The Historical Development of the Classification of the Family Scrophulariaceae.

Wendy Metelerkamp.
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1. INTRODUCTION.

What are the aims of a classification system and how do we go about forming one ? Man has always found the need to group similar organisms together, firstly to attain some feeling of order in the diversity of living organisms and secondly to be able to refer back to the groups formed and identify new specimens. Classification systems have been evolving over a long time and two basic systems have developed : a) a monothetic system of grouping where specified characters are required to be present in every member of a group (single thesis based). This is an 'artificial' grouping because it allows vastly different organisms to be brought together on a single common feature : it is neverthe-less extremely valuable for making identifications. b) a polythetic system of grouping where, of the characters used to define a group, no single one need be present in all members, but most should be present in each (multiple thesis based). This is a natural system as organisms showing a range of similarities are classed together, often in the same way in which they have evolved in groups determined by ancestor-affinities. This leads on to the phylogenetic system of classification where polythetically defined groups are arranged in presumed evolutionary sets and sequences. This involves postulating about ancient forms using fossil material where possible, and assessing primitive and advanced characters in living forms. This is geared towards an understanding of evolutionary changes and is often not ideal for identification purposes

In this seminar, I aim to show how the various classification systems have treated genera of the Family Scrophulariaceae, to show their downfalls and to propose how a better, possibly phylogenetic system could be developed.

2a. LINNAEUS'S SEXUAL SYSTEM OF CLASSIFICATION.

Prior to Linnaeus, there were many notable Botanists who gradually broke away from traditional doctrines of the medieval times and developed new systems of classification and terminology. Linnaeus is definitely the most famous of the early botanists being reknowned for the introduction of binomial nomenclature. In his many botanical publications, he crystallized the vast amount of botanical knowledge that had accumulated and developed a classification system that was highly functional and was easy to use. This was called the sexual system of classification in which the plant genera recognized at the time were divided into 24 classes. These classes were based primarily on the number of stamens, but together with their relative lengths, distinctness or fusion, and their occurrence in the same flower as the pistil (see Table 1).

Table 1 : The 24 classes in Linnaeus's Sexual System.

1. *Monandria*—stamen 1.
2. *Diandria*—stamens 2.
3. *Triandria*—stamens 3.
4. *Tetrandria*—stamens 4.
5. *Pentandria*—stamens 5.
6. *Hexandria*—stamens 6.
7. *Heptandria*—stamens 7.
8. *Octandria*—stamens 8.
9. *Enneandria*—stamens 9.
10. *Decandria*—stamens 10.
11. *Dodecandria*—stamens 12.
12. *Icosandria*—stamens more than 12, attached to the calyx.
13. *Polyandria*—stamens more than 12, attached to the receptacle.
14. *Didynamia*—stamens didynamous (2 long, 2 short).
15. *Tetradynamia*—stamens tetradynamous (4 long, 2 short).
16. *Monadelphia*—stamens monadelphous (in 1 bundle).
17. *Diadelphia*—stamens diadelphous (in 2 bundles).
18. *Polyadelphia*—stamens polyadelphous (in several bundles).
19. *Syngenesia*—stamens syngenesious (with united anthers).
20. *Gynandria*—stamens gynandrous (adnate to the pistil).
21. *Monoecia*—plant monoecious (unisexual flowers on the same plant).
22. *Dioecia*—plant dioecious (unisexual flowers on separate plants).
23. *Polygamia*—plants polygamous.
24. *Cryptogamia*—flowers concealed (the cryptogams).

These primary divisions were subdivided according to the number of styles of the gynoecium to give the subgroups monogynia, digynia, trigynia etc. within each of the above groups.

The major downfall of this system, as Linnaeus himself realized, was that it was completely artificial with plants being differentiated on a single character with no consideration of other characters such as flower structure or vegetative parts of the plants. However, it served its purpose very well as it was not difficult to use and greatly facilitated the identification and classification of the vast number of new species that were constantly being discovered at the time.

Where do the members of the Scrophulariaceae Family, as they are known today, fit in? They are probably exclusively bisexual with many of them having zygomorphic flowers. There are four stamens (sometimes two or five),with the anterior pair being longer than the posterior pair (didynamous) which are fused to the corolla. The style is single but often bilobed (Heywood, 1973).

This is all the basic information needed to be able to place a particular plant in a Linnean Class. As most Scrophulariaceae are didynamous, they would be placed in Class 14, Didynamia (see Fig. 1).

XIV DIDYNAMIA

Mariti quatuor, quorum 2 longiores & 2 breviores
Stamina quatuor : quorum 2 proxima, longiora sunt.
(TWO POWERS
Four husbands, two taller than the other two
Four stamens : of which the nearest two are longer)

Fig. 1 : The stamen characters used to describe the Class Didynamia (from Stearn, 1957).

However, there are some Scrophulariaceae that have five stamens eg. Verbascum and some that have only two eg. Veronica. These two genera would be placed in the Class Pentandria and Diandria respectively (Table 2).

Table 2 : Position of some modern genera of the Scrophulariaceae and related families in Linnaeus's Sexual System.

