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PHENETICS OF THE TAXA AND SYSTEMATIC POSITION OF THE AFRICAN *SWERTIA* (GENTIANACEAE)

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ABSTRACT: Twenty eight OTUs (Operational Taxonomic Units) were studied and a phenogram is established based on a Coefficient of Association (COA) to reveal the infrageneric divisions of *Swertia*, an African Genus of Gentianaceae. Two clusters (subgroups of the genus) were recognized at 0.65 level of COA above the base of the phenogram supporting the idea developed on the basis of a traditional intuitive synthetic taxonomic method. Two subgenera and two sections are proposed for the infrageneric taxonomy of *Swertia*. A relatively closer association of the OTUs *S. abyssinica* - ABY (1) and *S. brownii* - BRO (3) is attributed to their distinctively protruding parietal placentae. Close phylogenetic affinities between *Swertia* and *Lomatogonium* is suggested. The phylogenetic affinities of *Swertia* to *Gentianella* and *Gentiana* are discussed.

Key words/phrases: Coefficient of Association, Gentianaceae, OTUs, phylogenetics, *Swertia*

INTRODUCTION

In Africa the genus *Swertia* comprises twenty eight taxa. These are distributed between 14° N and 30° S latitude in sub-Saharan countries from west Africa to Madagascar. The species inhabit White's (1983) afromontane and afroalpine archipelago-like regional centre of endemism. Three geographical distribution patterns for the African taxa of the genus were identified and critically considered along with phenetic character states of the group as a whole (Sileshi Nemomissa, 1994). These geographical distribution patterns are: a) species which are widely distributed without any sign of infraspecific speciation due to continuous variations in the taxonomically useful character states (e.g., *S.*

fimbriatata, S. kilmandscharica and *S. quartiniana*); b) species which are common to Ethiopia and Tropical East Africa (TEA) and exhibit infraspecific segregation (e.g., *S. crassiuscula* s.l.); and c) endemic species.

The phenetic variation in the genus is further complicated by (climatic) variations along an altitudinal gradient. Fries (1923) recognized two infrageneric groups in the African *Swertia*. He did not, however, realize that his binectariate group is unnatural and the assemblage of unrelated groups. *S. macrosepala, S. uniflora, S. volkensii* and *S. subnivalis* were put under binectariate sensu Fries (1923) despite the fact that these species have a single naked nectary per corolla lobe. The next attempt to segregate the African *Swertia* was undertaken by Hedberg (1957) who mainly dealt with the Afroalpine species. He recognized three major groups in his study area and refrained from theoretical extensions of his results to the species at relatively lower altitudes.

This study: a) deals mainly with the results of a simple statistical analysis of phenetic data with regard to an infrageneric division of the African *Swertia;* b) pursues a different synthetic approach to arrive at a sound systematic decision; and c) discusses the systematic position of *Swertia* in the family Gentianaceae.

MATERIAL AND METHOD

The herbarium material of *Swertia* was acquired on loan from the following institutions: B, BR, C, E, EA, ETH, FT, K, P, S, UPS, W, WU (abbreviations of the institutions follow Holmgren *et al.*, 1990). Twenty eight taxa and thirty three character states were studied (Table 2) to elucidate the affinities and variations of the species of *Swertia*. The species were given acronyms and arabic numbers (Table 1). For the construction of the phenogram (Fig. 1), the Coefficients of Association (COA) of unweighed character states (Stuessy, 1990) was computed to assess resemblance or similarities among the taxa of *Swertia*.

The taxonomy of the taxa of *Swertia* follows Sileshi Nemomissa (1994). The terminologies adopted to describe gross morphological character states are according to Stearn (1983) and that of pollen grains follow Erdtman (1969).

Data on the systematic position of *Swertia* in the family Gentianceae was compiled both from the present study and literature. A comparative approach was followed to assess the phylogenetic similarities and variations of the genera comprising the subtribe Gentianinae in relation to *Swertia*, the alliance to which the genus belongs. The generic constitution of the subtribe Gentianinae follows Gilg (1895).

