or alpine zones.

Key words: altitudinal range, diversity centres, endemism, floral nectaries, migration routes

## INTRODUCTION

Understanding differences in plant species diversity requires discovering of underlying ecological and evolutionary factors. Among alternative research objects and approaches, studying of large genera is a relatively recent development (Sanderson and Wojciechowski 1996). By doing this a synthetic ecological research direction seems to arise relating global species distributions to phylogenetic informations and spatial environmental parameters (Beaman 1998, Cornejo 1998, Guala 1998).

For the present research the genus *Swertia* L. from the family Gentianaceae was selected because of previous phylogenetic studies done in this family (Mészáros 1994, Mészáros, de Laet and Smets 1996, Mészáros *et al.* 2002) and because *Swertia* is one of the most divers genera of the family. The most divers

one is *Gentiana* L. with c. 360 species classified into many (15) sections, for which the possibility of giving them generic status is at least discussed.

Taxonomically *Swertia* belongs to the tribe Gentianeae of the five monophyletic tribes of the family (Struwe 1999), its most closely related species-rich genera being *Gentianella* Moench and *Halenia* Borkhausen. The generic circumscription of *Swertia* was earlier narrower, distinguishing e.g. *Anagallidium* Grisebach, *Frasera* Walter, *Ophelia* D. Don as distinct genera, but we agree with Pringle (1990) and the monographer Shah (1990, 1992) that even the North American *Frasera* should be included in *Swertia*. The number of species was also decreased during taxonomic revisions, especially in Africa (Hedberg 1957, Sileshi 1998). So the extant species number takes today about 150 (148 in Shah 1990 and c. 150 in Ho and Pringle 1995). In addition, there are some uncertain, less known species, in his monograph Shah lists ten, while Sileshi (1998) seven such swertias.

Previous ecological studies of *Swertia* focused partly on single species, especially North American ones, investigating geographical ecology (Threadgill *et al.* 1979), life cycle (Threadgill *et al.* 1981) or pollination (Beattie *et al.* 1973). Pioneers of a more complex approach studied morphological variation of certain traits (Hedberg 1957) or correlation between chromosome numbers and morphological characters (Khoshoo and Tandon 1963, Pringle 1990). The recent taxonomic revisions available (Sunita 1987, Shah 1990, 1992, Ho and Pringle 1995, Sileshi 1998) established preconditions for an ecological approach with a global coverage.

In this paper firstly we detect geographical differences in species diversity and endemism. Second, we calculate morphological advancement indices for *Swertia* species (in the absence of a generic phylogeny). Thirdly, we study variations and correlations of phenotypic and environmental traits. Contrasting our results with evidence from literature we also try to draw some conclusions for the evolution and migration within the genus.

## METHODS

From the literature morphological and ecological data were collected supplemented with some measurements of herbarium exemplars from Budapest and Mainz. Sources of data, beside taxonomic revisions mentioned in Introduction, were the followings: Clarke (1885), Fries (1923), Card (1931), St. John (1941), Grossgeim (1952), Hedberg (1957), Pissjaukova (1961, 1963), Khoshoo and Tandon (1963), Toyokuni (1963), Smith (1965, 1970), Geesink (1973), Maiti and Banerji (1976a, b), Ubolcholaket (1983), Pringle (1993), Sileshi (1997).

Species numbers were assessed within the generic area for important countries, states (USA) or provinces (China) and calculated to an 100,000 square kilometre unit. Relative species richness, taking logarithms of area of political units into account, was also calculated according to Evans *et al.* (1955) (not shown here).

Number of endemic species for the same geographical units were counted and the usual percentage rate of regional species endemism were settled. Cowling and Hilton-Taylor (1997), in their detailed analysis for the Southern African flora highlighted the importance of considering higher and lower rates of endemism along with its average degrees. Therefore we assessed also the normal rate of endemism for the geographical units in question, depending on their size, based on Bykov's nomogram (Major 1988). Comparison of actual and normal rates of endemism resulted in indices of endemism.

Advancement indices (AI-s) of species were calculated according to the "groundplan divergence method" (Wagner 1980). The indices are based on distinguishing different character states, coding them according to assumed phylogenetic trends and summing up codes of each character with equal weights. The range of indices are then transformed to vary from zero (an absolutely primitive species) to 1 (a fully advanced species).

The following eight morphological characters were taken into consideration in calculating advancement indices.