Linnaean Genus	No. of stamens	Class	Modern Family
Calceolaria Feuill (1725)	2	Diandria	Scrophulariaceae
Elytraria Mx (1803)	2	Diandria	Acanthaceae
Veronica Fuchs (1542)	2	Diandria	Scrophulariaceae
Antirrhinum Diosc.	4	Didynamia	Scrophulariaceae
Bignonia Plum (1703)	4	"	Bignóniaceae
Digitalis Fuchs (1 542)	4	"	Scrophulariaceae
Acanthus Theophr.	4	"	Acanthaceae
Gesneria Plum (1703)	4	"	Gesneriaceae
Linaria Brun (1532)	4	"	Scrophulariaceae
Nemesia Venten. (803)	4	"	Scrophulariaceae
OrobancheDiosc.	4	"	Scrophulariaceae
Salpiglossis Ruizeet Pav (1794)	4	"	Solanaceae
Scrophularia Brunf (1532)	4	"	Scrophulariaceae
Selago Dalech. L. (1737)	4	"	Scrophulariaceae
Solanum Plin.	5	Pentandria	Solanaceae
Verbascum Plin.	5	"	Scrophulariaceae

By thebeginning of the 19th century, the sexual system was rapidly losing popularity because it brought together plants showing no common traits besides the number of stamens. An example is in the Diandria, a grass genus Anthoxanthin, a genus in the Scrophulariaceae Veronica and Salix, a genus in the Salicaceae are all grouped together. This shows clearly why monothetic groups are artificial. However, it must be realized that the sexual system was an essential precurser to the development of natural groupings. The artificial groups formed a base from which similar plants in widely spaced monothetic classes could be picked and then placed in groups defined by a set of characters.

2b. DE JUSSIEU AND HIS CONCEPT OF THE FAMILY.

De Jussieu published his Genera Plantarum in 1789 and in it he grouped together the genera that he considered to be similar into Orders. These Orders are analagous to the Family of today. He formed the Family Scrophulariaceae (thus the name de Juss. after the family in any textbook) composed of 33 genera of which two were not present in the 6th Edition of Linnaeus's Genera Plantarum (1764) one was in Octandria, three were in Tetandria, six were in Diandria and 24 were in Didynamia. He divided the Family into four groups (to which he gives no rank), based on the number of stamens and the arrangement of the leaves. The family itself is natural as he gives a description of it but the subgroups are defined by a single term and are thus still monothetic. However, the concept of a fairly large group of genera having a set of common features rather than a single one had been formed and formed an important step in the development of a more natural classification system.

Table 3 : The divisions of the Family Scrophulariaceae defined by de Jussieu and some of the 33 genera.

Group	Genera
I Stamina quatuor didynama.	Scrophularia, Digitalis, Antirrhinum (17)
II Stamina duo.	Calceolaria (3 genera)
III Genera Scrophulariis affinia, oppositefolia.	Gratiola, Mimulus (10 genera)
IV Genera Scrophulariis affinia, Alternifolia.	Browalia (3 genera)

Some of the genera in the modern Family Scrophulariaceae that were mentioned by Linnaeus (see Table 2) were not placed in this family by de Jussieu :- Veronica and Orobanche were placed in Family II, Pediculares, Verbascum was placed in the Family Solanaceae, which is subsequent to Scrophulariaceae, while Nemesia was only formed in 1803 and was therefore not mentioned at all.

In one of the latest editions of Linnaeus's Genera Plantarum published in 1830 and edited by Curtio Sprengel, an attempt to update the Linnaean system by applying de Jussieu's families can be seen. At the beginning of each class eg. Didynamia, the genera that fall into de Jussieu's families are listed. The Personatae (= Scrophulariaceae) in Didynamia consist of three groups :-

Rhinantheae : genera 2393 -2403
Scrofularinae : genera 2404 - 2442
Orobancheae : genera 2447 - 2454

while Personatae in Diandria consist of genera 77 - 94. In addition, an index at the back gives the names of all the families with the numbers of the constit- genera listed.

2c. THE CLASSIFICATIONS of BENTHAM AND VON WETTSTEIN.

The work of Bentham, published in De Candolle's Prodromus of 1846, is the first treatment of the Scrophulariaceae where definite groups, called suborders, were formed which are equivalent to sub-families of today. They are I SALPIGLOSSIDEAE II ANTIRRHINIDEAE andIII RHINANTHIDEAE (see Table 4).and are still defined monothetically on aestivation of the corolla. However, each sub-family is divided into tribes which are natural groups of genera having a set of common characters eg. the Tribe Veroniceae has members with centripetal, racemose inflorences with at least the lower leaves opposite. The stamens are separate but the anthers can be bilocular or confluent and unilocular.

Bentham's treatment forms the basis of all subsequent revisions of the Family Scrophulariaceae. It is a comprehensive analysis giving descriptions of all genera and species known at the time, comprising some 500 pages as opposed to the brief six pages describing the genera in de Jussieu's Genera Plantarum. Bentham grouped the genera to the best of his knowledge into natural classes but his system has had few major changes since then with new species merely being added to the existing framework. The hetergeneity of the tribes has expanded and the need for an investigation and redefinition of the polythetic limits is long overdue.

Von Wettstein (1897) produced a modified version of Bentham's plan published in Engler and Prantyl's Natürlichen Pflanzenfamilien. This is an even more detailed account than Bentham's, with diagrams to illustrate the floral and anatomical structures. He arranges the groups and subgroups in the form of a dichotomous key. He does not however, give any rank to the divisions but they may be presumed to be analagous to Bentham's suborders and tribes, and thus the modern sub-families and tribes.

Table 4 : The Sub-families and Tribes of the Family Scrophulariaceae by Bentham (de Candolle Prodromus, 1846).

Subordo I. **SALPIGLOSSIDEÆ**

Tribus I. SALPIGLOSSEÆ. — Æstivatio corollæ plicata vel imbricato-bilabiata, labio postico (quoad axin primarium) exteriore sinubus sæpius plicatis. Inflorescentia ab initio centrifuga. . Gen. I-IX.

Subordo II. **ANTIRRHINIDEÆ**

Æstivatio corollæ imbricato-bilabiata, labio postico exteriore. Inflorescentia vel undique centripeta vel composita, partialis in cymâ centrifuga (cymis raro ad florem unicum in pedunculo articulato opposite bibracteato reductis), primaria in thyrso centripeta.