Table 1. **List of 28 OTUs studied to construct a phenogram of 33 taxonomic character states with the three letter acronym and arabic numbers given for each species of *Swertia*.**

ABY	*S. abyssinica*	MAP, 14	*S. macrosepala* subsp. *microsperma*
ADO, 2	*S. adolfi-friederici*	PSE, 16	*S. scandens*
BRO, 3	*S. brownii*	PLG, 15	*S. pleurgynoides*
CRC, 4	*S. crassiuscula* subsp. *crassiuscula* var. *crassiuscula*	PUM, 17	*S. pumila*
CRL, 5	*S. crassiuscula* subsp. *crassiuscula* var. *leucantha*	QUA, 18	*S. quartiniana*
CRR, 6	*S. crassiuscula* subsp. *robusta*	SCO, 20	*S. scottii*
ENE, 7	*S. engleri* var. *engleri*	SUB, 22	*S. subnivalis*
ENW, 8	*S. engleri var. woodii*	TET, 23	*S. tetrandra*
FIM, 9	*S. fimbriata*	UNI, 24	*S. uniflora*
INT, 10	*S. intermixta*	USA, 25	*S. usambarensis*
KIL, 11	*S. kilimandscharica*	VOB, 27	*S. volkensii* var. *baleensis*
LUG, 12	*S. lugardae*	VOV, 26	*S. volkensii* var. *volkensii*
MAM, 13	*S. macrosepala* subsp. *macrosepala*	WEL, 28	*S. welwitschii*
SCL, 19	*S. Schliebenii*	SQM, 21	*S. squamigera*

Table 2. **Taxonomic character states used for the construction of a taxonomic character states phenogram of the African *Swertia* species.** A total of 14 characters with their states labelled from a - d.

Character states	
1	Basal rosette leaves: **a.** present; **b.** absent.
2.	Terminal inflorescences on the main axes: **a.** 1-flowered; **b.** 3-flowered; **c.** > 3-flowered.
3.	Corolla lobes: **a.** more than twice as long as the calyx lobes; **b.** less than twice as long as the calyx lobes.
4.	Nectaries: **a.** two per corolla lobe; **b.** one per corolla lobe.
5.	Margin of the nectaries: **a.** wholly fimbriated; **b.** partly fimbriated; **c.** naked.
6.	Anther: **a.** apiculate; **b.** not apiculate.
7.	Scale-like projections at the attachment point of the filament to the corolla lobe: **a.** present; **b.** absent.
8.	Style: **a.** distinct; **b.** subobsolete to absent.
9.	Seed number per capsule: **a.** < 13; **b.** between 25–40; **c.** numerous (> 40).
10.	Seed size (diameter or length): **a.** > 1 mm; **b.** < 1 mm.
11.	Seed surface: **a.** reticulate; **b.** no distinct reticulation; **c.** with interrupted ridge-like outgrowths; **d.** with continuous ridge-like outgrowths.
12.	Exine: **a.** spinulose; **b.** striato-reticulate.
13.	Parietal placentae: **a.** conspicuous; **b.** indistinct.
14.	Habit: **a.** Cushion-forming plant; **b.** not cushion-forming plant.

RESULTS

Two clusters are revealed at 0.65 level of COA (or 65% phenon line in the terminology of Sneath and Sokal, 1962) above the base of the phenogram (Fig. 1). The first cluster is formed by the OTUs ABY - ENW (1–8). Except for the specific character states for each OTU all of them share: a) two nectaries per corolla lobes; b) exotesta which could be considered as smooth, i.e., without distinct exotestal cells outgrowth; and c) spinulose exine sculpture. This first cluster of the genus is rather heterogenous. It is possible to recognize four subgroupings in the group OTUs ABY - ENW (1–8) above 89% phenon line. These are OTUs ABY - TET (1–23), PLG - USA (15–25), CRC - LUG (4–12) and

