VIII. *A Contribution to the Study of the Evolution of the Flower, with special reference to the* Hamamelidaceæ, Caprifoliaceæ, *and* Cornaceæ.

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(Plates 28–30 and 13 Text-figures.)

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Contents.

	Page
1. Introduction	239
2. Hamamelidaceæ	245
3. Caprifoliaceæ	251
4. Cornaceæ	261
(a) *Cornus*	261
(b) *Alangium* and *Marlea*	265
(c) *Aucuba*	269
(d) *Garrya*	274
(e) *Helwingia*	278
(f) *Corokia*	282
(g) *Melanophylla*	284
(h) *Griselinia*	284
(i) *Nyssa*	287
5. Final Discussion	291
Argument:—The Interpretation of Resemblances and Differences. Origins. Phylogeny of the Hamamelidaceæ. Phylogeny of the Caprifoliaceæ. Phylogeny of the Cornaceæ. The Vascular Structure of the Flower in Angiosperms. The Ovule in Angiosperms. Ovular connections. Ovular Vascular System. The Phylogeny of Angiosperms	291–302

1. INTRODUCTION.

The structure of the flower of *Davidia*, a genus referred to the Cornaceæ in 'Die Natürliche Pflanzenfamilien,' has been already described by the author* in a paper dealing with the structure and affinities of *Davidia involucrata*, published in the 'Transactions of the Linnean Society,' in 1909. During the study of *Davidia* there was occasion to examine the flowers of several genera of Cornaceæ, and in so doing striking structural differences were discovered not only between representative genera of the subfamilies but also between the genera that have been grouped in a particular subfamily, such as, for instance, the Cornoideæ. At the same time, as reference had

* A. S. Horne in Linn. Soc. Trans. 2nd ser., Bot. vii. (1909) 303–326, t. 31–33.

been repeatedly made to the Hamamelidaceæ and Caprifoliaceæ in the attempt to arrive at an interpretation of the floral morphology and a solution of the phylogeny of *Davidia*, it soon became evident that a close scrutiny of the evolutionary tendencies exhibited by these families would lead to a broader conception of the significance of the new discoveries, and shed considerable light upon the origin of the flower in several genera of Cornaceæ. Influenced by these considerations, the author has undertaken an elaborate and extended investigation of the Hamamelidaceæ, Caprifoliaceæ, and the Cornaceæ (as defined by Harms), notwithstanding the fact that these families are arranged in different cohorts in Engler's System—with the object of elucidating the true phylogeny of the Cornaceæ, and in the belief that the investigation would have a direct bearing upon the whole question of the phylogeny of the Angiosperms.

It is the object then of the present paper to record the facts that have been observed, and to present the conclusions that have been deduced from a comparative study of the evolutionary changes which are evident among the Hamamelidaceæ, Caprifoliaceæ, Cornaceæ, Araliaceæ, and other nearly associated families.

The composition of the family Hamamelidaceæ varies but little in the chief systematic works. Of the eighteen genera enumerated by Niedenzu *, in 'Die Pflanzenfamilien,' fifteen are recorded by Bentham and Hooker †, sixteen by Baillon ‡, and nine of the ten genera known to science at the time, by Endlicher §. Our knowledge of the general morphology is largely due to Baillon's ‖ researches, which are described in 'Adansonia.' Daniel Oliver ¶ contributed a valuable paper on *Sycopsis*, a new genus of Hamamelidaceæ, in 1860, and a note ** relating to the structure of the anther in *Hamamelis* and *Loropetalum* in 1862. The embryology of several genera was studied by Shoemaker †† in 1905.

The composition of the family Caprifoliaceæ has also varied little in the different systems. Of the eleven genera enumerated by Fritsch ‡‡ in 'Die Pflanzenfamilien,' all are recorded by Bentham and Hooker, and nine by Endlicher. *Adoxa*, appearing in Bentham and Hooker's list, is not retained by Fritsch. F. Höck §§ proposed the transference of *Sambucus* to a new family, the Sambucaceæ, but his suggestion has not received general acceptance.

The literature is chiefly systematic, or of a strictly morphological character. Maximowicz ‖‖ contributed an extensive monograph on the Caprifoliaceæ to the 'Bulletin de l'Académie Impériale des Sciences de Saint Pétersbourg.' Oersted ¶¶ revised the grouping

* F. Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2*a* (1891) 115–130.

† G. Bentham et J. D. Hooker, Gen. Pl. ii. 664–669.

‡ H. Baillon, Histoire des Plantes, iii. (1872) 456–461.

§ S. Endlicher, Gen. Pl. (1836–1840) 803.

‖ H. Baillon in Adansonia, i., v., xi.

¶ D. Oliver in Linn. Soc. Trans., Bot. xxiii. (1860) 83.

** D. Oliver, *l. c.* (1862) 457.

†† D. N. Shoemaker in Bot. Gaz. xxxix. (1905) 248.

‡‡ Fritsch in Engl. u. Prantl, Nat. Pfl., Teil iv. Abt. 4 (1891) 156.

§§ F. Höck in Bot. Centr. li. (1892) 233.

‖‖ C. J. Maximowicz in Bull. Acad. Imp. Sci. St. Pétersbourg: xxiv., *Lonicera* (1878); xxvi., *Viburnum* (1880); xxvii., *Triosteum* (1881); xxxi., *Linnæa*, *Diervilla* (1887).

¶¶ Oersted in Vidensk. Meddel. Naturh. Foren. Köbenh. vi. & vii. (1861) 267–305.

of the species of *Viburnum*, according to the character of the fruit, in 1861. E. A. Newell Arber * interpreted several cases of synanthy in *Lonicera*, in 1903. The embryology of the family has been neglected since the records that appear in the memoirs of Hofmeister † (1858, 1859), Vesque ‡ (1878, 1879), and Guignard § (1882).

The composition of the family Cornaceæ, unlike that in the above-mentioned families, does vary considerably in different systems. With the object, therefore, of making the exposition more intelligible, a table (see p. 242) has been drawn up, to collate the classification of the Cornaceæ adopted by Harms in 'Die Pflanzenfamilien' with those of other systematists.

It will be noted that the genera aggregated by Harms in the Cornaceæ were distributed among several families in the systems of Endlicher, De Candolle, and Lindley; thus the Cornaceæ comprise only five genera in De Candolle's ‖ 'Prodromus' (*Cornus*, *Aucuba*, *Griselinia*, *Mastixia*, and *Curtisia*); while other genera known to science at the time were segregated in the families Garryaceæ, Alangiaceæ, Helwingiaceæ, and Araliaceæ.

Benjamin Clarke ¶ described some observations upon the flowers of *Marlea* in a paper contributed to Hooker's 'Journal of Botany' so long ago as 1850, and came to the conclusion that the Alangieæ (*Alangium* and *Marlea*) are closely related to *Cornus*. Clarke's paper seems to have been overlooked.

Bentham and Hooker** include the Corneæ, Alangieæ, Garryaceæ, and Nyssaceæ of earlier systematists in the Cornaceæ. They define the Cornaceæ in terms of the ovule. Thus the genera are characterized by possessing ovules of the ventral type (with dorsal raphe), in contradistinction to the Araliaceæ where the ovules are of the dorsal type (with ventral raphe). But this criterion has proved to be unsound for two reasons: first, because the structure of the ovule in certain genera (*Helwingia*, *Nyssa*) was at the time imperfectly known, and, secondly, in that the so-called dorsal ovules are not necessarily homologous and do not strictly conform to a single type.

Baillon †† contributed important additions to our knowledge of the morphology of the family. He was the first to point out the peculiar morphology of the supposed calyx in *Garrya*, and worked out the development ‡‡ of the flower in both *Garrya elliptica* and the hybrid, *Garrya Thuretii*. But his interpretations of floral structure and affinities in the Cornaceæ were profoundly influenced by the results accruing from his researches §§ relating to the organogeny of the flower in the Amentiferæ. He found

* E. A. Newell Arber in Journ. Linn. Soc., Bot. xxxv. (1903) 463–474.

† W. Hofmeister in Pringsh. Jahrb. i. (1858) 120–121; and in Abhandl. Königl.-Sächs. Gesell. Wiss. (1859), 533–672, t. 1–27.

‡ J. Vesque in Ann. Sci. Nat., Bot. 6me sér. vi. (1878) 237–285, viii. (1879) 261–390.