Tribus II. CALCEOLARIEÆ. — Corolla biloba, lobis integris concavis. Calyx valvatim 4-divisus. Inflorescentia composita. Folia opposita aut verticillata. . . . . Gen. X-XI.

Tribus III. VERBASCEÆ. — Corolla rotata, bilabiata, lobis planis, efossulata. Stamina declinata. Inflorescentia centripeta, uniformis. Folia omnia alterna. Gen. XII-XV.

Tribus IV. HEMIMERIDEÆ. — Corolla rotata vel rarius tubulosa (1), bilabiata, fossulata saccata vel calcarata. Capsula bivalvis. Inflorescentia centripeta, uniformis. Folia saltem inferiora, opposita. Gen. XVI-XXII.

Tribus V. ANTIRRHINEÆ. — Corolla tubulosa, sæpe saccata vel calcarata. Capsula poris dehiscens. Inflorescentia centripeta, uniformis. Folia, saltem inferiora, opposita aut verticillata. Gen. XXIII-XXIX.

Tribus VI. CHELONEÆ. — Corolla tubulosa, non saccata nec calcarata. Capsula 2-4-valvis (rarius baccata indehiscens). Calycis lobi vel segmenta æstivatione imbricatâ. Inflorescentia composita. Gen. XXX-XLVI.

Tribus VII. ESCOBEDIEÆ. — Corolla tubulosa nec saccata nec calcarata. Capsula bivalvis. Calycis ampli æstivatio valvata. Inflorescentia centripeta pedunculis opposite bibracteatis. Folia saltem inferiora opposita . . . . Gen. XLVII-L.

Tribus VIII. GRATIOLEÆ. — Corolla tubulosa rarissime (in Sphenandrâ) subrotata, non saccata nec calcarata. Capsula bivalvis, rarissime indehiscens. Calycis lobi vel segmenta æstivatione imbricatâ. Inflorescentia centripeta, uniformis, rarissime (in Manuleâ) irregulariter composita. . . . . Gen. LI-XCIV.

Subordo III. **RHINANTHIDEÆ**

Æstivatio corollæ imbricata, labio postico nunquam exteriore. Inflorescentia vel undique centripeta, vel composita, vel rarissime (in Buddleieis perpaucis) undique centrifuga. — In trib. 9-13 antheræ semper muticæ; in trib. 9-14 corollæ lobi plani.

Tribus IX. SIBTHORPIEÆ. — Folia alterna vel cum floribus ad nodos fasciculata, vel rarius opposita non connata, floralia aut conformia aut superiora decrescentia. Flores in axillis solitarii vel fasciculati, rarius cymosi. . . . . Gen. XCV-CVII.

Tribus X. BUDDLEIEÆ. — Folia opposita, membranâ vel linea transversa connexa. Flores cymosi vel rarius in axillis solitarii. . . . . Gen. CVIII-CXIII.

Tribus XI. DIGITALEÆ. — Inflorescentia centripeta, racemosa. Folia omnia alterna, ima conferta petiolata. . . . . . . Gen. CXIV-CXX.

Tribus XII. VERONICEÆ. — Inflorescentia centripeta, racemosa. Folia, saltem inferiora, opposita. Stamina distantia. Antheræ biloculares vel confluentim uniloculares. . . . . . . Gen. CXXI-CXXIV.

Tribus XIII. BUCHNEREÆ. — Inflorescentia centripeta, racemosa. Folia, saltem inferiora, opposita. Stamina per paria approximata. Antheræ dimidiatim uniloculares. . . . . . . Gen. CXXV-CXXIX.

Tribus XIV. GERARDIEÆ. — Inflorescentia centripeta, racemosa. Folia, saltem inferiora, opposita. Stamina per paria approximata. Antheræ biloculares, loculis sæpe mucronatis, æqualibus majusculis vel altero casso. . . . . Gen. CXXX-CXLVI.

Tribus XV. EUPHRASIEÆ. — Inflorescentia centripeta, racemosa. Corollæ labium posticum galeatum aut concavum, erectum (excepta forte Tozziâ) . . . . Gen. CXLVII-CLXXIII.

Table 5 : The Sub-families and Tribes of the Family Scrophulariaceae by von Wettstein. A. from Natürlichen Pflanzenfamilien, 1897 (in German). B. from Willis, 1980 (in English).

A

A. Die 2 rückwärtigen (der Achse zugewendeten) Corollenzipfel oder (bei Verwachsung derselben) die Oberlippe decken in der Knospenlage die seitlichen Corollenzipfel.
- a. Alle B. wechselständig, vereinzelte Ausnahmen bei *Celsia*. In vielen Fällen das 5. Stb. vorhanden . . . . **I. Pseudosolaneae.**
  - α. Blkr. röhrenlos od. mit sehr kurzer Röhre, radfg. oder kurzglockig **1. Verbasceae.**
  - β. Blkr. mit verlängerter Röhre . . . . **2. Aptosimeae.**
- b. Wenigstens die unteren B. gegenständig. Das 5. Stb. umgebildet oder fehlend **II. Antirrhinoideae.**
  - α. Blkr. 2lippig, mit blasig aufgetriebenen, concaven Lippen . **4. Calceolarieae.**
  - β. Blkr. fast aktinomorph oder 2lippig, mit flachen oder convexen Lippen.
    - I. Fr. eine mannigfach sich öffnende, vielsamige Kapsel (nur bei wenigen *Cheloneae* eine vielsamige Beere).
      - 1° Blkr. gespornt oder am Grunde sackartig erweitert.
        - † Blkr. ohne Röhre . . . . **3. Hemimerideae.**
        - †† Blkr. mit Röhre . . . . **5. Antirrhineae.**
      - 2° Blkr. weder gespornt, noch sackartig erweitert.
        - † Blütenstand cymös zusammengesetzt . . . . **6. Cheloneae.**
        - †† Blütenstand nicht cymös, meist einfach.
          - * A. zuletzt 1fächerig . . . . **7. Manuleae.**
          - ** A. auch zuletzt 2fächerig . . . . **8. Gratioleae.**
    - II. Fr. eine saftige Steinfr. oder eine nicht aufspringende, wenigsamige Kapsel **9. Selagineae.**

