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CURRENT ANATOMICAL RESEARCH IN LILIACEAE, AMARYLLIDACEAE AND IRIDACEAE*

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ABSTRACT

Cutler, D.F. and Gregory, Mary (Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, England) 1983. Current anatomical research in Liliaceae, Amaryllidaceae and Iridaceae. Telopea 2(4): 425-452, Fig.1—An annotated bibliography is presented covering literature over the period 1968 to date. Recent research is described and areas of future work are discussed.

INTRODUCTION

In this article, the literature for the past twelve or so years is recorded on the anatomy of Liliaceae, Amaryllidaceae and Iridaceae and the smaller, related families, Alliaceae, Haemodoraceae, Hypoxidaceae, Ruscaceae, Smilacaceae and Trilliaceae. Subjects covered range from embryology, vegetative and floral anatomy to seed anatomy.

A format is used in which references are arranged alphabetically, numbered and annotated, so that the reader can rapidly obtain an idea of the range and contents of papers on subjects of particular interest to him. The main research trends have been identified, classified, and check lists compiled for the major headings.

Current systematic anatomy on the 'Anatomy of the Monocotyledons' series is reported. Comment is made on areas of research which might prove to be of future significance.

CURRENT RESEARCH

Work on the taxonomy of Liliaceae and their close relatives is entering an interesting period. Now that it is well recognised that a synthetic approach to classification is necessary (e.g. Huber 1977; Thorne 1976, 1977; Cronquist 1968; Traub 1975; Clifford 1977; Dahlgren 1975, 1977, 1980) there are signs of progress.

Of course, the specialists in disciplines like anatomy, palynology and phytochemistry will be hard to satisfy. They will probably feel that undue emphasis is still given to subjects other than their own. Having said this, it is perfectly clear to the plant anatomist that those attempting synthesis of data are hampered by incomplete or unconfirmed observations in the anatomical realm. It is evident that there is still scope for careful, accurate recording of anatomical data for systematic purposes. Attempts to construct schemes purported to show affinities between genera in Liliaceae, Amaryllidaceae, Iridaceae and related small families will inevitably be only partly successful until the anatomical data are presented in a comprehensive way. There are numerous papers which deal with the anatomy of one or two genera, or even several species within a genus, but few that make a wide survey. Some of these specialized articles are very helpful, e.g. Niehaus (1980) on the *Brodiaea* complex, De Vos (1970-9) on *Romulea* and other Iridaceae and Artyushenko's series of papers

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on *Galanthus* and *Zephyranthes* (Artyushenko 1969, 1974, 1980; Artyushenko & Dzidziguri, 1979). But there are few recent comprehensive anatomical reviews available. Of these Artyushenko (1970) has surveyed the morphology and anatomy of several genera of Amaryllidaceae, and Ambrose (1980) has written on the Melanthioideae using numerical analyses of morphological and anatomical data.

During the past twelve years progress has been made towards a volume in the series 'Anatomy of the Monocotyledons' (ed. C.R. Metcalfe) which will include Liliaceae, Amaryllidaceae, Iridaceae and smaller related families. The volume will be an example of international co-operation. Direct contributions to the descriptions on Amaryllidaceae will come from Dr N.L. de Menezes (Brazil) and Dr S. Arroyo (Argentina). Dr de Menezes (1980) has made observations on the relationships between Velloziaceae and Amaryllidaceae. Dr Arroyo has concentrated on affinities between members of the family from S. America and S. Africa (1981).

For the Liliaceae, Ambrose's (1980) paper will provide the basis for the Melanthioideae, and Cutler has been concentrating on other groups. Much of Cutler's published work has been on the Aloineae, in particular on leaf surface studies (Cutler 1972, 1978, 1979, Cutler & Brandham 1977, Cutler et al. 1980). There are also contributions by Dr Baijnath (S. Africa) on *Bulbine* and its relatives and *Kniphofia* (Baijnath 1977, 1980).

The Iridaceae are currently being examined anatomically by Dr P. Rudall (Kew) and *Iris* by Mr Wu Gi-gen (China). In this family, leaf transverse sectional outlines and sclerenchyma distribution are of particular interest. Also, the range of vascular bundle types may provide data of taxonomic significance.

Miss M. Gregory is working on the Alliaceae, where the arrangement of the vascular bundles and position of laticifers in the leaf are of use taxonomically.