Life form: perennial (0), monocarpic (1), annual (2)

Stem leaves phyllotaxy: opposite (0), whorled (1), alternate (2)

Stem leaf base: pedicellate (0), sessile (1), amplexicaule (2)

Floral mery: pentamerous (0), tetramerous (1)

Horizontal position of nectary(ies) on the corolla lobe: two nectaries far from each other (0), two nectaries close to each other (1), two nectaries but partly united (2), one single (evolutionarily united), nectary (3)

Vertical position of nectary(ies) on the corolla lobe: at the base of the lobe (0), between the base and the middle of the lobe (1) at the middle of the lobe (2)

Shape of nectaries: orbicular (0), oblong (1), elongated (2)

Coverage of nectaries: naked (0), covered by scales of fringes (1).

We also tried to include other characters into calculation of advancement indices (stem, inflorescens, seed, chromosome number) but failed, mainly because not being able to detect their phylogenetic trends.

Phylogenetic trends (polarities) of character states were generally taken over from previous studies of the evolution of the family (mentioned earlier). A special attention deserve the applied characters of horizontal and vertical positions of nectaries on the corolla lobes. Identification keys for species in the majority of cases contain a distinction of two or single nectary on the corolla

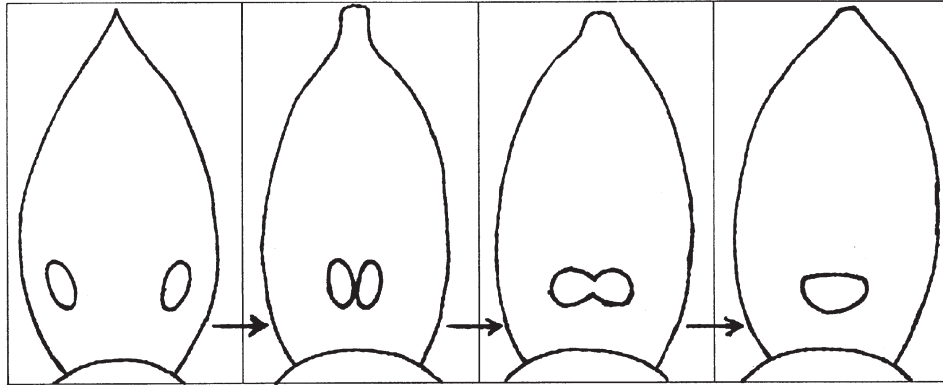


Fig. 1. Assumed phylogenetic trends in the position of nectaries. A = *Swertia lurida* (D. Don) Clarke; B = *S. thomsonii* Clarke; C = *S. longifolia* Boiss.; D = *S. adolfi-friderici* Mildbr. et Gilg

lobe, only sometimes referring to their vertical position. At detecting, phylogenetic trends of nectaries we considered their position in closely related genera of *Swertia* having epipetalous nectaries (*Comastoma*, *Gentianella*, *Gentianopsis*, *Halenia Jaeschkea*, *Lomatogonium*) all with two nectaries at the base of corolla lobes with the exception of *Halenia* where a single spur developed from each lobe. At the same time we accepted some of phylogenetic trends elaborated by Maiti and Banerji (1976a) based on Himalayan species of *Swertia*. The here assumed phylogenetic trends in the position of nectaries are illustrated in Figures 1 and 2.

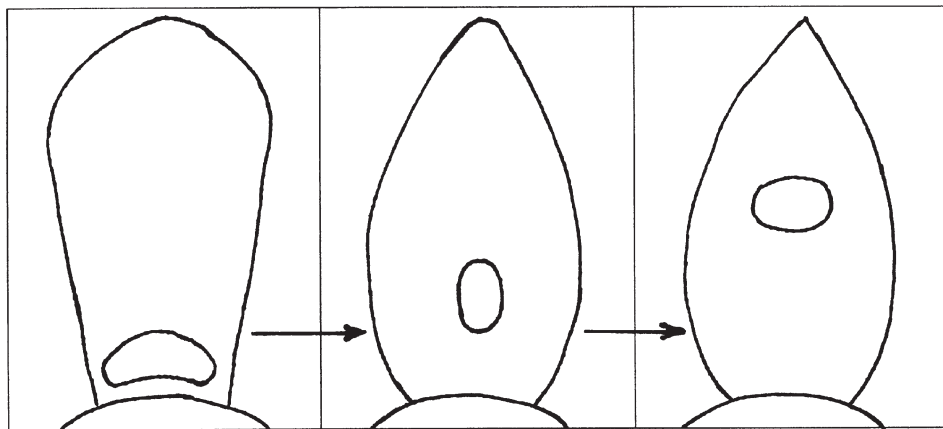


Fig. 2. Assumed phylogenetic trends in the position of nectaries. A = *Swertia hookeri* Clarke; B = *S. cordata* (G. Don) Clarke; C = *S. shintenesis* Hayata

Trait correlations with further quantitative phenotypic characters (plant height, length of corolla lobe, capsule and seed) and with ecological variables such as altitude, latitude, habitat and endemism were also calculated, for more than 100 species. Trait means and coefficients of variation (c.v.) were computed using the untransformed data, while for correlation and regression analysis trait values were natural-log transformed prior to statistical analysis to eliminate heteroscedasticity.