B. Die 2 rückwärtigen Blumenkronenzipfel oder die Oberlippe werden in der Knospenlage von einem oder beiden Seitenzipfeln gedeckt . . . . **III. Rhinanthoideae.**
- a. Blumenkronenzipfel alle flach und abstehend oder die 2 oberen aufrecht.
  - α. Antherenfächer zuletzt an der Spitze vereint. Die 2 oberen Blumenkronenb. oft aufrecht stehend. Nicht Parasiten . . . . **10. Digitaleae.**
  - β. Antherenfächer immer getrennt, manchmal ein Fach reduciert. Blumenkronenb. alle flach abstehend. Vielfach Parasiten und Halbparasiten **11. Gerardieae.**
- b. Die 2 oberen Blumenkronenb. bilden eine helmartige Oberlippe. Vielfach Parasiten und Halbparasiten . . . . **12. Rhinantheae.**

B

A. Two post. C-teeth (or upper lip) cover lat. teeth in bud.
- I. ***Verbascoideae*** (**'*Pseudosolaneae*'**) (all ls. usu. alt.; 5 sta. often present):
  - 1. VERBASCEAE (C with very short tube or none, rotate or shortly campanulate): *Verbascum, Celsia.*
  - 2. APTOSIMEAE (C with long tube): *Aptosimum.*
- II. ***Scrophularioideae*** (***Antirrhinoideae***) (lower ls. at least opp.; the 5th sta. wanting or staminodial):
  - α. C 2-lipped; lower lip concave, bladder-like.
  - 2. CALCEOLARIEAE: *Calceolaria.*
  - β. C almost actinom., or 2-lipped with flat or convex lips.
  - 2. HEMIMERIDEAE (dehisc. caps.; C spurred or saccate at base, with no tube): *Alonsoa.*
  - 3. ANTIRRHINEAE (as 2, but with tube): *Linaria, Antirrhinum, Maurandia, Rhodochiton.*
  - 4. SCROPHULARIEAE (CHELONEAE) (dehisc. caps. or many-seeded berry; C not spurred or saccate; infl. cymose, cpd.): *Russelia, Wightia, Collinsia, Scrophularia, Chelone, Penstemon, Paulownia.*
  - 5. MANULEAE (dehisc. caps.; C as in 4; infl. not cymose; usu. simple; anthers finally 1-loc.): *Zaluzianskia, Sutera.*
  - 6. GRATIOLEAE (as 5, but anthers finally 2-loc.): *Mimulus, Gratiola, Torenia.*
  - 7. SELAGINEAE (drupe or indehisc. few-seeded caps.): *Hebenstretia, Selago.*

B. Two post. teeth (or upper lip) of C covered in bud by one or both of the lat. teeth.
- III. ***Rhinanthoideae***:
  - α. C-teeth all flat and divergent, or the 2 upper erect.
  - 1. DIGITALIDEAE (anther-loc. finally united at tip; 2 upper C-lobes often erect; not paras.): *Veronica, Digitalis.*
  - 2. GERARDIEAE (anther-loc. always separate, one often reduced; C-lobes all flat, divergent; often paras.): *Gerardia.*
  - β. 2 upper C-teeth form a helmet-like upper lip. Often paras.
  - 3. RHINANTHEAE: *Castilleja, Melampyrum, Tozzia, Euphrasia, Bartsia, Pedicularis, Rhinanthus.*

There are three sub-families, I Pseudosolaneae, II Antirrhinoideae and III Rhinanthoideae, again primarily based on the aestivation of the corolla. However, Sub-family I, Pseudosolanaceae is not analagous to Bentham's Salpiglossideae but consists of genera with apparent Solanacious affinities having five stamens and almost regular flowers. Von Wettstein has placed Salpiglossideae in the Solanaceae, where it can be found today. Comparison of Table 4 and 5 show that he has maintained the main Benthamian tribes but has reduced the number from seven to three in the Rhinanthoideae. Table 5A shows the original treatment of the Scrophulariaceae by von Wettstein in 1897, and 5B shows the latest treatment from Willis (1980). There is absolutely NO difference apart from three name changes.

The fact that the sub-family and tribe divisions of the Scrophulariaceae has not changed for over 80 years indicates one of two things :- 1) Von Wettstein produced a system that subsequent taxonomists have not been able to improove or 2) modern taxonomists have been concentrating on revisions of genera and have simply not attempted a review of the family because there are so many more species and the task is enormous.

2d. MODERN CLASSIFICATIONS.

A number of attempts at reclassifying the Scrophulariaceae have been made since von Wettstein, but they have not been generally accepted. Hallier (1903) made the first attempt at a phylogenetic arrangement. He abandonned the character of aestivation as the basis for dividing the family into subfamilies and divided it into 16 tribes. He enlarged it to include the Plantaginaceae, Lentibulariaceae and Orobanchaceae (formerly treated as families). He considered the almost actinomorphic flower with five stamens, as in Verbascum to be the most primitive form. To represent the two lines of development from this type he placed Selagineae at the beginning, Verbasceae near the middle and Orobancheae at the end (see Table 6). Selagineae have a similar flower structure to other Scrophulariaceae, but the ovary is specialized having a single pendulous ovule in both locules which develop into a schizocarp when mature. The normal ovary has many axile ovules in a bilocular strucure that dehisces loculicidally or septicidally (Thieret, 1967). The other line of specialization is an increasing tendency towards parasitism, culminating in the Orobancheae which are almost exclusively parasitic (Tiagi, 1952).