Mesophyll in many of the genera of all three major families may provide characters of some importance. It is known that mesophyll, in particular the number of palisade layers, can be influenced markedly by leaf environment. This has tended to make anatomists cautious about using mesophyll features as potential taxonomic characters, and may explain why this tissue is relatively neglected in the literature on Liliales. Cutler's studies of a wide range of genera indicate that, when observed in L.S., otherwise undistinguished 'rounded' mesophyll cells may have a characteristic appearance. Further, additional and often quite striking features may be seen if the mesophyll is viewed paradermally—preferably through the epidermis, since attempts to cut paradermal sections may disarrange the cells (Fig. 1).

In addition to 'classical' systematic studies, there are other areas of work which will all contribute to a greater understanding of interrelationships between these families. Cheadle and colleagues have been making a long series of studies on vessel elements (1968-71). The types and their distribution, whether in root only, or root and stem, or all vegetative parts are of considerable interest, and may enable us to deduce the 'direction' of evolution for some groups. Huber has made extensive studies of seeds (1969) and those results and other observations have enabled him to formulate ideas on relationships within his Liliales (1977). The phylogenetic significance of the structure of the floral nectary in monocotyledons has been discussed by Daumann (1970), and that of embryos by Khokhryakov (1971, 1975). Behnke's (1972) work on sieve-tube plastids has drawn evidence of inter-relationships from a new source which has proved of considerable interest.

Kaplan has made extensive developmental studies both on the nature of the monocotyledonous leaf (1973) and of unifacial leaves in monocotyledons (1975). Guédès (1972, 1980) and Bugnon & Mbaya (1976) are also involved in this area of research. This work is most important, since it aids an understanding of the nature of the organs we are dealing with, and complements studies on comparative anatomy. Other developmental studies have concentrated on branching, vascular systems and intercalary meristems (e.g. Fisher & French 1976, 1978).

Examples of the interest in bulb and inflorescence morphology and anatomy can be found in the works of Ekberg (1972), Müller-Doblies (1971, 1977, Müller-Doblies, D. & U. 1978) and Baranova (1976). Sterling, from 1972 onwards, has produced a

series of papers concerned with the anatomy of carpels in the Liliacae, and the floral vascular system of a number of members of this family has been studied by Utech (1978-9, Utech & Kawano 1975-1980).

Phytochemical papers are, on the whole, outside the range of this review, but mention should be made of works on crystal types and their distribution, e.g. Samara & Terpó (1980) and Amico et al. (1977, 1979).

Few recent accounts exist about the importance of stomatal types within the monocotyledons. Tomlinson (1974) wrote on this topic in general, but most workers deal with rather well-defined, small groups, e.g. Bresky (1975), who reported on stomatal types in some South American members of Amaryllidaceae, Alstroemeriaceae, Iridaceae and Liliaceae, Pande (1980), who worked on Iridaceae, Qualo (1976), who examined the stomata of 27 spp. of *Haworthia,* and Shah & Gopal (1970), who studied various species of Amaryllidaceae.

Embryological studies are very time-consuming, and have tended to be fewer in number than those for most other anatomical aspects during the past twelve years. Examples include those of Björnstad (1970), Cave (1974, 1975), Lakshmanan & Philip (1971), and Sokolowska-Kulczycka (1973-80), but all seen by the present authors are listed in the annotated bibliography, together with papers on all the other aspects mentioned above, as well as some of which space would not permit discussion.

FUTURE RESEARCH

Although classical studies can be rather drawn out and the routine discipline of making careful observations and records somewhat daunting, undoubtedly they will be of increasing importance in the next few years, as data are gathered together, gaps in knowledge found and filled. The scattered nature of current information—and the surprising lack of it on certain groups—make this task essential.

H. Rasmussen (in preparation) has demonstrated how essential it is to study stomatal development in each species before data are incorporated into systematic and phylogenetic studies. Purely descriptive studies on mature stomata have value at the diagnostic level, and will continue to be published, but the additional information to be obtained for the little extra work on development is well worthwhile. Since most monocot leaves have a basal meristem, this is relatively easy to do from live material.

Other developmental studies are normally very time-consuming. This limits their application in systematics, but not their importance. In particular, studies on branching systems and entire vascular systems show considerable promise.

Recent discussion on the value of studies on flower development (see Kaplan 1971) have aroused interest in this field. Carpel and inflorescence vasculature have yielded very valuable data in the past, and, with due care over interpretation, should continue to do so.

The potential of comparative, developmental embryological studies in the Liliales has by no means been exhausted. Seed and seedling anatomy have also more to yield to the research worker.