## RESULTS

### *Species (lineage) diversity and endemism*

The generic area of *Swertia* covers four continents, namely Asia, Africa, North America and Europe, its species are missing only from South America, Australia and New Zealand. The ca 150 species are characteristic for "lineage diversity" (Sanderson 1998) of the genus as a whole but evenness in species distribution is largely unequal, so continental species richness differs markedly: maximal in Asia (with half of species in China alone), less in Africa (25 species) and North America (ten percent) while in Europe there is a single species.

Regional diversity expressed as species number per 100,000 square kilometre were mapped (Fig. 3), distinguishing five diversity classes. The highest diversity was found in Nepal (Himalaya) with 16.3 species per 100,000 square kilometre while the second highest one in the province of Yunnan (China) with an 8.4 figure (taking higher but distorted, extrapolated values of political units less than 100,000 square kilometre not into consideration).

Two diversity centres of *Swertia* can be distinguished based on the map, one in Asia and another in Africa. The first one consists of East Himalaya (Nepal, Bhutan, Sikkim) and Chinese provinces of Yunnan and Sichuan, practically overlapping the fourth maximum phytodiversity centre of Earth (Eastern Himalaya – Yunnan Centre (Barthlott *et al.* 1996)). Within Africa highest species diversities can be found in Malawi (6.8) and Uganda (5.4) being parts of the East African Rift Valley Region, while Ethiopia where two third of African species are present has a diversity figure of only 1.3 giving an example for the conflict between continental evenness and regional density of species as components of the applied diversity measure. Within North America highest diversities (1.8 – 3.2.) were found in four pacific states i.e. Washington, Oregon, Idaho and California constituting parts of the Rocky Mountains and ranging from north border of the United States to Mexico.