Table 6 : The Phylogenetic arrangement of the tribes of the Family Scrophulariaceae by Hallier (1903).

1. Selagineae.	
2. Plantagineae.	
3. Manuleeae.	increase in seed size,
4. Digitaleae.	decrease in number of seeds.
5. Verbasceae.	
6. Leucophylleae.	
7. Cheloneae.	
8. Aptosimeae.	
9. Hemimerideae.	
10. Calceolarieae.	
11. Antirrhineae.	
12. Lentibularieae.	increase in parasitism.
13. Gratioleae.	
14, Gerardieae.	
15. Rhinantheae.	
16. Orobancheae.	

The problems imposed on trying to represent good polythetic groups in a developmental sequence can be illustrated by this example. This can be shown in three different ways :-

a) a list, which is one dimensional, can only show one line of development from the primitive form at the beginning through to the advanced form.

b) a map, which is two dimensional, can represent two lines of development. Hallier achieved this by placing the primitive form in the middle of a linear sequence.

c) a modal, which is three dimensional, is the best available representation but is still inadequate because the relationship between groups is in fact multi-dimensional.

Information is lost by compressing these relationships into one,two or three dimensions, for example, the linear sequence above can not express the specialization of flower structure into the bladder-like bottom lip in Calceolarieae, or the elaborate seed structure in Antirrhinoideae. Hallier's treatment is an important one because he placed emphasis on natural groupings and discarded monothetic delimitations, but it is not as easy to use as von Wettstein's system and has not been widely implememted.

Van Tieghem (1903, cited by Thieret, 1967) proposed a major division of the family based on staminal characters. The two groups were :-

a) stamens with tetrathecal anthers which are dorsifixed, pendulous, bifid with four longitudinal pollen sacs eg. Antirrhinum, Linaria, Mimulus.

b) stamens with dithecal anthers which are basifixed, erect with only two transverse pollen sacs eg. Scrophularia, Verbascum, Celsia, Nemesia.

He claims that the dithecal anther can be developed from the tetrathecal type and cited some genera that were intermediate eg. Zaluzianskia. This however indicates that staminal characters can not be used as a character for a major division but should rather be used along with other features to assess the degree of advancement of species.

Bellini (1907, cited by Thieret, 1967) proposed a classification based on characters of the nectary and the degree of parasitsm. Non-parasitic genera were placed in the sub-family Scrophulariaceae and parasitic and semi-parasitic ones were placed in the Rhinanthaceae. There are four different types of nectary :-

a)nectary situated upon the hypogyn ous disc, and is found only in the Rhinanthaceae.

b) nectary originates from the aborted fifth stamen.

c) nectary originates from the bases of the filaments of the larger stamens.

d) nectary is petaloid or lacking.

Types b), c) and d) are found only in the Scrophulariaceae. Many of the tribes are equivalent to those of von Wettstein (Thieret, 1967). In theory, nectary characters may be useful, but determination of the origin may be practically difficult and become subjective.

Pennell (1935)cited by Thieret, 1967) has reclassified portions of the Family Scrophulariaceae on a more phylogenetic basis. However, his work has been based on genera in the New World and do not take into account any of the Old World genera which means his contributions can only be regarded as preliminary.

There have been no more recent revisions of the Scrophulariaceae. With much new evidence available and many new species described, there is a strong case for a revision of the Family. All its genera should be critically analysed to show what changes have been made to them and to point out where further investigations need to be carried out. Corroboration between experts on generic revisions will be required before a review of the Family Scrophulariaceae above the generic can be achieved.

3. RELATIONSHIPS BETWEEN SCROPHULARIACEAE AND OTHER FAMILIES.

The Family Scrophulariaceae is closely allied to a number of other families, notably the Solanaceae, Bignoniaceae, Gesneriaceae, Globulariaceae, Lentibulariaceae and Acanthaceae. A few examples will be discussed in order to show the approaches being taken in current taxonomic practice.

The Pseudosolanoideae were placed in the initial position in von Wettstein's system to indicate the affinity with the Solanaceae. The best example is that of Verbascum which is nearly actinomorphic and has a full complement of five stamens. However, there are a number of features which show this affinity to be apparent not real. The slight zygomorphism expressed in Verbascum is characteristic of other scrophulariaceae (Robyns, 1931 cited by Thieret, 1967). The other genera in the Tribe Verbasceae have only four stamens, the posterior one being lost or reduced while the anterior stamen is lost or reduced in the Salpiglossideae, Family Solanaceae. The oblique alignment of carpels contrasted to the median alignment in the Scrophulariaceae further characterizes the Solanaceae : in practice, however this may be very difficult to determine especially if the floral axis is not clear. In addition, Solanaceae have plicate aestivation and bicallateral vascular bundles while Scrophulariaceae have imbricate aestivation and collateral vascular bundles.

The Bignoniaceae show a definite affinity with the Scrophulariaceae, the main difference between them being the woody nature of the former and the herbacious nature of the latter. Paulownia is a genus of woody species and therefore belongs in the Bignoniaceae but the seed has a copious endosperm which is anomalous in the group but is characteristic of the Scrophulariaceae. This genus has been transferred backwards and forwards between the two families a number of times (Cambell 1930 ; Thieret,1967). Adetailed study of seeds of Bignoniaceae especially herbacious forms (eg. Incarvillea) is needed to determine if absence of endosperm is constant in this family.