ENE - ENW (7–8). At this level the cluster ABY - TET (1–23) forms a phenon with cluster PLG - USA (15–25). The OTU SCO (20) does not cluster with any of the subgroups at this phenon line and it links the two aforementioned clusters with the third cluster CRC - LUG (4–12). This third cluster forms a phenon with cluster ENE - ENW (7–8). The OTUs ENE (7) and ENW (8) are taxonomic varieties of *S. engleri*. The cluster ENE - ENW (7–8) associates with the remaining clusters at 40% phenon line above the base of the phenogram because of its unique states such as partly fimbriated nectary margin. It is, however, unnatural to erect any formal taxonomic subcategories within the cluster ABY - ENW (1–8) because the difference involves quantitative characters which could be used for statistical analysis (which may not be employed by field taxonomists). It is, thus, categorized under a single infrageneric status, namely, Subgenus I.

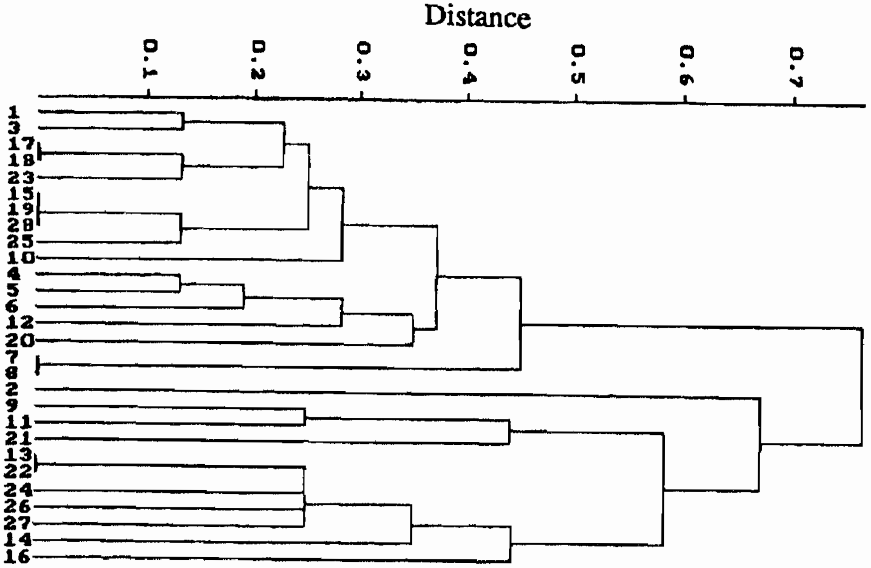

Fig. 1. Phenogram of relationships among OTUs of *Swertia* based on simple matching coefficient and unweighed arithmetic averages. Further explanations in the text.

The second rather broad cluster formed by OTUs ADO - PSE (2–16) is believed to constitute the second subgenus of the African *Swertia* (see Discussion). The recognition of two subcategories within subgenus II is also supported by numerical analysis (Fig. 1). These two subcategories are to be erected at the level of a taxonomic section; the sections form phenons of their own at 55% phenon line above the base of the phenogram. The traditional intuitive approach is thus supported by numerical data. An exception to this generalization is the OTU ADO (2) which does not associate with any of the clusters at this phenon line. ADO (2) is more closely related to the OTUs FIM - SQM (9–21) than SUB - PSE (22–16). Thus, it is rather natural to put OTUs ADO - SQM (2–21) under section A.

It is clearly noted (Fig. 1) that the OTUs SUB - VOB (22–27) exhibit closer affinities to each other than to either MAP (14) or PSE (16). The separation of MAP (14) from OTUs SUB - VOB (22–27) at 35% phenon line above the base of the phenogram is attributed to the unique states of MAP (14), i.e., relatively smaller seed size and ± reticulate seed surface. PSE is not related to OTUs SUB - MAP (22–14) at 45% due to the unique states of its seeds. Nonetheless, OTUs MAM - PSE (13–16) constitutes section B of subgenus II (Fig. 2).