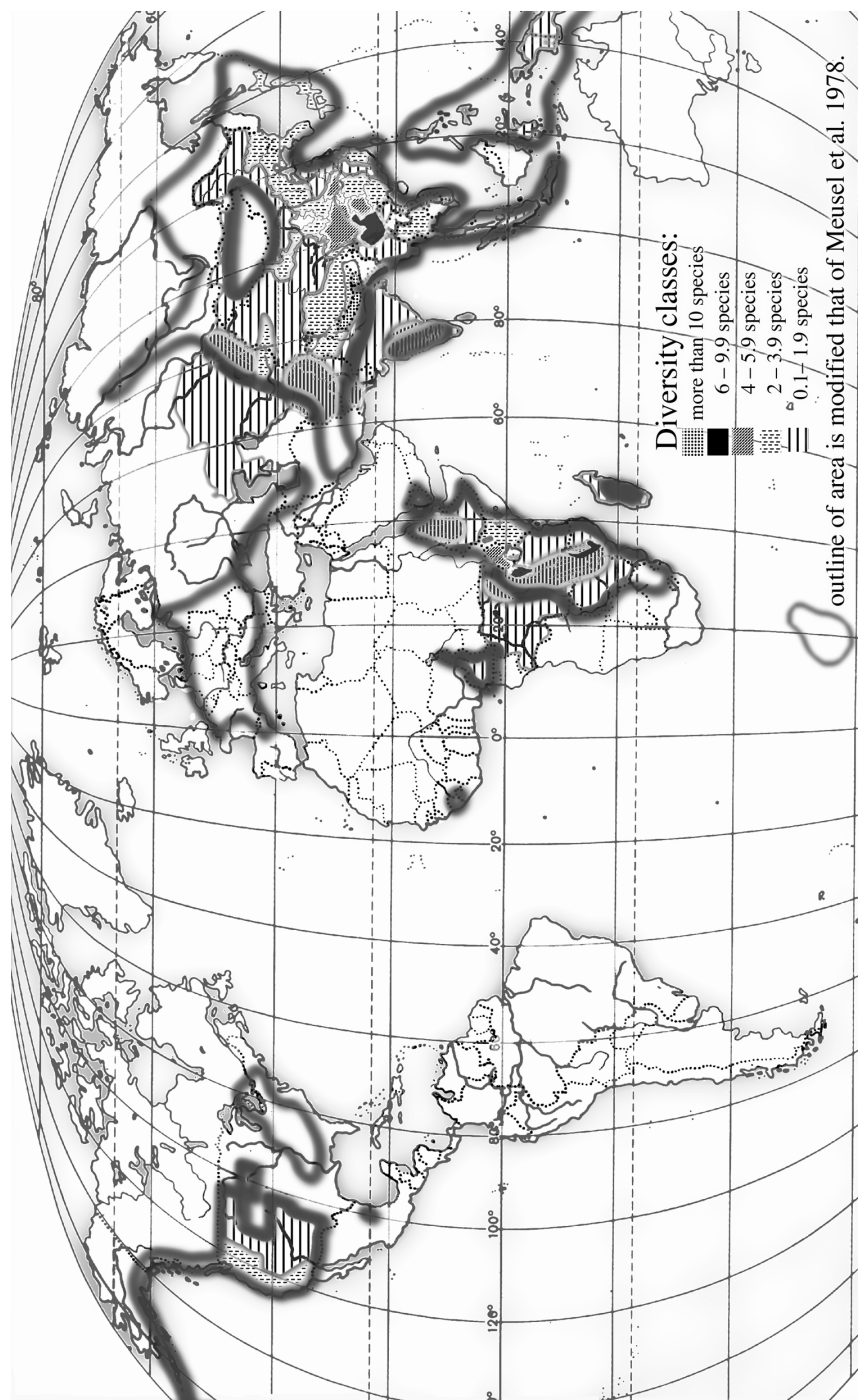


Fig. 3. Area of *Sverbia* with species diversity classes: number of species per 100,000 km<sup>2</sup>

Highest factual rates of endemism were found on smaller islands with low species numbers, e.g. Taiwan has four swertias, three of them being endemic (75 percent). But highest figures for mainland were settled for Asia, namely Yunnan had a 34.8, while East Himalaya a 30.0 percentage endemism taking 3.2 and 3.0 times of the normal rate of endemism (index of endemicity). In this case the centre of endemism overlapped with the Asian diversity centre. However, this overlapping was not valid for every province. On other continents figures of endemism were rather lower. So in Africa three states: Tanzania, Ethiopia and Kenya, each having more than ten swertias, had 14.3, 12.5 and 7.1 percent of endemism, respectively, in all three cases below the normal rate. In North America the factual rate of endemism, interestingly, exceeded the normal rate in all states where swertias occurred. In California, with the largest number of species (9), the figure of endemism was maximal (44.4 percent) achieving four times of the normal rate.

#### *Morphological advancement of species*

Within the theoretically possible limits (from zero to 1) the realised range of advancement indices for *Swertia* species is wide, extending from 0.12 to 0.78,

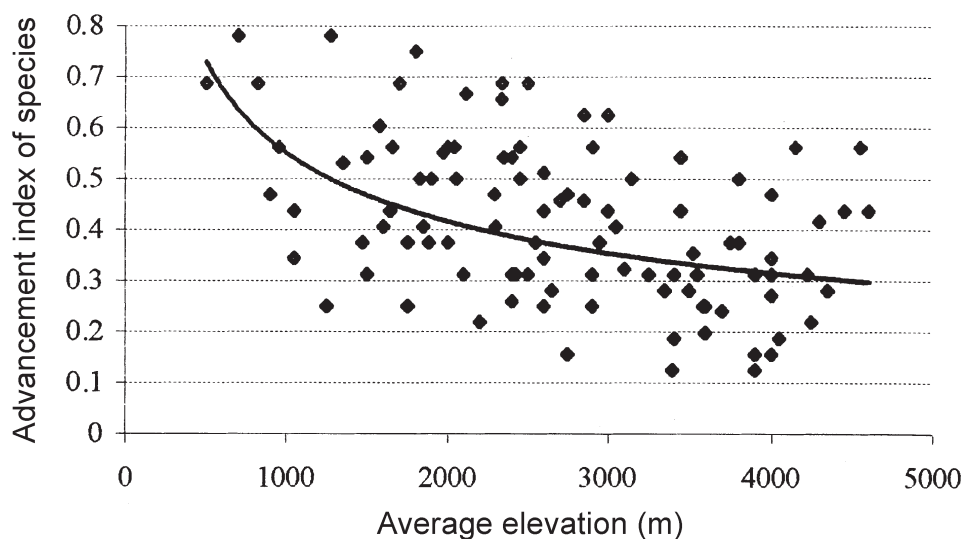


Fig. 4. Correlation between elevation and morphological advancement of *Swertia* species (with a regression line based on power function)