The Acanthaceae are closely related to the Scrophulariaceae with the irregular, five-part flowers, reduction in stamen number and a bicarpellate, superior ovary being common features (Heywood,1978). Elytraria is a transitional form being distinct from most Acanthaceae by having a well developed endosperm, as in the Scrophulariaceae. However, the funiculus is not developed into the typical jaculater which expels the seeds in most genera of Acanthaceae, so, like Paulownia above, Elytraria has been juggled between the two families.

The Gesneriaceae are often regarded as the tropical counterparts of the Scrophulariaceae, which is an essentially temperate family. Gesneriaceae are only separated from Scrophulariaceae by having a unilocualar ovary but Burtt (1977) has found some other differences :- Scrophulariaceae have anisocytic stomata and iridoid glycosides while Gesneriaceae have anomocytic stomata and do not have iridoid glycosides (see also Metcalfe and Chalk, 1950). He found a monotypic genus, Jerdonia that was placed in the Gesneriaceae because the ovary is unilocular but there are four parietal placenta, quite unlike the bifid lamellate placenta of most Gesneriaceae. It also displays some distinct Scrophulariacious features :- the seeds are large, with well developed endosperm and the inflorescence is a pair flowered cyme, found in several Scrophulariaceae genera. Jerdonia forms an intermediate between the two families, but can not be easily assigned to either.

There are some groups that have had their rank status swopped back and forth between tribe and family by various workers, Selaginaceae, Orobanchaceae and Globulariaceae being well known examples. The family rank of Selaginaceae was upheld by Bentham and Hooker (1876) but reduced to tribal level by von Wettstein (1891). It has subsequently been reinstated as a family by Hutchinson (1973) and Dyer (1975) because it has a single ovule in each locule. However, there are a few species of Selago that have two ovules in each locule and are placed medianly, one turned upwards and the other turned downwards with neither occuppying the apical position of single ovule of typical Selago.(Junell, 1961 cited by Burtt, 1977). The Tribe Manuleae is placed by von Wettstein next to the Tribe Selagineae, and on investigation by Junell (1961, cited by Burtt,1977) was found to contain a monotypic genus, Glumicalyx, with some species having fewer ovules than the rest of the species. The upper ones were found to be turned upwards, and the lower ones turned downwards, as in the atypical Selago species. Another possible link is in Glumicalyx, each locule contains up to six ovules all located in the upper part of the axile placenta. However, only the upper 1-3 develop into seeds. Further sterilization of this ovary might lead to the single apical ovule of Selago. This evidence shows a close relationship between Selagineae andManuleae but the difference between the two is no more than between Manuleae and other tribes, so Selagineae can not be maintained as a separate family (Burtt, 1977).

Globulariaceae have flowers that follow the basic Scrophulariaceae plan but are arranged in capitula surrounded by an involucre. They are related to the Selagineae by having a pendulous ovule but there is only a single locule. For this reason the Globulariaceae have been regarded as a separate family by Heywood (1978) and Hutchinson (1975). Cronquist (1968) includes the Selagineae in his Globulariaceae while Van Tieghem (1891, cited by Thieret, 1967) included Globulariaceae in his Selaginaceae.

The Orobanchaceae form an ecologically distinct group as they are all parasitic plants, almost completely lacking green colouration (Heywood, 1978). However, Some Scrophulariaceae are parasitic or semi-parasitic and the two families share almost all floral characteristics. The Orobanchaceae should be regarded as an advanced group of the Scrophulariaceae, as done by Hallier (1903).

4. AIMS FOR A PHYLOGENETIC CLASSIFICATION AND PROBLEMS NEEDING FURTHER STUDY.

Just as workers criticized Linnaeus's artificial system of classification, so the existing system of classifying the Scrophulariaceae must be critically analysed in the light of new information and new species. As von Wettstein's arrangement is the most generally accepted one, a few of the weak points will be discussed.

As the Sub-family Pseudo-solanaceae was based on a supposed but now unsupported affinity to the Solanaceae, this sub-group should be dissolved, leaving the two sub-groups Antirrhinoideae and Rhinanthoideae. These two are differentiated on aestivation characters (see Table 5B) :-

A. Two posterior corolla teeth (or upper lip) cover lateral teeth in bud
Antirrhinoideae

B. Two posterior corolla teeth covered in bud by one or both lateral teeth
Rhinanthoideae

Besides being amonothetic character, this is a trivial difference on which to base such a major division but 'appears to be of great racial value' (Pennell, 1935 cited by Thieret,1967). However, Hartl (1957, cited by Thieret,1967) reported that the anterior lobes of Lindenbergia, a genus of the Antirrhinoideae, are external in bud which indicates that this feature may be of little importance for determining relationships. A division based on an overall assessment of primitive and advanced characters would be more satisfactory for a phylogenetic system. A wide diversity of characters could be investigated to look for features to facilitate such a division.

Two of the 12 Scrophulariaceae tribes, the Cheloneae and Digitaleae are known to be particularly heterogeneous (Thieret,1967). Some of the genera included in Cheloneae by von Wettstein possess features that show them to be closely related to taxa other than Cheloneae eg.

Paulownia has been transferred to Bignoniaceae,
Brookea and Uroskinnera to Gesneriaceae, and
Leucocarpus, Berendtiella and Hemichaena to Gratioleae.

With the above genera removed, the Cheloneae Tribe is still heterogeneous having members with baccate and capsular fruits, loculicidal and septicidal capsules and only some possessing staminodes (Thieret,1967).