§ Guignard in Ann. Sci. Nat., Bot. 6me sér. xiii. (1882) 136–198.

‖ A. de Candolle, Prodromus, iv. (1830) 271.

¶ Benjamin Clarke in Hooker's Kew Journ. vol. ii. (1850) 129.

** Bentham et Hooker, 'Genera Plantarum,' vol. i. part iii. (1867) 947.

†† H. Baillon in Adansonia, v. (1864) 179–203; x. (1871–1873) 112–117.

‡‡ H. Baillon in Bull. Soc. Linn. Paris (1877), 139.

§§ H. Baillon in Adansonia, xi. (1873–1876) 163–174; xii. (1876–1879) 1–20.

TABLE I.—THE ARRANGEMENT OF THE CORNACEÆ OF HARMS IN OTHER SYSTEMS.

Wangerin, 1910 *.	Harms, 1898 †.	Baillon, 1877–1879 ‡.	Bentham & Hooker, 1867 §.	Endlicher, 1847 ‖.	Lindley, 1847 ¶.	Endlicher, 1836–1840 **.	De Candolle, 1830 ††.
Garryaceæ.	I. Garrya.	Cornaceæ ser. II.	Cornaceæ sec. II.	Garryaceæ.	Garryaceæ.	Garryaceæ antedesmeis affines.	Garryaceæ.
Nyssaceæ.	II. Nyssa.			Nyssaceæ.	Alangiaceæ.	Nyssaceæ; genera Santalaceis affinia.	— —
	Camptotheca.			— —	— —	— —	— —
	III. Davidia.	Combretaceæ.	— —	— —	— —	— —	— —
Alangiaceæ.	IV. Alangium.		Cornaceæ sec. I.	Corneæ.	Alangiaceæ.	Alangieæ.	Alangiaceæ.
	Marlea.						
	V. Mastixia.	Umbelliferæ.		Corneæ Aucubeæ.	Cornaceæ?	genera dubia Cornaceis affinia cum Polyosmate Votomita.	Corneæ.
	VI. Curtisia.	(Araliеæ.)		Corneæ veræ.			
Cornaceæ.	VII. Helwingia.	Cornaceæ ser. I.	Araliaceæ.	Helwingiaceæ.	Helwingiaceæ.	Helwingiaceæ; genera Santalaceis affinia.	Helwingiaceæ.
	Corokia.		Cornaceæ sec. I.	Corneæ Aucubeæ.	Cornaceæ.	genera Rhamnaceis affinia.	— —
	Cornus.			Cornæ.		Corneæ.	Corneæ.
	Benthamia.			Corneæ veræ.			
	Toricellia.			Araliaceæ.	Araliaceæ.	Araliaceæ.	Araliaceæ.
	Melanophylla.	— —	— —	— —	— —	— —	— —
	Kaliphora.			— —	— —	— —	— —
	Aucuba.	Cornaceæ ser. I.	Cornaceæ sec. II.	Corneæ Aucubeæ cum Quadriala & Decostea.	Cornaceæ.	genera Corneis affinia cum Decostea.	Corneæ.
	Griselinia.			Araliaceæ.	— —	genera dubiæ sedis.	— —

* W. Wangerin in 'Das Pflanzenreich,' 41 Heft, 1910.
† Harms in Engl. u. Prantl, Nat. Pfl. Teil iii. Abt. 8, 1898.
‡ H. Baillon, Histoire des Plantes, vii. 1879 (Cornaceæ and Umbelliferæ), and vi. 1877 (Combretaceæ).
§ G. Bentham et J. D. Hooker, Gen. Pl. i. pt. iii. (1867).
‖ S. Endlicher, Gen. Suppl. iv. pts. ii. & iii. 1847.
¶ J. Lindley, The Veg. King. 2nd ed. 1847.
** S. Endlicher, Gen. Pl. 1836–1840.
†† A. De Candolle, Prodr. iv. 1830.

that the ovary of *Quercus*, *Castanea*, and other genera becomes multilocular during development, owing to the inward or centripetal growth of the parietal placentæ, and, hence, was led to the belief that the bilocular ovaries found in certain genera of Cornaceæ originated from unilocular types. But the ovary, in Cornaceæ, as will be subsequently shown, has advanced beyond the evolutionary phase described by Baillon for the Amentiferæ, and presents instead advanced stages in progressive abortion.

Harms * brings together the largest grouping of genera ever included in the Cornaceæ. He asserts that intermediate forms exist between ovules of the dorsal and ventral types, and hence there is no adequate reason for excluding genera with the Aralian type of ovule (*Nyssa* and *Davidia*) from the Cornaceæ. But Harms's opinions carry little weight, owing to the fact that the criteria upon which he relies are insufficient to express the diverse structural forms of ovule obtaining in this family.

Walther Wangerin † contributed a lengthy paper, entitled "Die Umgrenzung und Gliederung der Cornaceæ," to Engler's 'Jahrbücher,' in 1906. This paper describes in detail the chief morphological and anatomical characters of the family, gathered from the works of Sertorius, Baillon, and others, and from an examination of herbarium material. This paper forms the basis of Wangerin's monograph ‡ contributed to 'Das Pflanzenreich' in 1910. The Cornaceæ of Harms are, in this monograph, resolved into four old families, the Garryaceæ, Alangiaceæ, Nyssaceæ, and Cornaceæ. Two of these, the Nyssaceæ (*Nyssa* and *Davidia*) and Alangiaceæ, according to Wangerin, are distinguished by two integuments. The present author §, however, recorded only a single integument for *Davidia* in 1909, and is now able to show that *Nyssa* also is unitegumentary. Hence Wangerin has relied upon a morphological error with regard to the Nyssaceæ, and, in consequence, has failed to present a convincing case for the re-establishment of both families.

The present investigation reveals several hitherto-unrecorded details in the floral organization, the special morphology of the ovary and ovule, and the course of the vascular tissue in the families under consideration. A striking evolutionary series has been traced in the Caprifoliaceæ, where, owing to progressive abortion, the *parietal portion of the ovary* that is well represented in *Leycesteria* has become reduced until, in *Sambucus*, only vestiges remain. Progressive abortion, in the Caprifoliaceæ, is accompanied by progressive sterilization—the ovules are not only reduced in number, but transitional stages occur from ovules physiologically sterile to be found in *Lonicera* to the merest rudiments discovered in *Sambucus*. Owing to reduction the ovary or loculus, in several genera, becomes monospermous, with a terminal seed, but in each case the one-seeded condition has been attained by a different method. Comparison with an analogous sterilization series in the Hamamelidaceæ shows that the terminal seed in the Caprifoliaceæ is constantly axially suspended, or in the exceptional case of *Viburnum* axially borne by origin, whereas in the latter family it is situated parietally.

* Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8.

† W. Wangerin in Engl. Bot. Jahrb. Band xxxviii. Heft 2 (1906).

‡ W. Wangerin in Engl. Das Pflanzenreich, Heft 41 (1910).

§ A. S. Horne in Trans. Linn. Soc. ser. 2, Bot. vii. (1909) 323.

Passing then to the Cornaceæ, the author selected *Corokia* and *Marlea*, genera with unilocular or bilocular ovaries, and traced the structural changes accompanying the reduction from two loculi to one. With the aid of all the available facts it was then possible to analyse and interpret the uniovulate Cornaceæ, and the single terminal ovule was found to be of multiple origin. The sterilization series evident in the Caprifoliaceæ extends by way of *Sambucus* to the Cornaceæ, where vestiges of ovules are unknown, and the conclusion reached that the ovaries or loculi of the Cornaceæ were primitively pluriovulate is supported by the direct evidence deduced from their own structural peculiarities.

A series has been traced in the direction of the loss of carpellary autonomy by way of the Araliaceæ, Caprifoliaceæ, and Cornaceæ that culminates in the reduced ovary of *Aucuba*, which in appearance and structure simulates a single inferior carpel.

Structural synthesis in the flower is accompanied by a corresponding economic advance in the development of the vascular system. The dorsal and lateral bundles of the carpels, and the traces of the perianth and stamens that exist as independent series in *Aralia* are in the Caprifoliaceæ represented by one series, and the latter family exhibits a still further economical advance reaching in *Viburnum* the condition obtaining in the Compositæ, where the bundles in the single series are reduced to half the sum of the petals and stamens. Two lines of advance towards the evolution of the single series have been traced, one presented by *Aralia*, *Davidia*, and *Marlea*, and the other exemplified by the Hamamelidaceæ.