In dicotyledons, venation patterns (Hickey 1980) have extensive taxonomic and phylogenetic implications. There is an undoubted potential for comparable work in the monocotyledons.

Recent studies on leaf surfaces with the SEM (Cutler et al. 1980) have demonstrated the wealth of new characters to be found which are of taxonomic interest. It is not clear yet whether these will have taxonomic significance beyond the generic level, or whether they will prove to be of more interest to the student of ecological anatomy. Consequently more surveys and experimental studies could yield important results. Similarly, petal surface features are very well demonstrated by the SEM (Stirton 1981), and here is an almost virgin field of study, since Barthlott & Ehler have looked at only a few monocot petals in their 1977 paper. Huber's (1969) survey of seed anatomy could be extended by use of the SEM. Vessel elements also show up very clearly in the SEM.

ANNOTATED BIBLIOGRAPHY

All of the references have been seen in the original, except where abstracting sources are cited in square brackets.

The following abbreviations are used:

Alliaceae	All.
Amaryllidaceae	Amar.
Haemodoraceae	Haem.
Hypoxidaceae	Hypox.
Iridaceae	Irid.
Liliaceae	Lili.
Ruscaceae	Rusc.
Smilacaceae	Smil.
Trilliaceae	Trill.
LM	light microscopy
SEM	scanning electron microscopy
TEM	transmission electron microscopy

For subject index see p.451.

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introductory section on criteria used, eg. growth habit, leaves, stomata, nodal anatomy, wood anatomy, inflorescences, floral structure. Families listed, with brief notes on relationships.

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336. Tamberg, T.G. (1975) [Anatomical structure of the stem of *Gladiolus*.] *Byull. Vses. Ord. Lenina Inst. Rast. N.I. Vavilova 54,* 69-72. [Russian] Irid. 2 cvs.
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343. Thompson, M.F. (1978) Studies in the Hypoxidaceae. II. Floral morphology and anatomy. *Bothalia 12,* 429-35. *Empodium, Pauridia, Spiloxene.*
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crystalliferous idioblasts in the carpels of *Ornithogalum caudatum*. *Ann. Bot. 46,* 533-9. Lili. SEM, TEM.

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365. Utech, F.H. (1979) Floral vascular anatomy of *Scoliopus bigelovii* Torrey (Liliaceae-Parideae = Trilliaceae) and tribal note. *Ann. Carnegie Mus. 48* (4), 43-71. [*Biol. Abstr. 68* (1979) No. 13647.] Comparison with *Medeola*.
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373. Valsecchi, F. (1974) Osservazioni embriologiche, sistematiche ed ecologiche su *Allium parciflorum* Viv. *G. bot. Ital. 108,* 81-93. All.
374. Vasil, I.K. (1974) The histology and physiology of pollen germination and pollen tube growth on the stigma and in the style. pp.105-18 in: Fertilization in higher plants (ed. Linskens, H.F.) North-Holland Publ. Co.: Amsterdam & Oxford. Includes Lili. *Lilium.* Transmitting tissue in style.
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377. Ventner, A.M. (1972) 'n Morfologiese ondersoek van drie aalwyne. *Aloe 10* (4), 49-96. [English summary 48.] Lili. *Aloe,* 3 taxa, leaf anatomy.
378. Wagner, P. (1977) Vessel types of the monocotyledons: a survey. *Bot. Notiser 130,* 383-402. Includes All., Amar., Haem., Hypox., Irid., Lili., Smil. Survey of literature and discussion of relationships. Roots, stems, leaves.
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380. Werner, P.A. (1978) On the determination of age in *Liatris aspera* using cross-sections of corms: implications for past demographic studies. *Amer. Nat. 112,* 1113-20. Lili. 'Growth rings' = bands of sclerenchyma.
381. Williams, R.F. (1975) The shoot apex and leaf growth. A study in quantitative biology. 256 pp. Cambridge Univ. Press. [*Biol. Abstr. 60* (1975) No. 10948.] Includes Lili. *Dianella.*
382. Wilson, K. & Anderson, G.J.H. (1979) Further observations on root contraction. *Ann. Bot. 43,* 665-75. Lili. *Hyacinthus* mainly, also Amar. *Narcissus* and Irid. *Gladiolus.* LM and TEM.
383. Yasui, K., Miyata, K. & Konishi, K. (1974) [Histological studies on formation and thickening growth of gladiolus corms.] *J. Jap. Soc. hort. Sci. 42,* 371-9. [Japanese; English summary] Irid.
384. Yasui, K., Miyata, K., Kunisada, J. & Konishi, K. (1974) [Histological studies on corm development in *Freesia.*] *J. Jap. Soc. hort. Sci. 43,* 150-60. [Japanese; English summary] [*Bibl. Agric. 39* (1975) No. 151710.] Irid.
385. Yates, I.E. & Duncan, W.H. (1970) Comparative studies of *Smilax,* Section Smilax of the southeastern United States. *Rhodora 72,* 289-312. Smil. Leaf anatomy of 8 spp.
386. Zahariadi, C. (1977) Notes on the intrageneric classification of the genus *Ornithogalum* L. (Liliaceae). *Bot. Zh. SSSR 62,* 1624-39. [Russian] Includes some characters of seed anatomy.
387. Zeiger, E. & Cardemil, L. (1973) Cell kinetics, stomatal differentiation, and diurnal rhythm in *Allium cepa. Dev. Biol. 32,* 179-88. [*Biol. Abstr. 56* (1973) No. 63158.] All.