Table 1 (continued)

Adv. ind.	Asia according to Shah (1990, 1992)			Other Asian territories (ex Soviet Union, Japan, Iran, Thailand)
	Africa (incl. Madagascar) according to Sileschi (1998)	North America according to Shah (1990, 1992)	China	
0.35–0.44	<i>S. adolfi-friderici</i> Mildbr. et Gilg <i>S. wetsitschii</i> Engl. <i>S. rosulata</i> (Baker) Klack.	<i>S. perennis</i> L. (also in Europe and Asia)	<i>S. virescens</i> H. Smith <i>S. verticillifolia</i> T. N. Ho et S. W. Liu <i>S. obtusa</i> Ledebour <i>S. forrestii</i> H. Smith <i>S. cordata</i> (G. Don) C. B. Clarke <i>S. macrosperma</i> (C. B. Clarke) C. B. Clarke <i>S. diluta</i> (Turez.) Benth. <i>S. hispidicalyx</i> Burkill <i>S. delavayi</i> Franch. <i>S. patens</i> Burkill <i>S. franchetiana</i> H. Smith <i>S. pubescens</i> Franch. <i>S. pseudochinensis</i> Hara	<i>S. striata</i> Collett et Hemsl. <i>S. papuana</i> Diels <i>S. burmanica</i> H. Smith <i>S. javanica</i> Bl. Bijdr. <i>S. swertopsis</i> Makino
0.45–0.54	<i>S. squamigera</i> Sileschi <i>S. manni</i> Hook. <i>S. kilimandscharrica</i> Engl. <i>S. fimbriata</i> (Hochst.) Cuf. <i>S. tetrandra</i> Hochst		<i>S. yunnanensis</i> Burkill <i>S. decora</i> Franch. <i>S. emietensis</i> Ma <i>S. shinttenensis</i> Hayata <i>S. racemosa</i> (Wallich ex Grisebach) G. B. Clarke <i>S. patula</i> H. Smith <i>S. leducii</i> Franch.	<i>S. longifolia</i> Boiss <i>S. calicicola</i> Kerr <i>S. pinetorum</i> Kerr <i>S. tashiroi</i> (Maxim.) Makino <i>S. gonczaroviana</i> Pissjauk.

Table 1 (continued)

Adv. ind.	Africa (incl. Madagascar) according to Sileschi (1998)	North America according to Shah (1990, 1992)	Asia		
			China	India and Himalayas	Other Asian territo- ries (ex Soviet Un- ion, Japan, Iran, Thailand)
0.55–0.78	<i>S. intermixta</i> A. Rich. <i>S. schliebenii</i> Mildbr.	<i>S. radiata</i> (Kellogg) Kuntze <i>S. neglecta</i> (Hall) Jepson <i>S. carolinensis</i> (Walt.) Kuntze <i>S. albomarginata</i> (Wats.) Kuntze <i>S. parryi</i> (Torr.) Kuntze <i>S. montana</i> (Muhl.) St. John <i>S. albicaulis</i> (Griseb.) Kuntze <i>S. fastigiata</i> Pursh <i>S. tubulosa</i> (Coville) Jepson <i>S. puberulenta</i> (Davidson) Jepson	<i>S. tetraptera</i> Maxim. <i>S. musotii</i> Franch. <i>S. nervosa</i> (G. Don) C. B. Clarke <i>S. scapiformis</i> T. N. Hoand et S. W. Liu <i>S. arisanensis</i> Hayata <i>S. tetrapetala</i> Pallas <i>S. angustifolia</i> Ham. ex. D. Don	<i>S. corimbosa</i> (Griseb) C. B. Clarke <i>S. luriida</i> (G. Don) C. B. Clarke <i>S. chirayta</i> (Roxb. ex Fleming) Karsten	

with an average of 0.40 and a coefficient of variation (c.v.) of 37 percent. Table 1 lists species of *Swertia* according to magnitude of their advancement.

The most primitive group of species (AI < 0.25), all perennial ones, live in Africa (4 species) and Asia (7 species), not extending to North America. The areas of the Asian species are included into the mentioned diversity centre, only *S. marginata* Schrenk occurs also in Mongolia and Russia.