The ovule in the Caprifoliaceæ and Cornaceæ has advanced far beyond the evolutionary stage exhibited by the Hamamelidaceæ, but whereas there is little deviation from a single type in either the Hamamelidaceæ or Caprifoliaceæ, the ovules of Cornaceæ present diverse forms and structures. The nucellus of Cornaceæ presents some resemblance to that of the Rosaceæ on the one side, and on the other through *Helwingia* to the reduced nucellus of *Lilium* or *Inula*.

Considerable emphasis is laid upon the fact that similar stages and methods of floral construction recur, not only in the same but different families, and upon the fact that similar ends are attained in the same or different families by dissimilar methods. The separation of the sexes occurs in several genera of Hamamelidaceæ, Rosaceæ, and numerous other families. Epigynous structures have arisen in numerous groups and even in the same group by more than one device. The centripetal development of parietal placentæ, rendering the ovary multilocular, occurs in *Castanea*, *Quercus*, *Rhodoleia*, and many other genera. Similar stages in the evolution of the vascular system have recurred in *Castanea*, the Caprifoliaceæ, and Cornaceæ, whilst similar arrangements of ovules are found and the details of the vascular supply are nearly identical in different families. Neither is the ovule by any means exempt. The separation of one type from another; the transition from bi- to unitegumentary forms, and the evolution of the exalbuminous seed has happened again and again in the racial experience of Angiosperms. Convergence and parallel development are established doctrines, but many authors have failed to grasp their significance. Convergence in

one or a few characters may not prove of much importance, but when the action of evolutionary forces has achieved a like resultant or effect, and similar combinations of characters are found, the problem of origins becomes almost insoluble.

The author is led, from the facts presented here, to express the strong conviction that the structural peculiarities to be perceived in both the Caprifoliaceæ and Cornaceæ are indicative of different origins; that certain genera in each family have pursued independent but similar lines of development, and hence both families are convergent and polyphyletic. The case for the polyphyletic origin of Cornaceæ has already been stated before the Botanical Section of the British Association at Portsmouth in 1911 *.

The author, in conclusion, indicates the bearing of modern experimental work upon the field of enquiry pursued here, discusses the affinities of the three families specially studied, outlines the general features in the evolution of the floral vascular system and of the ovule, and, finally, sums up the position created by this investigation in relation to the natural classification of Angiosperms.

This research was commenced at the Royal College of Science, London, and finished at the Wisley Laboratory, and my thanks are due to the President and Council of the Royal Horticultural Society and the Director of the Laboratory for the opportunities they have given me for pursuing my study on this subject at Wisley.

I am chiefly indebted to Professor J. B. Farmer, F.R.S., and to Mr. A. W. Hill, F.L.S., Assistant Director of the Royal Botanic Gardens, Kew, for the material used. Specimens of *Griselinia lucida* were kindly collected and preserved for the purpose of this investigation by Miss Heywood, in New Zealand, at the request of Dr. O. V. Darbishire; and flowers of *Griselinia littoralis* were contributed by Mr. J. W. Hamilton of Hamwood, Dunboyne, Ireland. For the rare female catkins of *Garrya elliptica*, the author is indebted to Messrs. Veitch, and inflorescences of several rare Caprifoliaceæ were obtained from the Gardens of the Royal Horticultural Society.

2. HAMAMELIDACEÆ.

Since the writer aims at a comparison of origins, considerable importance is attached to details of floral organization, and for this reason special attention is given to variability in the position occupied by the ovary in relation to the remaining floral whorls, to details in the internal structure of the ovary, to the number and structure of the ovules, and to sterilization in the ovary; special interest also attaches to an instance of the transformation of the petals into stamens that he has observed in *Corylopsis* and to the elucidation of the morphology of the bracts found in *Parrotia*, whilst the course of the vascular tissue in the flower has also been traced.

The variability in the position occupied by the ovary in relation to the outer whorls will be considered first. *Distylium* is hypogynous, *Hamamelis* and *Corylopsis* are perigynous, and the perianth and stamens are seated upon a circular ridge of tissue attached to the ovary below mid-height. *Trichocladus* also is perigynous, but the ridge

* A. S. Horne in Proc. Brit. Assoc. Adv. Sci. Portsmouth (1911), p. 585.

is inserted at a higher level. *Eustigma*, from the illustration accompanying Seeman's * "Botany of the Voyage of H.M.S. 'Herald,'" is subepigynous. Thus the ovaries of the above-mentioned genera fall into a complete series varying from a hypogynous to an epigynous structure. *Sycopsis*, as originally noted by D. Oliver †, differs from all the remaining Hamamelidaceæ. Oliver states that the ovary appears to be inferior, owing to the fact that it is surrounded by a closely adpressed tube, which bears at its margin the remaining floral whorls. He remarks that when the tube is laid open by dissection the ovary is clearly superior. Hence *Sycopsis* forms the only other member of a second series, beginning with a *Distylium*-like form in which the perigynous ridge has become specially developed and adpressed to the ovary-wall. Very frequently, organs originally adpressed become congenitally united, so that the step from the structure in *Sycopsis* to a truly epigynous flower is not a great one. *Loropetalum* is epigynous, according to the figures of *Hamamelis chinensis* given by Robert Brown in Abel's ‡ 'Narrative of a Journey to China' and to the published illustration of *Loropetalum chinense* §. The probable origin of the epigynous condition has not yet been investigated. In proceeding to pass in review the structure of the ovary itself, it may be remarked that the Hamamelidaceæ are divided by Niedenzu ‖ into two subfamilies, the Bucklandioideæ (ovaries with pluriovulate loculi) and the Hamamelidoideæ (ovaries with uniovulate loculi)—a method of grouping that corresponds to the one adopted by Endlicher ¶ in 1836. Now the ovary of *Rhodoleia*, a genus of the Bucklandioideæ, is specially noteworthy: that of *R. Championi* is described as bilocular in Walpers's ** 'Annales Botanices Systematicæ' and in Curtis's †† 'Botanical Magazine,' but Bentham ‡‡, in his 'Flora Hongkongensis,' records that it consists of two carpels united at the base into a one-celled ovary with parietal placentæ. Baillon §§ states that the ovary of *Rhodoleia* is either completely or incompletely two-celled, that it is especially incomplete below, where often the placentæ do not even touch; that in the Sumatran species (*R. Teysmannia*) they are more or less fused higher up, but in the Chinese (*R. Championi*) they are only in contact and may be separated without rupture; thus they are really parietal as in so many of the Saxifragineæ. J. G. Boerlage ‖‖, in 'Flora van Nederlandsch Indie,' records that the ovary is bilocular and sometimes unilocular owing to the disappearance of the dissepiment, and, finally, Niedenzu ¶¶ states that it is either

* Seeman, Botany of the Voyage of H.M.S. 'Herald,' Tab. 95.

† D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83; *Sycopsis sinensis* in Hook. Ic. 1931 (1891).

‡ Robert Brown in Abel's 'Narrative of a Journey to China,' fig. 4.

§ In Icon. Select. Horti Thenen. pl. 58. fig. 8.

‖ Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2 (1891) 121.

¶ S. Endlicher, Gen. Pl. (1836–1840) 803.

** In Walpers's 'Annales Botanices Systematicæ,' Tom. iii. 842 (1850–1853).

†† In Curtis's Bot. Mag. vi. Tab. 4509 (1850).

‡‡ Bentham, 'Fl. Hongkongensis,' p. 131 (1861).

§§ H. Baillon, Histoire des Plantes, iii. 393 (1872).

‖‖ J. G. Boerlage, 'Flora van Nederlandsch Indie,' i. Polypetalæ, 454 (1890).

¶¶ Niedenzu, *l. c.* p. 122; fig. 68 (p. 123).

unilocular, completely bilocular, or bilocular in the superior portion only. The above-mentioned descriptions appear to the writer to afford clear evidence that the ovary of *Rhodoleia* is varying in the degree of centripetal development of the placentæ, and in so doing exhibits a tendency to break into different types distinguished by the presence and absence of a septum respectively. The ovaries of the Hamamelidoideæ possess a septum which renders them bilocular.