DISCUSSION

Phenetics and infrageneric groups in Swertia

Phenetic (quantitative) analysis of selected character states resulted in the recognition of two subgenera in the genus. They are named as subgenus I and subgenus II, leaving aside the coining of formal taxonomic epithets of the subgenera for further communications. The distinctive features of the subgenera are tabulated below (Table 3).

It should be noted, however, that the two sections are interlinked by some character states (see below). Nevertheless, the recognition and segregation of these sections pose no difficulty at all in the field. Such a segregation is not possible in subgenus I although some species exhibit closer associations to each other than to another species group (Fig. 2).

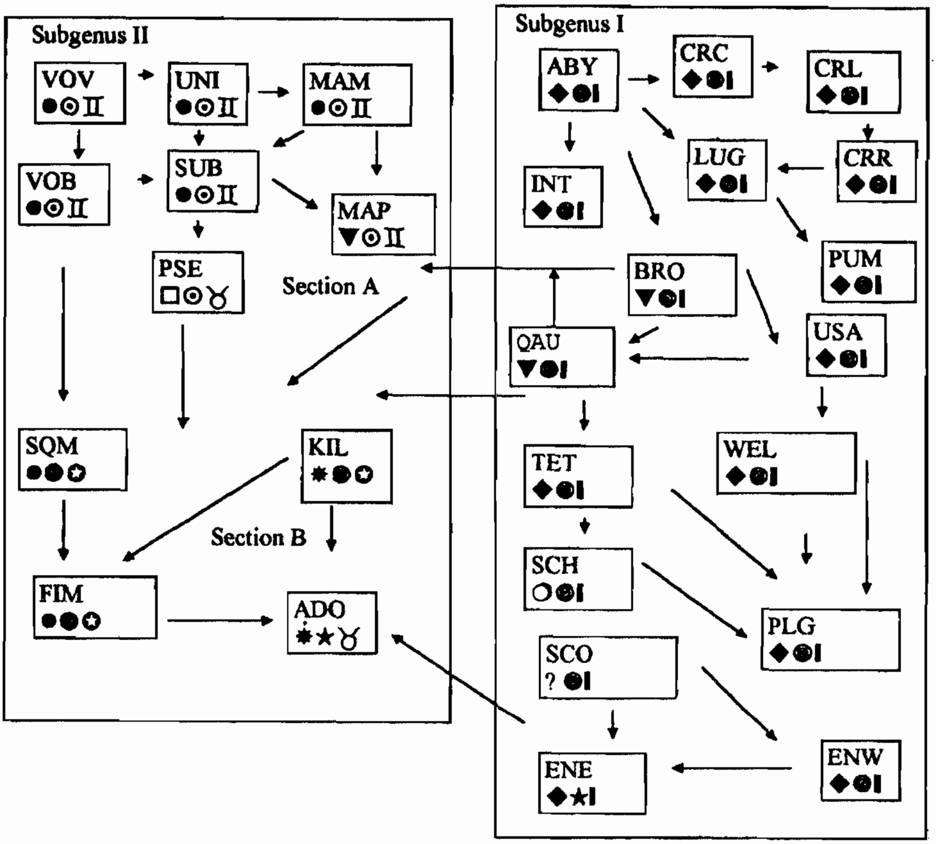

Fig. 2. Presumed relationships with in the African *Swertia* and distribution of some selected character states. Further explanations in the text. Seed surface (exotesta): ◆, faintly reticulate; ▼, conspicuously reticulate; O, wavy line; ✱, continuous undulating outgrowth; ●, broken striation; □, continuous but not wavy. Nectary margin: ⊙, naked; ◉, fully fimbriated; ★, only lower margin fimbriated. Exine: ▮, spinulosey; II, coarsely striato-reticulate; ✪, finely striato-reticulate; ♉, transitional exine type.