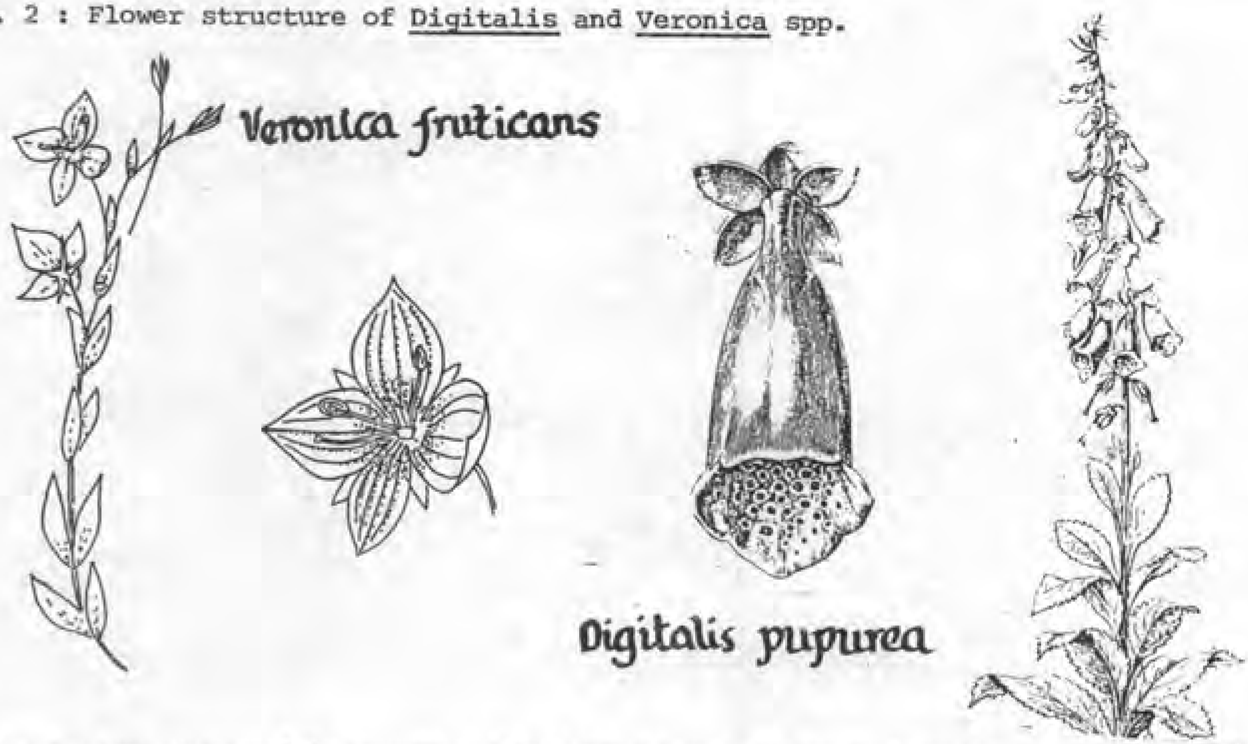
The Digitaleae is the least coherent of all the tribes as exemplified by the following key to two of the main genera :-

stigmas distinct, anther cells divaricate, capsule woody, septicidal
Digitalis.

stigmas united, anther cells parallel, capsule hardly or not woody, loculicidal
Veronica.

This tribe thus comprises of genera that should not be considered together even though they have the common features of not being parasitic and having anther locules united at the top (see Table 5B). This is a good example of a polythetic grouping being artificial. To be effective, a polythetic grouping must cover the majority of characters, for example, if the stigmas, alignment of anther cells and capsules had been taken into account, Veronica and Digitalis would never have been placed in the same tribe. Looking at the flower structure, further evidence for supporting Bentham's original division into two separate tribes, the Veroniceae and the Digitaleae, can be seen. In the genus Veronica, the posterior sepal is missing and the two posterior petals are fused into a single large one. The corolla tube is usually short and there are two stamens while Digitalis has four stamens and the corolla is rather expanded becoming wide at the mouth.

Fig. 2 : Flower structure of Digitalis and Veronica spp.



The flowers are arranged in racemes that become one sided by twisting in Digitalian species. However, a lot more study on the two groups is necessary before the dismemberment of the Digitaleae (sensu von Wettstein) can be made.

These few examples show that although the Scrophulariaceae are generally considered a 'well known' family, they are in fact far from it and taxonomic work on the group has only just begun (Thieret,1967).

To obtain a phylogenetic classification of the Scrophulariaceae, a world monograph of all the constituent genera is essential. Existing family divisions must be ignored to prevent any bias judgements, and relationships between the genera must be found by investigating a wide range of characters. For each of these characters, a hypothetical primitive form must be recognised, using fossil evidence where possible, The degree of departure from this primitive form must then be assessed and polythetically amalgamated to form developmental groups. As evolution usually proceeds by changes involving reduction, fusion and specialization (Stebbins,1974), these are modifications indicative of an advanced form. However, the possibility of reversal to a primitive (ancestral) state must not be forgotten.

The Verbasceae can not be regarded as the primitive form,as done by Hallier (1903), as they have united stigmas and relatively complex seeds which are advanced characters. The search for a putative primitive form must be carried out in the Antirrhinoideae as the Rhinanthoideae appear to be advanced, having developed elaborate zygomorphic flowers and the parasitic mode of life. The simplest seeds in this sub-family are found in Gratioleae. Thieret (1967) therefore proposes this group to represent the primitive form as it has additional unspecialized characters of distinct stigmas, septicidal capsules, distinct sepals, racemose inflorescence and opposite arrangement of the leaves.