The ovules in the Bucklandioideæ are arranged in series attached, in unilocular forms of *Rhodoleia*, to parietal placentæ. In *Liquidambar*, according to Shoemaker *, they are developed on marginal placentæ. The writer attaches some importance to the method of placentation in the Hamamelidoideæ. Sargent † states that the ovules in *Hamamelis* are suspended from the septum. Niedenzu ‡ gives a representation of them attached to the septum in *Hamamelis* and *Corylopsis spicata*, but the writer, after a careful examination of several species (notably, *Hamamelis virginica*, *arborea*, and *Zuccariniana*, *Corylopsis spicata*, *Parrotia Jacquemontiana*, and *Fothergilla Gardeni* and *major*), finds that they are not thus attached, but borne upon parietal placentæ that are situated immediately above the septum.

There are some interesting points connected with the number of ovules, and it is possible to arrange certain genera in a series from those in which the ovules are numerous in each loculus to those with uniovulate loculi. Shoemaker § records two series in each loculus of *Liquidambar styraciflua*. Le Maout and Decaisne || note that the ovules of the Hamamelideæ (including *Bucklandia*) are either solitary or numerous, but in the latter case only the lower are fertile, whilst in *Disanthus cercidifolius*, from Baillon's ¶ description, the number of ovules in each series is reduced to three. Reduction reaches an extreme in the Hamamelidoideæ. Here it is generally stated that the ovaries possess uniovulate loculi, although Baillon ** long ago described two instances in which the loculi are, at first, biovulate, but later uniovulate, owing to the arrestment of one of the pair, thus in *Hamamelis virginica*, "Dans l'angle interne de chaque loge, il y a un placenta vers le haut duquel s'insérent un ou deux ovules descendants. Dans ce dernier cas, l'un d'eux s'arrête de bonne heure dans son développement"; and in *Distylium* "Il y a dans chaque loge deux ovules dont un seul prend tout son développement." Le Maout and Decaisne †† even figure a four-seeded fruit of *Hamamelis*. Shoemaker ‡‡ found only one example of an ovary with biovulate carpels in *H. virginiana*, although he examined several hundred flowers and suggests

* D. N. Shoemaker in Bot. Gaz. xxxix. (1905) 262.

† Sargent, Silva of N. Amer. v. (1893) 1.

‡ Niedenzu in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 2 (1891), figs. 65 (*Hamamelis*) and 72 (*Corylopsis spicata*).

§ D. N. Shoemaker, *l. c.* 262.

|| Le Maout and Decaisne, Gen. Syst. Bot. ed. Hook. 410 (1876).

¶ H. Baillon, Histoire des Plantes, iii. 396 (1872).

** H Baillon, *l. c.* 390 (*Hamamelis*); 395 (*Distylium*).

†† Le Maout and Decaisne, *l. c.* 409.

‡‡ D. N. Shoemaker, *l. c.* 251.

that the condition described by Baillon may occur more frequently in places from which he had not obtained material. The writer has hitherto failed to find even traces of a second ovule in *H. virginica*, *Zuccariniana*, and *arborea* (Text-fig. 1, A 3, A 4), but he has observed biovulate loculi in *Fothergilla Gardeni* and *major*, *Corylopsis spicata*, and *Parrotia Jacquemontiana* (Text-fig. 1, C 2). Parallel instances to these occur among the Araliaceæ and Umbelliferæ: thus two ovules suspended from terminal parietal placentæ develop in each loculus of *Aralia* and *Acanthopanax* and, according to Tanfani *, of *Apium*; and one of each pair aborts as it does in the Hamamelidoideæ cited above.

According to Baillon's† description, reduction in the ovary proceeds still further, thus in *Hamamelis* the ovary is sometimes completely sterile:—"Dans un grand nombre de fleurs, le gynécée demeure petit, stérile, on ne renfermant que des rudiment d'ovules"; again, in *Corylopsis*, "Il y a tous les passages quant au gynécée entre des ovaires complètement stériles et vides; et ceux que contiennent des ovules bien constitués, dans les fleurs femelles ou hermaphrodites." Here, in two distinct genera, separation of the sexes is recorded as actually taking place, a feature highly significant when it is remembered that several genera of Hamamelidaceæ possess polygamous flowers and in certain others the flowers are unisexual.

The development of the ovule of *Hamamelis virginiana* and *Liquidambar styraciflua* was described by Shoemaker‡ in 1905, who found a nucellus of considerable bulk invested by two integuments and a parietal layer of cells similar to that formed in the nucellus of the Saxifragaceæ and Rosaceæ. The writer has examined the ovules of *Fothergilla*, *Corylopsis*, and *Parrotia*, and finds that they are constructed like those of *Hamamelis*.

Comparisons have been made from time to time by various writers between the genera of the Hamamelidaceæ and Cornaceæ that are provided with conspicuous involucral bracts. The writer has examined the bracts of *Parrotia*, and finds that they differ morphologically from those of the Cornaceæ. The bracts of *Parrotia* are tripartite, but this character cannot be easily observed, owing to the special development of one or other of the three segments. Since the foliage leaves and the lowermost bracts are stipulate, it appears that the coloured portion of the bract may correspond either to a stipule or the lamina of a leaf, and so differs from the bracts of the exstipulate genera, *Cornus* and *Davidia*.

The disposition and transformations of the stamens furnish other characters of interest from an evolutionary point of view. According to Baillon §, eight stamens are present in *Dicoryphe*, but the four alternipetalous ones are sterile, and again, in *Tetrathyrium subcordatum* and *Corylopsis*, glands occur in the interval between the stamens. Shoemaker ‖ points out that abortive pollen is sometimes developed in the nectaries present in the flowers of *Liquidambar styraciflua*, and he regards these

* E. Tanfani in Nuov. Giorn. Ital. vol. xxiii. (1891) 451–469, t. 4–7.

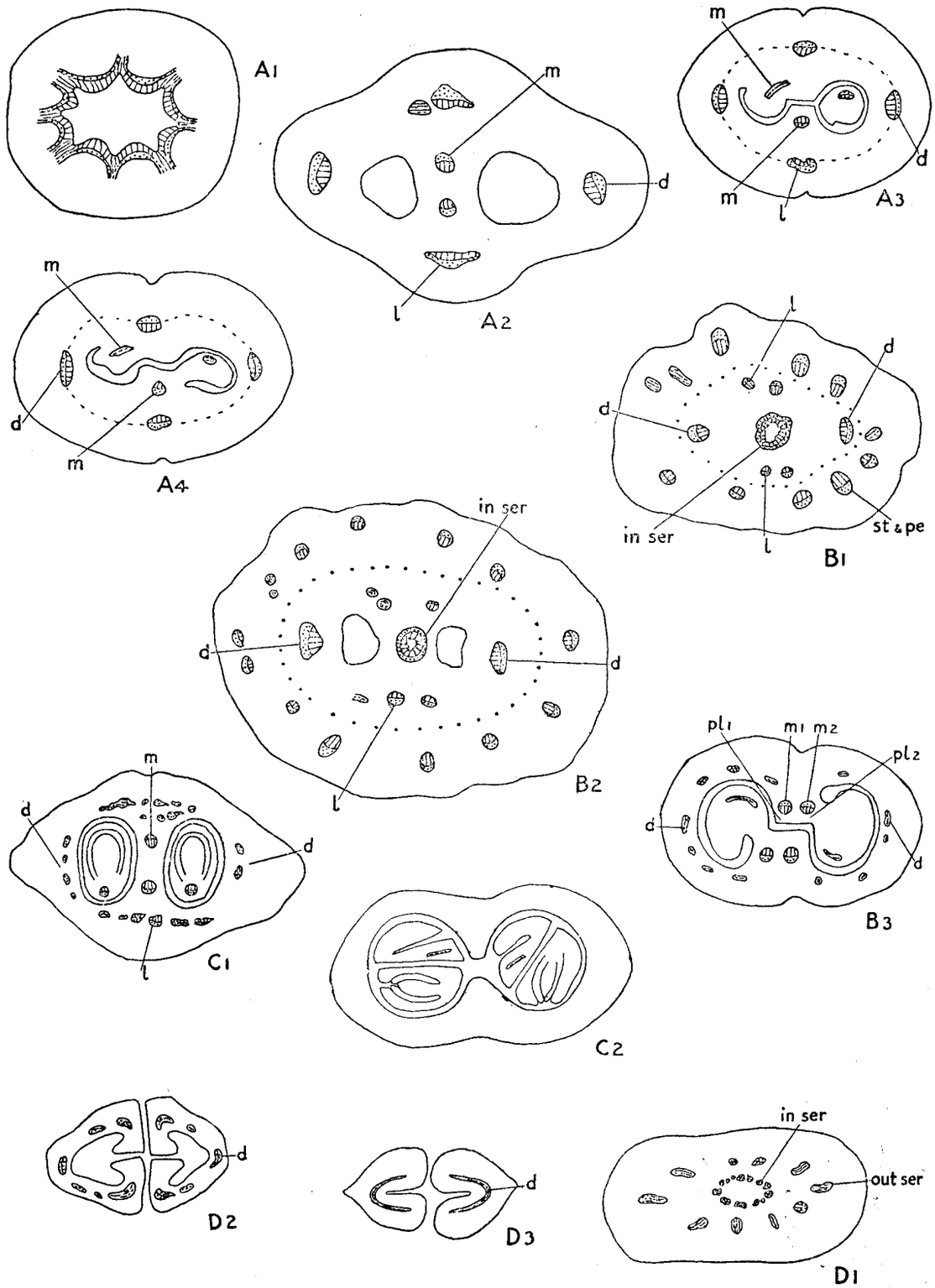
† H. Baillon, Histoire des Plantes, iii. 390 (*Hamamelis*); 391 (*Corylopsis*).