The two phenetic associations within subgenus II (Fig. 1) suggest two natural subgroups which could be treated at sectional level. The characterization of the two sections and their respective species composition is given in Table 4.

Table 3. Comparison of the two subgenera of *Swertia* using three morphological character states.

Character states	Subgenus I	Subgenus II
Number of nectary/corolla lobe	two	one
Seed surface	Exotestal cells without distinct outgrowth	Exotestal cells with remarkable outgrowths
Exine sculpture	spinulose	striato-reticulate

Table 4. Character states of the sections of the genus *Swertia* subgenus II.

Character states	Section A	Section B
Margin of nectary	fimbriated	naked
Exine fine detail	fine	coarse
Species	*S. adolfi-friederici* *S. fimbriata* *S. kilimandscharica* *S. squamigera*	*S. scandens* *S. macrosepala* *S. subnivalis* *S. uniflora* *S. volkensii*

Noteworthy is the recording of linkage character states which may suggest the operation of mosaic evolutionary processes in the genus as a unit while each subunit pursues a separate course of evolution.

Distribution of some selected character states within Swertia

The two subgenera are markedly separated from each other as presented in Fig. 2. There are, however, linking species which connect the two subgenera. Subgenus I is linked to subgenus II by a reticulate seed surface, a feature which is unexceptionally recorded in the populations of *S. macrosepala* subsp. *microsperma*. Furthermore, the seed size in this species is comparable to that of the other species of subgenus I. This species is, thus, considered to be a linking species. The presence of half-fimbriated nectary margin in *S. engleri* var. *engleri* is another character state which links subgenus I to subgenus II (Fig. 2). The margin of the nectary of *S. adolfi-friederici* could also be cited as an additional example with regard to this character state. Fully fimbriated nectary margin is also an argument in the same direction. *S. fimbriata*, *S. kilimadscharica* and *S. squamigera* have fully fimbriated nectary margins, a universal characteristic of subgenus I. Although the two subgenera are probably following different courses of evolution, it is also easy to visualize mosaic character states which show linkage between them.

The within subgenera segregation is more remarkable in subgenus II than I (Fig. 2). There is a very close association among the species with fully fimbriated nectary margin on one hand and those with naked nectary margin on the other. The two sections of the subgenus II are, however, connected through *S. scandens* and *S. adolfi-friederici*; the linkage character states are found to be exine sculpturing and its fine details.

Systematic position of Swertia *in the family Gentianaceae*

1. *Swertia* and *Lomatogonium*

Both genera are characterized by calyx and corolla lobes which are free for most of their length and two fimbriated nectaries per corolla lobe. One remarkable difference between them is that the stigmatic groove runs down the length of the ovary at either side of the suture between carpels in *Lomatogonium*, i.e., commissural stigma (Gilg, 1895; Lindsey, 1940; Toyokuni and Yamazaki, 1993).

In *Lomatogonium* like in *Swertia*, each carpel is supplied by 1 dorsal and 2 ventral bundles. Furthermore, spinulose and striate exine sculptures characterize the two genera (Nilsson, 1964; 1967) although the micromorphological details may vary. Regardless of these palynological similarities, *Swertia* is perhaps more advanced than *Lomatogonium* in view of its more specialized carpel structure because: a) the carpels are incompletely fused; and b) the stigma is not restricted to the distal end of the gynoecium in *Lomatogonium*.

Löve and Löve (1986) recorded the somatic chromosome number $2n=16$ and $2n=32$ in *Lomatogonium rotatum* (L.) Fries and *L. carinthiacum*, respectively. This suggests a chromosome base number of $x=8$ for the genus. In contrast, the base numbers of *Swertia* species are $x=n=10$ and $x=n=13$. Theoretically, $x=n=10$ could be derived from $x=8$ as the result of ascending dysploidy effected by "fission" of chromosome segments. Although no morphological data on the chromosomes of the genera are on record, increasing and decreasing dysploidies have played a great role in shaping the evolution of higher vascular plants (Ehrendorfer, 1976). Nevertheless, both genera appear to be very closely related to each other.