There are many diverse techniques and new characters available to aid the modern taxonomist but purely morphological features are still vitally important. The chemical composition of the Scrophulariaceae have not been investigated, but further analysis may reveal important trends.: the officinal properties of Digitalian leaves containing the poisonous alkaloid digitalin is well known (Thomson, 1978). The cytology of the Scrophulariaceae has only been investigated in the cultivated forms because they are economically important (see Table 6) Analysis of chromosome numbers of the wild types in association with the geographic distribution sho ld reveal very important relationships and elucidate trends of development. Lower chromosome numbers are presumed to be the primitive forms, the higher ones being derived by polyploidy and chromosome multiplication (Stebbins, 1974). From Table 6, a number of polyploid forms can be seen : Digitalis ($2n = 56$) and Scrophularia ($2n = 36,40,80$), but the highest base numbers are found in Orobanche ($n = 19$), and Bartsia ($n = 12$), which are advanced genera. However, extrapolation from horticultural forms is not advisable because they have been synthetically induced to produce polyploid forms.

The Scrophulariaceae is a highly specialized family showing unique features such as the development of parasitism and the adaption of floral structure to bird and insect pollination. A classification based on the degree and type of pollination specialization was proposed by Müller (cited by Willis, 1908, 1960).

Table 6 : Base and Diploid Chromosome Numbers of some cultivated genera of the Scrophulariaceae (from Darlington and Ammal,1945).

Genus	Base No.	Diploid No.
Zaluzianskyia	6	12
Linaria	6,7,8,	12,24
Digitalis	7,28	56
Chelone	8	16
Antirrhinum	8	16
Verbascum	8,15,18	20,32,36,34,48,64
Nemesia	9	18
Calceolaria	8,9,30	18,36,32,60
Bartsia	12	24
Orobancheae	19	38
Scrophularia	9,10	36,40,80
Globularia	10	~20

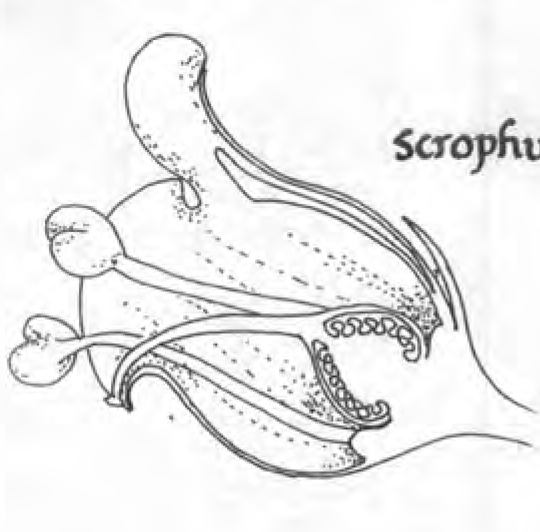
The pollination groups are based on how the pollinator picks up the pollen :-

1. Verbascum or Veronica type with an open flower and a short tube. Insects such as bees and flies can easily alight to eat or collect pollen (Robertson, 1892) which becomes attached to the underside of the insect.

(from von Wettstein, 1897)

Verbascum thapsus Veronica fruticans.

2. Scrophularia type with stamens and style bent towards the lower lip. Pollen will again become dusted onto the underside of the insect.



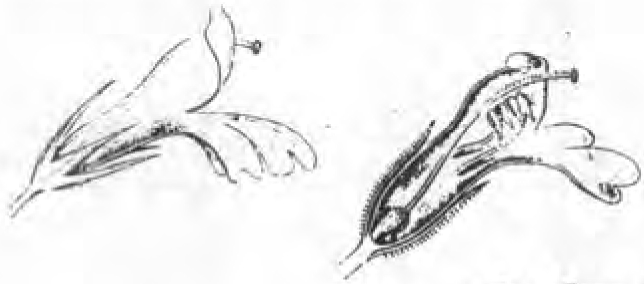
Scrophularia nodosa.

3. Digitalis and Linaria type, or gullet blossom where the stamens are placed so as to touch the back of the insect eg. bee, as it pushes its way into the flower. Linaria is more specialized as the gullet is closed and con only be opened by insects that are heavy enough.

Linaria alpina

Digitalis purpurea

4. The loose pollen type eg. Euphrasia, where pollen is loose and powdery. The anthers are protected by the upper lip of the flower and are provided with spine so that they can be shaken when an insect enters and recieves a shower of pollen on his head.



Euphrasia rostkoviana.

Specialized pollination mechanisms involve the degree of fusion of petals, development of corolla tube and/or nectar spur, degree of zygomorphy, position of stamens and type of inflorescence and could be considered as a 'built in phylogenetic scale'. Unfortunately, the rate of evolution is never constant and it is quite possible that two very dimilar pollinating mechanisms developed independantly. On the other hand, two closely allied species or genera may exhibit completely different pollination syndromes.

5. CONCLUSIONS.

Artificial systems of classifications based on monothetic divisions were essential precursers to the development of natural, polythetic systems. Botanists of the 17th-19th Century collected large amounts of data and produced such good classifications that they are still in use today. However, these systems were based only on information known at the time and constant addition of new species to the old framework has resulted in a breakdown of the polythetic groupings into heterogeneous collections of genera having few common traits. Modern taxonomists must divert their attention beyond the generic level and concentrate on combining existing information about Scrophulariaceae genera. Fully polythetic groups can then be formed and arranged according to a developmental scheme. It is essential to realize that as modern research reveals new information and relationships, so the classification must adapt to accommodate the changes. The ultimate goal is a phylogenetic classification, but there is little concrete evidence of primitive forms, any attempt is merely hypothetical and performs the main function of satisfying man's insatiability for patterns.

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