‡ D. N. Shoemaker, in Bot. Gaz. xxxix. (1905) 262.

§ H. Baillon, *l. c.* 392 (*Dicoryphe*); 391 (*Tetrathyrium*).

‖ D. N. Shoemaker, *l. c.* 262.

Text-fig. 1.



Diagrams illustrating the course of the floral vascular tissue in four genera of the Hamamelidaceæ:—A 1, *Hamamelis arborea*; A 2–A 4, *H. Zuccariniana*; B 1–B 3, *Fothergilla major*; C 1, C 2, *Parrotia Jacquemontiana*; D 1–D 3, *Corylopsis spicata*. (Abbreviations, see p. 308.)

nectaries as reduced stamens. Oliver* states that the "didynamous squamæ" in *Eustigma* replace petals. An instance of the transformation of petals into stamens was observed by the writer in flowers of *Corylopsis spicata* gathered from Kew plants in 1909. The normal flowers possess five petals and five stamens. A complete transitional series occurred between the normal and the entirely apetalous flowers. The transitional flowers possessed foliose stamens, each consisting of a broad filament and rudimentary anther lobes. The genus *Fothergilla* possesses a number of stamens arranged in a single verticil. These emerge from a perigynous collar, which surrounds the ovary. The writer finds from seventeen to twenty-two in *F. Gardeni* and *major*. Baillon† investigated the development of the stamens and found that they represent several distinct whorls. Since *Fothergilla* is apetalous, it is possible that the outer whorls are really transformed sepals and petals.

The course of the vascular tissue has been followed in four genera:—*Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia*. The vascular cylinder (Text-fig. 1, A 1) separates, at the base of the ovary, into an outer and an inner series of bundles (D 1). The bundles of the outer series branch just below the level of the insertion of the perigynous ridge of tissue, to form externally the stemonal and perianth traces, *st* and *pe*; and internally the dorsal and lateral carpellary bundles, *d* and *l* (B 1, B 2). The former then leave the ovary. The inner bundles vary in number and disposition in different genera. In *Fothergilla*, two bundles are present in the septum as shown in C 1 (*Parrotia*), and each divides before leaving it to form two, which traverse the corresponding placentæ, B 3. Thus the bundle *m* (C 1) forms *m* 1 and *m* 2, which traverse *pl* 1 and *pl* 2 respectively (B 3). A single branch from *m* 1 supplies an ovule in the left-hand loculus and one from *m* 2 an ovule in the right-hand loculus. But in *Hamamelis Zuccariniana*, where the loculi are uniovulate, only one placenta corresponding to *pl* 1 and *pl* 2 is found, and the septal bundles, *m*, pass into it unbranched (A 3, A 4). In this case, one branch passes to the ovule from the bundle, *m*.

The above-described system is of a similar type to that which is found in the genus *Saxifraga*. It resembles in some details that of *Carpinus betulus*, described by Benson‡ and Welsford.

Summary.

1. A complete series from hypogynous to epigynous forms of flower exists in the Hamamelidaceæ, ranging from *Distylium*, by way of the perigynous genera *Hamamelis*, *Corylopsis*, and *Trichocladus* to *Eustigma*. Another series ranging from a *Distylium*-like form is only represented by *Sycopsis*, a genus which simulates epigyny owing to the fact that the ovary is invested by a closely adpressed perigynous tube. *Loropetalum* is epigynous, but the origin of this condition needs investigation.

2. The genus *Rhodoleia*, according to published descriptions, exhibits variability in the internal structure of the ovary.

* D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83.

† H. Baillon in Adansonia, x. (1871) 127.

‡ Benson and Welsford in Ann. of Bot. xxiii. (1909) 630.

3. The ovules in *Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia* are suspended from *parietal placentæ* that are situated immediately above the septum in each.

4. The Hamamelidaceæ exhibit a complete series in the reduction of the number of ovules, ranging from *Liquidambar*, with numerous ovules in each loculus, by way of *Disanthus*, in which Baillon records three ovules in each series, and *Fothergilla*, *Corylopsis*, and *Parrotia*, with two ovules (one abortive) in each loculus, as in several Araliaceæ and Umbelliferæ, to *Hamamelis*, in which each loculus is uniovulate.

5. According to Baillon, the ovaries of *Hamamelis* and *Corylopsis* are often arrested in development and remain small and sterile. This feature is of special interest, owing to the fact that genera with polygamous and with unisexual flowers are frequent in the Hamamelidaceæ.

6. The ovules of the Hamamelidaceæ possess a bulky nucellus which becomes invested by two integuments and resembles in structure that of the Saxifragaceæ and Rosaceæ.

7. The bracts of *Parrotia* are tripartite and correspond morphologically to a stipulate leaf. One or other of the segments becomes specially developed and conspicuous. Hence the conspicuous portion may be homologous with either a stipule or the lamina of a leaf.

8. A complete series in the metamorphosis of petals into stamens has been observed in *Corylopsis spicata*.

9. The course of the vascular tissue in the flower has been followed in four genera—*Hamamelis*, *Fothergilla*, *Corylopsis*, and *Parrotia*. The same type prevails in them all and is similar to that which is found in *Saxifraga*.