2. *Swertia* and *Veratrilla*

Free rotate corolla lobes and winged seeds may relate *Veratrilla* to *Swertia*. The former genus is, however, dioecious (Smith, 1970). From a phytochemical viewpoint, *Veratrilla* is perhaps more advanced than *Swertia*. Although tetraoxygenated xanthones are recorded in both genera, the difference lies in the degree of the oxygenation of ring B of their xanthones. Mészáros (1994) believed that oxygenation of all four positions of ring B and two of ring A is a primitive condition in the family Gentianaceae and reduction in the extensive oxygenation of ring B of xanthone compounds is assumed to be a derived character state. *V. baillonii* has one oxygenated position (position 7) on ring B (Buckingham *et al.*, 1994) unlike e.g. *Swertia bimaculata* where positions 5 and 8 are oxygenated (Ghosal *et al.*, 1975a; Fig. 22). Generally, multiple oxygenation of ring B (except position 6) is common in *Swertia* species. *S. chirata* (Ghosal *et al.*, 1973) and *S. purpurascens* (Ghosal *et al.*, 1975b) have both tetra- and penta-oxygenated xanthones. In the light of the above statements, therefore, the relationship between the two genera may not be as close as hitherto thought.

3. *Swertia* and *Halenia*

Allen (1933) reported that the most primitive group of *Halenia* (sect. *Swertiella* Allen) lacks a well developed spur at the back of the corolla lobes as a nectar storage tissue. Instead, each corolla lobe is beset with a single naked nectary pit (nectary) e.g., in *H. brevicornis* unlike in *H. deflexa* and *H. elliptica*. The author further suggested that the putative ancestor of *Halenia* could be found in *Swertia*.

The basic chromosome number of *Halenia* is $x=11$ (Löve, 1953). It is not the aim of this study to establish the origin of $x=11$ in this genus. It could, however, be suggested that the formation of a spur (at the back of the corolla lobes) is more advanced than the nectaries of *Swertia* in respect to pollination and/or pollinators (perhaps by advanced insect groups in *Halenia*). The possession of an unspecialized nectary pit on the adaxial surface of the corolla lobes, i.e., the lack of well developed spur in some members of *Halenia* may suggest that this character is a primitive character state.

Phytochemically, *Halenia* is more advanced than *Swertia* (Mészáros, 1994; Table 1) in that it has lost the ability to oxygenate position 8 of ring B in its xanthone compounds. The earlier report of 1,3,6,8-tetraoxygenated xanthones for *Halenia elliptica,* was found to be incorrect (Bennet and Lee, 1991; see also references therein). The possession of only one substituted position on ring B of its xanthones is also an argument in the same direction. Mészáros (1994) argued that the loss of oxygenation of position 6 of ring B had played a great role in the differentiation of the subtribe Gentianinae as a whole.

4. *Swertia* and *Gentianella*

Both genera have epipetalous nectary pits. *Gentianella,* however, has a relatively longer corolla tube, the throat of which is ciliated. Moreover, each carpel is supplied by one dorsal and one (fused) ventral bundles (Lindsey, 1940) unlike in *Swertia* where the ventral bundles are not fused (Sileshi Nemomissa, 1994).