It is further interesting from a distribution point of view that in Africa the two most advanced species have only indices of 0.56 while in North America the most primitive species (*S. neglecta* (Hall) Jepson), has almost the same advancement index (0.55) if we leave the Holarctic *S. perennis* L. with an index of 0.37 out of consideration.

The most advanced three species (AI > 0.75) live in North America (*S. albomarginata* (Wats.) Kuntze, and *S. tubulosa* (Corille) Jepson) and Japan, Korea, East Russia (*S. tetrapetala* Pallas), these are monocarpic or annual species with tetramerous flowers and one nectary per corolla lobe.

#### Morphological and ecological variation

According to Ricklefs & Renner (1994) "Ecological versatility of higher taxa may be indicated by the morphological and physiological diversity of their subordinate species". We tried to characterize and compare morphologi-

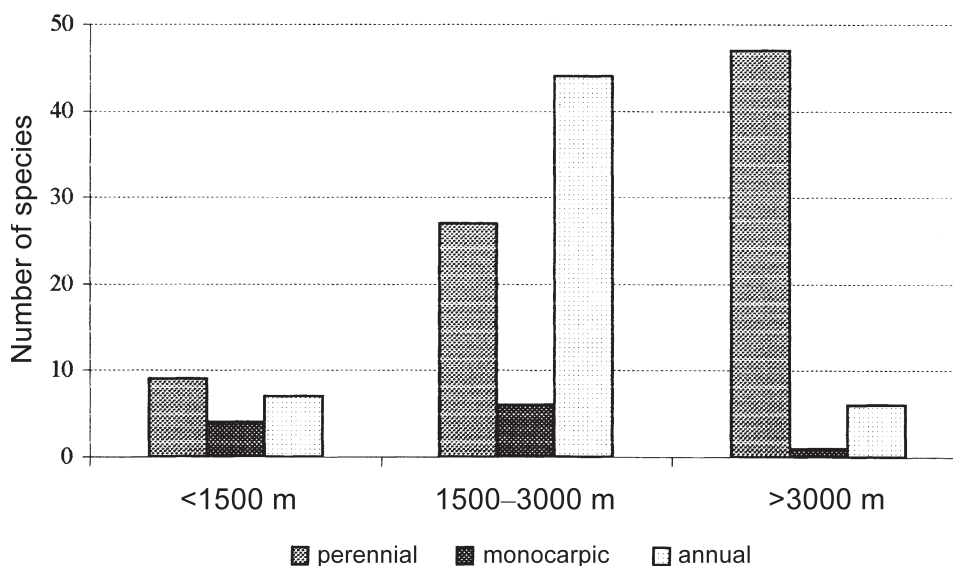


Fig. 5. Life form spectra of *Swertia* species in different altitudinal zones

cal and ecological diversity of the genus *Swertia* by simple statistic measures of interspecific variation such as ranges, averages and coefficients of variation (c.v.).

The interspecific variation of reproductive traits such as length of corolla lobes and that of capsule were quite normal with coefficients of variation of 47.5 and 41.3 percent, respectively. But remarkable high variabilities were found in cases of plant height (c.v. = 89.3 percent) and seed length (c.v. = 108.3). (The length of leaves was not investigated because of its great variation within individual plants.) In the case of plant height (stem length) at least one reason for high variability is the existence of different growth forms. While *S. acaulis* H. Smith is a cushion plant growing in the Himalaya with stems of only 1 to 2 centimetres, the maximum plant height takes 1.5 to 2 metres at the Himalayan perennial of *S. rex* Clarke and at two North American monocarpic species (*S. caroliniensis* (Walt.) Kuntze and *S. radiata* (Kellogg) Kuntze). But the maximum stem length of 3 to 4 metres has *S. scandens* T. C. E. Fr., a montane forest endemic species of Kenya, alone with this growth form in the genus. In the case of seed size (length) the generic average took 1.50 millimetres with the smallest seeds of *S. tetraptera* Maximowicz (<0.1 millimetres), resident of China, while the largest seeds belong to the North American *S. caroliniensis* attaining 9 to 10 mm in length.

For expression of ecological diversity quantitative characters such as altitude and latitude could be used. Average elevation of *Swertia* species took 2,695 metres with a wide generic range extending from 500 metres (*S. caroliniensis* (Walt.) Kuntze) to 4,850 metres (*S. younghusbandii* Burkill (China and Sikkim)). Nevertheless, the c.v. of average altitude had a low figure of 37.0 percent. But each species has also an altitudinal range, so this range was used as a second variable for elevation. The generic average of this interval slightly exceeded 1,000 metres but varied from zero to 3,800 metres, the widest amplitude found at *S. wolfgangiana* Grüning (China) ranging from 1,500 to 5,300 metres. Interestingly, c.v. of this specific altitudinal range was high showing a 81.4 percentage variability.