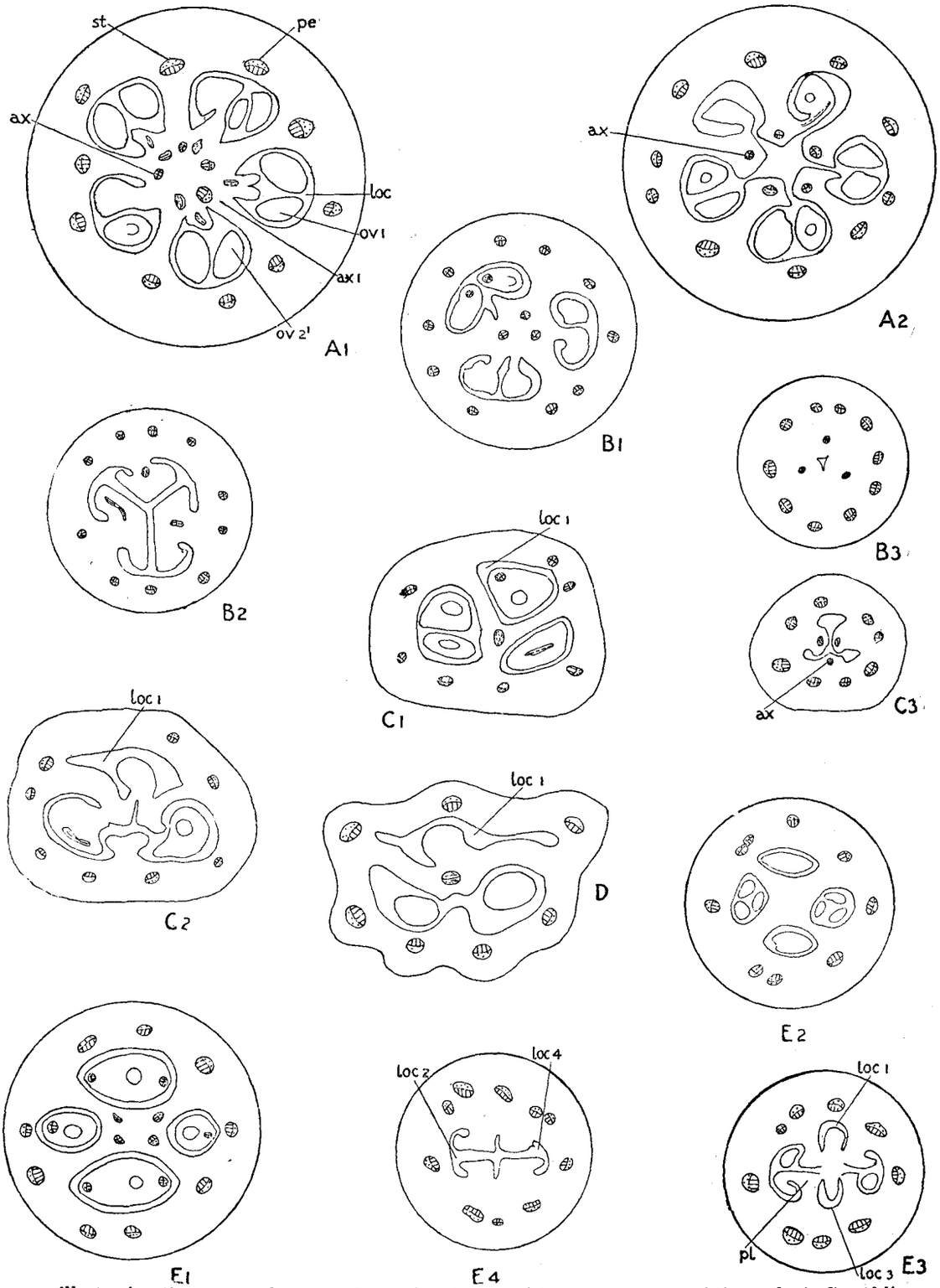
3. CAPRIFOLIACEÆ.

The general details of floral organization in the Caprifoliaceæ are so well known that they need not be recapitulated. Hence the morphology and vascular structure of the ovary and ovule will receive special consideration.

Morphology of the Ovary.

The ovary of *Leycesteria*, the type genus of the family, is five-chambered below, owing to the fact that the margins of the carpels are in this region congenitally united, forming a solid axial portion with radiating septa (Text-fig. 2, A 1), but the margins are free above, so that the accretion is incomplete (A 2). Hence the biseriate ovules are axially or parietally borne according to their situation. The fruit contains many seeds. *Lonicera* possesses a trilocular ovary, which is structurally similar to that of *Leycesteria* (B 1–B 3), but although the ovary is pluriovulate, few seeds are formed. Frequently in *L. Caprifolium* only one seed reaches maturity, the septa being ruptured or pushed aside by the developing seed, which eventually occupies the whole cavity of the ovary. Here the ovary does not undergo structural modification during growth in connection with the habit of producing few seeds. *Abelia* and *Linnæa* also possess trilocular ovaries of the *Leycesteria* type, but in each case one loculus is uniovulate, the ovule being

Text-fig. 2.



Diagrams illustrating the course of the floral vascular tissue and the arrangements of the ovules in Caprifoliaceæ:—A 1, 2, *Leycesteria formosa*; B 1–B 3, *Lonicera Periclymenum*; C 1–C 3, *Linnæa borealis*, *D. Abelia*; E 1–E 4, *Symphoricarpus racemosus* (continued in text-fig. 3).

suspended axially (D, C 1–C 3; *loc* 1). The structural agreement in this respect between *Abelia* and *Linnæa* is so close that it is impossible to distinguish between them. The genus *Dipelta*, established by Maximowicz *, possesses an ovary with two pluriovulate and two uniovulate compartments. Seeds are not formed in the pluriovulate loculi.

Symphoricarpus forms the next member of a remarkable series in which that portion of the ovary corresponding to the superior half in *Leycesteria* fails to develop. The adult flowers of *S. racemosus* are four-chambered below (E 1–E 3), but two-chambered in the very small upper portion, owing to the fact that the upper portion of the lateral carpel is incompletely developed (E 4; *loc* 2, *loc* 4). Each lateral chamber, *loc* 1, *loc* 3, contains a single axially suspended ovule. The loculi at right angles to these are pluriovulate, and the ovules which they contain are arranged in biseriate rows, suspended from the small adpressed parietal placentæ (E 3, *pl*) present in the upper portion of the ovary, with the exception of the lowermost ovule, which is axially borne. Only a single specimen of an entirely pentamerous flower was found; in this case the inferior portion of the ovary was five-chambered and the additional loculus uniovulate.

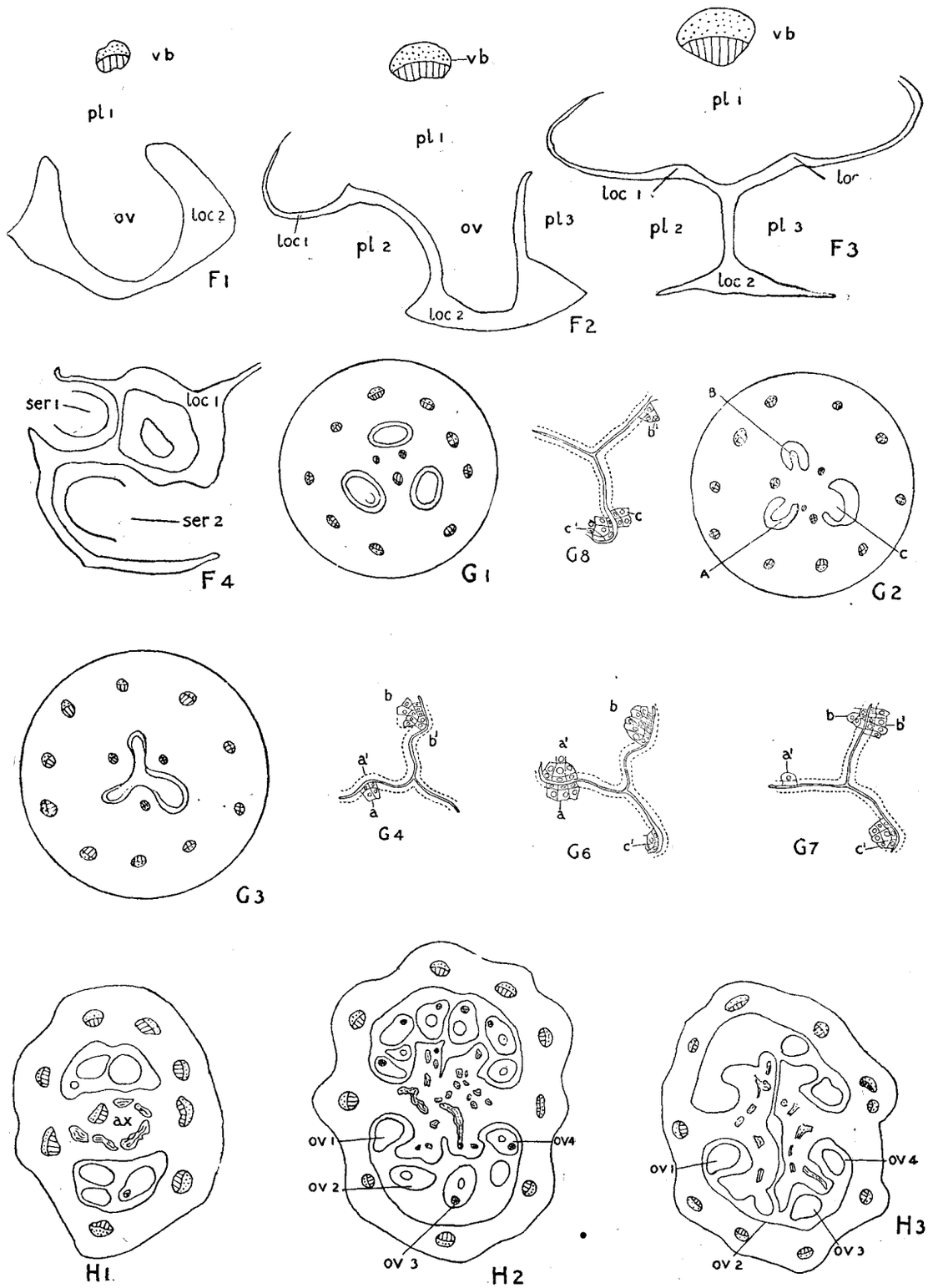
Abortion in the parietal portion of the ovary is carried still further in *Viburnum*, where, if the very young flowers of *V. Lantana* be examined, three united pairs of parietal placentæ may be observed (Text-fig. 3, F 2, F 3; *pl* 1, 2, 3). These are almost in contact with one another, so that they separate three compartments (*loc* 1, 2, 3). During subsequent growth only a single loculus (F 1–F 3; *loc* 2) develops as indicated in Text-fig. 4, leaving two upper arrested compartments (*loc* 1, 3). The latter are pluriovulate as previously recorded by Vidal †, and the ovules in each are arranged in two or more series (Text-fig. 3, F 4; *ser* 1, *ser* 2). At the same time Vidal, who made a special study of the development of the ovary in the Caprifoliaceæ, entirely overlooked the fact that the fertile ovule (F 1, *ov*) does not extend as it normally should do into either of the adjacent compartments (F 1–F 3; *loc* 1, 3), but into the loculus which has developed from the originally opposite compartment (F 1–F 3; *loc* 2). Again, the placentæ (*pl* 2, *pl* 3) do not bear ovules as they normally should do on the sides adjacent to *loc* 2. Finally, the fertile ovule does not actually form a member of the series of sterile ovules that arise from *pl* 1 and extend in *loc* 1 and 3. These features furnish an important clue to the interpretation of the peculiar morphology of *Viburnum*, which will be discussed after the vascular system has been described.