388. Zhestyanikova, L.L. & Zykina, A.V. (1974) [Anatomical structure of succulent layers in the bulbs of some wild species of the genus *Allium* L.] *Trudy. prikl. Bot. Genet. Selek. 51* (3), 136-47. [Russian; English summary.] All. 4 spp.
389. Zhestyanikova, L.L. & Zykina, A.V. (1976) [Anatomical structure of the fleshy scales of the most widely distributed species of *Allium*.] *Byull. Vses. Ord. Lenina Inst. Rast. N.I. Vavilova 64,* 35-40. [Russian] All. 7 spp.
390. Zubkus, L.P. & Sedel'nikova, L.L. (1977) [Anatomic and morphologic characteristics of juvenile-virgin plants of *Erythronium sibiricum*.] pp. 55-72 in: Dekorativnye rasteniia i ikh introduktsiia v zapadnuiu Sibir' (ed. Sobolevskaia, K.A.). [Russian] [*Bibl. Agric. 42* (1978) No. 082180.] Lili. Seedling anatomy.

ADDENDUM

Since this survey was written in June 1981, many papers have been published. We list here a few of the more important ones.

Arroyo, S.C. (1982) Anatomia vegetativa de *Ixiolirion* Fisch. ex Herb. (Liliales) y su significado taxonomico. *Parodiana 1*: 271-86.
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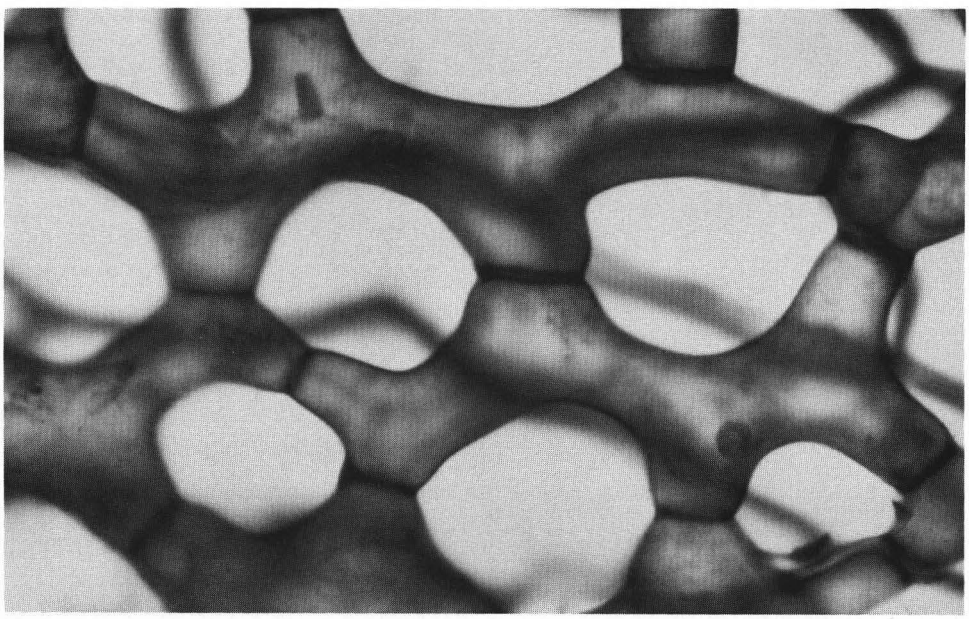

Fig. 1 *Clintonia uniflora* leaf, paradermal section showing shapes of chlorenchyma cells (x500).

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