Another applied quantitative ecological character was the horizontal distribution of species measured as geographic distances from the Equator and expressed in latitudinal degrees. The area of the genus *Swertia* extends from 30° S to further than 60° N and the generic arithmetic means of distances from Equator takes 26.8° (independently of northern or southern direction in distribution). The c.v. of this distance variable is also low, 46.0 percent similarly to altitudinal average. A range variable for horizontal distribution was also applied, the generic average of which was 11.0 latitudinal degrees. This variable indicated again high variability with c.v. of 102.2 percent.

For qualitative (coded) ecological characters the above statistical measures are not interpretable, nevertheless their distribution were interesting in ecological characterization of the genus. According to moisture regime 35.5 percent of taxa lived on wet habitats, 37.6 percent on mesic, 12.0 percent on dry ones while 14.9 percent of them occupied two habitat categories, so a strong preference for wet and mesic habitats was detectable for the genus and relatively few species adapted to dry environment.

#### *Environmental and phenotypic correlations*

Among environmental factors elevation proved to be the most important. The correlation between specific average altitude and AI-s was  $-0.44$ ; this result indicates that more primitive species live generally higher while more advanced ones are adapted to lower elevations (Fig. 4). There was also a similar negative correlation ( $-0.38$ ) between specific average elevation and life form meaning that perennial species occur generally higher while monocarpic or annual ones live lower, probably adapted to less mesic environments (Fig. 5). Finally, there was a positive correlation ( $+0.32$ ) between specific elevation and the degree of endemism, agreeing with the general increasing tendency of endemism of mountain plants with altitude (up to the subalpine zone, see Major 1988). The positive correlation of latitude with AI-s was less pronounced ( $+0.28$ ) indicating that more advanced species live further from Equator (mainly in the northern hemisphere).

Among phenotypic correlations allometric relationships deserve special attention. For expressing body size, plant height (stem length) seemed to be a proper variable. But the correlations were weak with plant height (capsule length  $+0.25$ , seed length  $+0.26$ , corolla lobe length  $+0.05$ ), probably because of high phenotypic plasticity of stem length. This conclusion may even be more correct in the light of strong correlation ( $+0.67$ ) found between corolla lobe length and that of the capsule, both variables having low interspecific c.v.-s (47.5 and 41.3 percent, respectively).

The corolla lobe length showed a relatively good correlation with life form ( $-0.40$ ) indicating shorter lobes of monocarpic and annual species. In the case of seed size (length) the AI of species was correlated ( $+0.33$ ) meaning that more advanced species had generally larger seeds.

## DISCUSSION

The lineage diversity of *Swertia* with its c. 150 species is incommensurable with such large genera as *Astragalus*, *Carex*, *Senecio*, *Euphorbia* and *Psychotria*

each having more than 1,000 species (Sanderson and Wojciechowski 1996). Its species richness also falls behind that of known north-temperate, alpine, herbaceous genera such as *Pedicularis* (350), *Primula* (400) or *Saxifraga* (440, species numbers are from Mabberley 1997). But the comparison is more realistic within its own family Gentianaceae. Here the most closely related species-rich genera have somewhat similar species number (*Gentianella* 125, *Halenia* 100, Ho and Pringle 1995) and *Gentiana* sect. *Chondrophyllae* has almost the same number of species (156, Ho and Pringle 1995). The similarity with *Gentiana* sect. *Chondrophyllae* extends also to their subcosmopolitan area, large share of non-perennial species and the preponderance of haploid chromosome numbers of  $n = 13$  and  $10$ . So explanations for rapid evolution (small population sizes, star phylogeny i.e. simultaneous speciation of many species given for *Gentiana* sect. *Chondrophyllae* (Yuan and Küpfer 1997)) may partly be valid also for *Swertia*, although there is an altitudinal difference, *Swertia* being rather a montane genus while *Gentiana* sect. *Chondrophyllae* prefers alpine conditions.