The absence of spinulose exine sculpture in *Gentianella* (Nilsson, 1967) may also suggest the relatively distant phylogenetic association of the two genera. Findings on the xanthone compounds of *Gentianella* showed the oxygenation of all (5,7, and 8) but position 6 of ring B (Mészáros, 1994; Table 1; cf. with that of *Swertia*). It is to be noted that multiple occurrences of xanthones in a single member of the family is common, i.e., not a single xanthone compound is oxygenated at all 5, 7 and 8 positions of ring B. Massias *et al.* (1982) suggested that during the evolutionary process substitution at position 5 might have replaced position 7 in *Gentianella.* These authors believed that xanthones substituted at position 7 on ring B occur in less advanced members of the genus and are merely relics. Therefore, the tendency towards the specialization of ring B of xanthones in *Gentianella* substantiates its evolutionary advancement over *Swertia* and their relatively distant phylogenetic relationships.

5. *Swertia* and *Gentiana*

As with *Gentianella,* the affinities of *Gentiana* to *Swertia* do not seem to be particularly close, either. In *Gentiana*: 1) the nectary is at the base of the ovary; 2) its pollination biology is perhaps more advanced (Webb and Pearson, 1993) than *Swertia* to ensure outcrossing; and 3) each carpel is supplied by 1 dorsal and 7 ventral bundles in some members of the genus (Lindsey, 1940). These character states of *Gentiana* are perhaps more advanced than those of *Swertia* species.

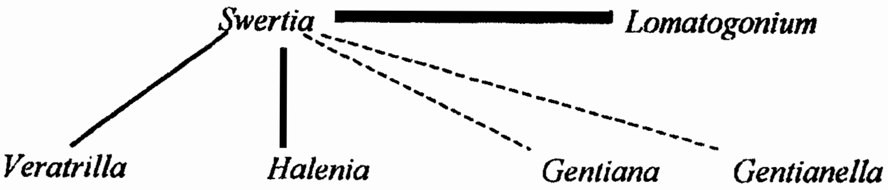

Fig. 3. Possible phylogenetic relationships of *Swertia* with other genera of the subtribe Gentianinae. The thickness of the lines indicate the degree of phylogentic associations in the generic pair and broken lines signify relatively distant relationships.

The genus *Gentiana* lacks oxygenated positions 5 and 6 in its xanthone compounds (Mészáros, 1994); some of its members have also lost the ability of oxygenation at position 8. On the other hand, Ghosal *et al.* (1975b) reported that *Gentiana* and *Swertia* display tetra- and pentaoxygenation systems of their xanthones except that extensive oxygenation of ring B of its xanthones is significantly reduced in *Gentiana*. The biochemical data again point towards a relatively distant phylogenetic relationship of *Gentiana* and *Swertia*. Within the subtribe Gentianinae, therefore, *Swertia* appears: a) to be closely related only to *Lomatogonim* and perhaps more advanced than that genus; and b) to be less advanced than *Halenia*, *Gentianella* and *Gentiana*.