Sambucus forms the extreme member of the series under discussion. The number of loculi in *S. nigra* varies from two to five, but there are usually three. A single terminal axially situated ovule occurs in each loculus (G 2). The area above the ovules, which appears to form a part of the lower tissue region of the style, is in reality an exceedingly rudimentary parietal portion of the ovary, wherein the ovules are reduced to tiny swellings, arranged in short biseriate rows above the normal ovules. Figs. G 4–G 8 show the ovular rudiments arranged in the series *a*, *a'*; *b*, *b'*; and *c*, *c'* above the ovules A, B, and C, respectively (G 2). Hence it appears that the terminal ovules of *Sambucus*

* Maximowicz in Bull. Acad. Imp. Sci. Saint Pétersbourg, xxiv. (1878) 50.

† Vidal in Bull. Soc. de Statistique, Grenoble, 4 sér. t. iv. (1899) 157.

Text-fig. 3.



Floral structure in F 1–F 4, *Viburnum Lantana*; G 1–G 3, *Sambucus nigra*; G 4–G 8, the same, biseriate ovular rudiments; H 1–H 3, *Diervilla Lonicera*. (Abbreviations, see p. 308.)

occupy in the ovary an equivalent morphological position to those of the pluriovulate loculi in *Symphoricarpus*.

In *Diervilla* the portion of the ovary corresponding to the parietal region in *Leycesteria* is specially developed, the axial portion (H 1) being relatively small. Hence the greater number of the ovules are parietally borne. The opposite placentæ are in close contact, so that the ovary is rendered bilocular (H 3). In *Diervilla Lonicera* the ovules in each loculus are multiseriate (H 2, H 3, *ov* 1, 2, 3, 4), but in other species this arrangement is less definite. *Diervilla*, in the adpressed placentæ and multiseriate ovules, differs from all other Caprifoliaceæ.

The Ovule.

Hooker and Thomson * describe the ovule of *Viburnum Tinus* as consisting in its early stages "of a minute curved nucleus encircled with an annulus which is the only integument." This description applies equally well to the Caprifoliaceæ considered in this paper. The nucellus develops more or less obliquely, and is of comparatively small bulk. At maturity the ovules tend to occupy a tangential position in the loculus—that is to say, the nucellus and the vascular bundle of the raphe rest in a plane at right angles to a radial plane. They are not displaced from this position owing to abortion, but in *Symphoricarpus* the lowermost ovule of each biseriate row may be radially situated with the raphe abaxial, not adaxial as in the Araliaceæ.

Vesque in 1878 and Guignard in 1882 record that in *Lonicera* the embryo-sac is produced from a linear row of three cells. The writer finds that the single megaspore-mother-cell in the sterile ovules of *Symphoricarpus*, which are morphologically similar to the fertile ovules, produces not a linear row but a group of megaspores (Pl. 29. figs. 51–54, *m.sp*). Complete embryo-sacs were not observed in the sterile ovules. This suggests that the sterile ovules in *Viburnum* have become structurally modified in consequence of the loss of fertility, and that the raphe, the integument, and the nucellus have become degenerate. The megaspores of the normal ovule of *V. Lantana* are arranged in a linear row, as described by Hofmeister in his memoir of 1858; but the sporogenous tissue of the imperfect ovules originates from one or more subepidermal cells, of which each may produce a group of four cells (Pl. 29. figs. 55-57). Each megaspore, as a result of germination, produces an even number of nuclei, usually four or eight; but it is often difficult to trace them to their respective "megaspores," since the nuclei, from eight to sixteen and even more in number, appear to be situated in a single mass of protoplasm (Pl. 29. figs. 58-60). The energids resulting from the division of the "megaspores" do not become specially modified as in normal embryo-sacs. At the time when the perfect ovule has reached maturity, the energids are grouped to form hollow protoplasmic sacs which subsequently disintegrate.

Progressive reduction reaches an extreme in *Sambucus*. The tissue swellings, which correspond in situation to biseriate rows of ovules as shown in Text-fig. 3, G 4–G 8, are caused by the radial elongation beyond the normal of a small plate of sub-epidermal cells

* Hooker and Thomson, in "Præcursores ad Floram Indicam" (1855), Journ. Linn. Soc., Bot. ii. (1858) 163.

(Pl. 29. fig. 62). At the time of megaspore formation in the ovule each cell of the plate is filled with a finely reticulate cytoplasm and contains a resting nucleus. The nucleus subsequently divides to form two or four daughter nuclei, which are evident during the early stages of endosperm formation in the young seed, but soon disintegrate (Pl. 29. figs. 63, 64).

Course of the Vascular Tissue.