The discovered two (Asian and African) species diversity centres raises the questions of their relation to each other and if one of them can be considered as centre of origin of the genus. The occurrence of the 11 most primitive *Swertia* species in or around these two diversity centres suggests that within the generic area the centre of origin should be either in the Eastern Himalaya – Yunnan Centre or in the East African Rift Valley centre. There was a slight difference in the AI-s of the 11 most primitive species (0.12–0.22 in Africa and 0.16–0.24 in Asia) but this was not decisive. Neither were chromosome numbers because both  $n = 13$  and  $n = 10$  species live in Asia and Africa. But there are more circumstantial arguments supporting one or the other centre. The Asian centre are favoured by the followings:

1. All other genera of the tribe Gentianeae Struwe (subtribe Gentianinae Gilg) have their centre of origin in Himalaya and SW China (Meusel *et al.* 1978).

2. The two highest species diversity figures was found here (Nepal 16.3, Yunnan 8.4)

3. High degree of regional endemism was found, e.g. 34.8 percent of *Swertia* species occurring in Yunnan are restricted to this province of China (area with more than 30% endemism are considered as centres of endemism by Linder 1983).

4. The minimum altitude of the 11 most primitive species takes 2,500 m, exactly coinciding with the lowest elevation given by Van Steenis (1964) for temperate genera on tropical mountains.

5. Herbaceous genera associated with African swertias are mostly Holarctic, at least in the alpine zone (Hedberg 1964).

There are two argument for the African centre:

1. *Swertia* is the only genus of tribe Gentianeae Struwe occurring in Africa (not considering one species of *Gentiana* sect. *Chondrophyllae* in the Atlas Mts).

2. There are some most primitive species also in Africa, contrasting with the absence of them from other migration routes (to North America, from Thailand to New Guinea).

So the evidence favour an Asian centre of origin but a disjunction of an earlier continuous area extending to both continents (vicariance biogeography explanation), cannot be excluded.

Concerning vertical extention of the genus *Swertia* it was an interesting result that while AI-s correlated with average elevation of species ( $r = 0.44$ ), they did not with their altitudinal ranges ( $r = 0.04$ ). Namely wide range of montane species was explained with zones of temporary and permanent establishment by Van Steenis (1961) and with adaptation to long-term climatic fluctuation by Wood (1971). Two explanations for the absence of correlation with altitudinal range can be given. Either the whole genus had performed such an adaptation without significant interspecific differences detectable among extant swertias. Or ecological diversification not parallel with that of phenotypic one, a case emphasized by several authors (e.g. West-Eberhard 1989).

Nevertheless, altitudinal range of species did correlated with their maximal ( $r = +0.45$ ) and minimal elevation ( $r = -0.34$ ). At a first glance these relationships may seem to be trivial but they are not. They can be interpreted that species penetrating to highest and/or lowest habitats have widest ranges and this phenomenon gives support to Wood's idea. Therefore, species having at least 2,000 metres altitudinal range were also considered separately. Of the 22 such swertias only one lives in North America and three occur in Africa while all other species belong to Asia. They are not endemic taxa but rather have wider distribution so their ample ecological amplitude are expressed not only in their vertical but also in their horizontal ranges.

Negative correlation of AI-s with specific average elevation and the minimal altitude of 2,500 metres of the 11 most primitive species speak in favour of a montane or alpine origin of the genus. Downward migration (and adaptation) of species was probably connected with cooling climate. But anemochor seeds allowed also horizontal extension of generic area, probably starting from the Asian centre of origin.

Four such migration routes are possible: 1. SE direction: Thailand, Myanmar, Indonesia, New Guinea (Van Steenis 1964, also for other genera). 2. SW direction to Africa and Madagascar (Goldblatt 1978). 3. NW direction: through Beringia to North America. 4. NE direction to W Asia, Europe (only *S. peren-*

*nis*). These migrations generally associated with speciation events except the case of the fourth route. This implication are supported by high endemism of some states such as Thailand, Indonesia and California (but interestingly, it is not the case for Africa).

Exact dating of these migration events is not possible. Establishment of migration routes gives only indication of earliest possible wanderings, so according to Billings (1974) rise of high mountains in Malaysia, New Guinea happened in late Pliocene while migration of the northern Eurasian flora into Africa was possible (once again) probably from the Miocene on because of closing of the Tethys Sea (Goldblatt 1978). But these long-range dispersals were probably generated by drastic climatic changes during the Pleistocene. This is supported by *Swertia*-fossils from Pleistocene of Western, Central and Eastern Europe (Mai 1985) while for East African volcanoes there are rather Holocene arrival dates for *Podocarpus* and *Hagenia*, trees often associated with some *swertias* (Sauer 1988).

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