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REFERENCES

1. Allen, C.K. (1933). A monograph of the American species of the genus *Halenia*. *Ann. Missouri Bot. Gard.* **20**:119–222.
2. Bennet, G.J. and Lee, H.H. (1991). *Halenia elliptica* xanthone: a structural revision. *Phytochemistry* **30**:1347–1348.
3. Buckingham, J., Macdonald, F.M. and Bradley, H.M., (eds) (1994). *Dictionary of Natural Products, R-Z,* Vol. 5, 1st ed., Chapman & Hall, London, pp. 5557–5558 and 5560.
4. Ehrendorfer, F. (1976). Evolutionary significance of chromosomal differentiation pattern in gymnosperms and primitive angiosperms. In: *Origin and Early Evolution of Angiosperms*, pp. 220–240, (Beck, C.B., ed.). Columbia Univ. Press. New York.
5. Erdtman, G. (1969). *Handbook of Palynology: Morphology - Taxonomy - Ecology.* Munksgaard, Copenhagen.
6. Fries, Th.C.E. (1923). Die *Swertia*-Arten der Afrikanischen Hochgebrige. *Notizbl. bot. Gart. Berl.* **8**:389–423.
7. Ghosal, S., Sharma, P.V., Chaudhuri, R.K. and Bhattacharya, S.K. (1973). Chemical constituents of Gentianaceae V: Tetraoxygenated xanthones of *Swertia chirata* Buch. Ham. *J. Pharm. Sci.* **62**:926–930.
8. Ghosal, S., Sharma, P.V. and Chaudhuri, R.K. (1975a). Xanthones of *Swertia bimaculata*. *Phytochemistry* **14**:2671–2675.
9. Ghosal, S., Sharma, P.V., Chaudhuri, R.K. and Bhattacharya, S.K. (1975b). Chemical constituents of Gentianaceae XIV: Tetraoxygenated and penta-oxygenated xanthones of *Swertia purpurascens* Wall. *J. Pharm. Sci.* **64**:80–83.
10. Gilg, E. (1895). Gentianaceae. In: *Die natürlichen Pflanzenfamilien* IV, Vol. 2, pp. 50–108, (Engler, A. and Prantl, K., ed.). Wilhelm Engelmann, Leipzig.
11. Hedberg, O. (1957). Afroalpine vascular plants: a taxonomic revision. *Symb. Bot. Upsal.* **15**:1–411, Pl. 1–12.
12. Holmgren, P.K., Holmgren, N.H. and Barnett, L.C. (1990). Index Herbariorum I. The herbaria of the world, ed. 8. *Regnum Vegetabile* **120**:1–693.
13. Lindsey, A.A. (1940). Floral anatomy in Gentianaceae. *Amer. J. Bot.* **27**:640–652.
14. Löve, A. and Löve, D. (1986). IOBP Chromosome number report 93. *Taxon* **35**:897–899.

15. Löve, D. (1953). Cytotaxonomic remarks on the Gentianaceae. *Hereditas* **39**:225–235.

16. Massias, M., Carbonnier, J. and Molho, D. (1982). Chemotaxonomy of *Gentianopsis*: xanthones, C-glycosylflavonoids and carbohydrates. *Biochem. Syst. Ecol.* **10**:319–327.

17. Mészáros, S. (1994). Evolutionary significance of xanthones in Gentianaceae: a reappraisal. *Biochem. Syst. Ecol.* **22**:85–94.

18. Nilsson, S. (1964). On the pollen morphology of Lomatogonium A. Br. *Grana* **5**:298–329.

19. Nilsson, S. (1967). Pollen morphological studies in the Gentianaceae-Gentianinae. *Grana.* **7**:46–145.

20. Sileshi Nemomissa (1994). *Swertia* L. (Gentianaceae) in North East Africa. Univ. Wien, Diss. Form. Naturwiss. Fak. 215p. PhD thesis.

21. Smith, H. (1970). New or little known Himalayan species of *Swertia* and *Veratrilla* (Gentianaceae). *Bull. Br. Mus. Hist. (Bot.)* **4**:239–258, Pl. 22–37.

22. Sneath, P.H.A. and Sokal, R.R. (1962). Numerical taxonomy. *Nature* **193**:855--860.

23. Stearn, W.T. (1983). *Botanical Latin: History, Grammar, Syntax, Terminology and Vocabulary*. David & Charles Ltd., London.

24. Stuessy, T.F. (1990). *Plant Taxonomy: The Systematic Evaluation of Comparative Data*. Columbia Univ. Press, New York.

25. Toyokuni, H. and Yamzaki, T. (1993). Gentianaceae. In: *Flora of Japan Vol. IIIa: Angiospermae, Dicotyledonae, Sympetalae (*a), pp. 139–157, (Iwatsuki, K., Yamazaki, T, Boufford, D.E. and Ohba, H., ed.). Kodansha Ltd., Japan.

26. Webb, C.J. and Pearson, P.E. (1993). The evolution of approach herkogamy from protandry in New Zealand *Gentiana* (Gentianaceae). *Pl. Syst. Evol.* **186**:187–191.

27. White, F. (1983). *The Vegetation of Africa: A Discriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. UNESCO, Paris. Courvoisier S:A, Switzerland.