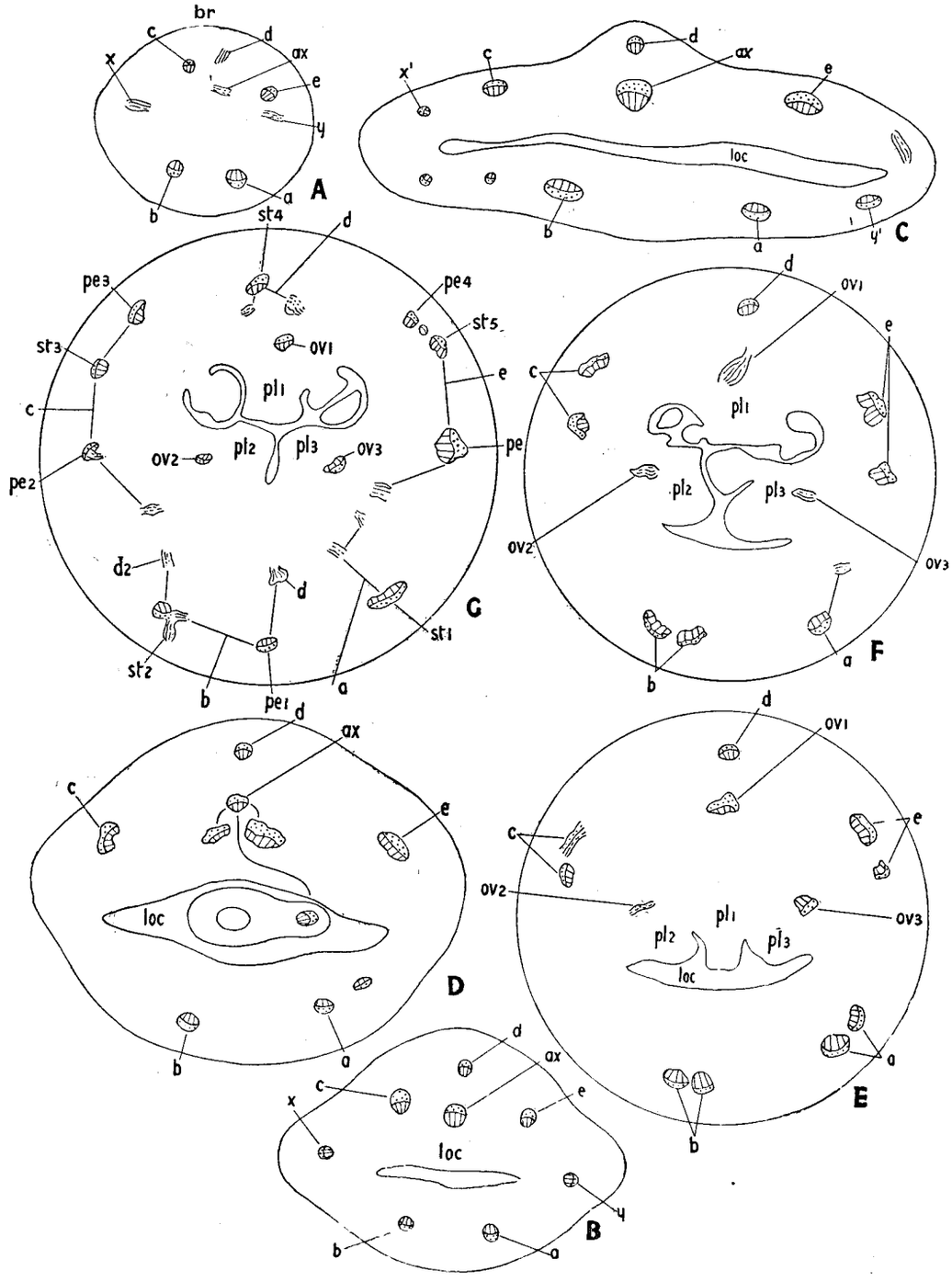
The vascular structure of the flower-stalk of *Leycesteria formosa* separates into an inner or axial (Text-fig. 2, A 1) and an outer or peripheral series of bundles. The bundles of the outer series extend upward in the wall of the ovary—those alternating with the loculi toward the stamens (*st*), those opposite the loculi toward the petals (*pe*)—and emerge from the terminal neck-like portion into the stamens and petals without entering into connection with the axial vascular strands. The presence of a single peripheral series of bundles is a feature which is constant for all the Caprifoliaceæ—in *Aralia* two distinct peripheral series are present, an outer relating to the perianth and stamens, and an inner composed of the dorsal and lateral carpellary bundles. But the number of bundles in the series is not constant: there are ten in *Leycesteria*, being equal to the sum of the petals and stamens; but in *Linnæa* (C 1) and *Diervilla* (Text-fig. 3, H) they are less than the sum, and only one-half the sum in *Viburnum* (Text-fig. 4, B, *a*, *b*, *c*, *d*, *e*).

The inner axial bundles are numerically equal to and alternate with the loculi in *Leycesteria*. They extend axially upward into the parietal placentæ (Text-fig. 2, A 2, *ax*) and finally into the style, where they alternate with the lobes of the stylar canal, as shown in C 3 (*Linnæa*). A similar grouping of the axial bundles obtains in the remaining genera. In *Lonicera*, where the ovary is trilocular, there are three axial bundles (B). In *Sambucus*, where the number of loculi varies from two to five, there is a corresponding variability in the bundles. In *Aralia* the absence of a loculus involves the absence of the corresponding axial and of the inner peripheral ovarian bundles, but in *Sambucus* only the axial bundles vary correspondingly.

Two ranks of ovules occur in each loculus of *Leycesteria*. It follows, therefore, that each axial bundle (such as, for instance, *ax* 1 in A 1) is adjacent to the rows of ovules (*ov* 1, *ov* 2′), the nearer series of each of the adjacent loculi, and receives corresponding series of vascular connections—one series from each row. Each ovule receives only a single bundle. A similar arrangement obtains in relation to the ovules in the pluriovulate loculi of *Symphoricarpus*, but the single ovule in each uniovulate loculus receives two connections, being in this respect the equivalent of a pair of ovules in the adjoining compartments. The vascular structure of the single ovule in *Sambucus* is similar to this.

Special attention has been given to the vascular structure of the flower of *Viburnum*, on account of its peculiar morphology. The floral vascular skeleton has been reconstructed from serial sections in a wax model (Pl. 30). This model will now be described, but the description should be followed with the aid of the diagrams of transverse sections

Text-fig. 4.



Diagrams illustrating the course of the vascular tissue in *Viburnum Lantana*. (Abbreviations, see p. 308.)

in Text-fig. 4. The position of the bracteole is marked *br*. Only five bundles, indicated by the letters *a–e*, extend throughout the ovary-wall. The bundles *a*, *b* are on the side opposite the bracteole, and the remainder on the side adjacent to it (A–D). The bundle *a* is connected with the stamen *st* 1; *b* with the petal *pe* 1 and stamen *st* 2; *c* with *pe* 2, *st* 3, and *pe* 3; *d* with *st* 4; and *e* with *pe* 4, *st* 5, and *pe* 5 (E, F, G). It is evident, therefore, that all the petals and stamens, with the exception of *st* 1, *pe* 1, and *st* 2, are connected with the bundles extending in one side of the ovary-wall—the side bearing the placentæ; so that a special enlargement of one part of the original wall—that opposite the placentæ—seems to have taken place. Besides the principal bundles, two smaller ones, *x* and *y* (B), are present, situated between *b* and *c* and *e* and *a* respectively. These die out upwards after branching and anastomosing with the adjacent principal bundles. Branches are shown at *x'* and *y'* (C). Figure G represents a transverse section of the model at the level *α–β* shown in Pl. **30**. It will be observed that small branches extend inward from the principal bundles just below the point of insertion of the stamens and petals—for instance, the branch *d* from *pe* 1 and *d* 2 from *st* 2. These branches represent the originally free dorsal and lateral carpellary bundles of the primitive flower. Similar branches occur in *Sambucus*, but they are entirely absent in *Leycesteria*, as mentioned above. Within the single series made up of principal and auxiliary bundles (*x*, *y*) there is another bundle, *ax* (A–D), which extends towards the placentæ and divides just below the ovule to form several small strands (D). Some of these collect to form the single ovular bundle. The remainder collect to form three strands, *ov* 1, *ov* 2, and *ov* 3, which extend upwards into the three placentæ, *pl* 1, *pl* 2, and *pl* 3 respectively (E). Thence they extend into the style, where they alternate with the above-mentioned dorsal branches. Hence it is clear that the bundle *ax*, owing to the extension of its branches into the placentæ, does not follow the course normally pursued by a peripheral bundle that relates specially to a parietally-borne ovule, but it is, on the contrary, analogous to the entire axial system of the Caprifoliaceæ with multilocular ovaries (Text-fig. 2). It is, therefore, not unreasonable to suppose that the bundle has been actually displaced from an axial to a peripheral position during the progressive abortion of the now rudimentary compartments. Assuming this to be the case, and taking also into consideration the morphological details already described relating to the ovule itself, together with the facts that rudimentary ovules are sometimes situated immediately above the fertile ovule and that rudimentary ovules do not arise from the placentæ (*pl* 2, *pl* 3) on the side of the fertile loculus, there is not the least doubt that the ovule now parietally situated was originally axially borne, but has suffered displacement concurrently with the displacement of the septa and axially extending vascular tissue. This solution of the morphology of the ovary brings *Viburnum* into line with the remaining Caprifoliaceæ.

Summary.

1. The Caprifoliaceæ show a complete series in the direction of abortion in that part of the ovary corresponding to the parietal portion in *Leycesteria*. The parietal region is rudimentary in the pluriovulate carpels of *Symphoricarpus* and in *Viburnum*. It is

extremely rudimentary in *Sambucus*, and obsolete in the uniovulate loculi of *Symphoricarpus*. The parietal region is also small in *Aralia* and the Hamamelidaceæ.

2. Progressive abortion in the ovary is associated with progressive sterilization. Physiological sterility occurs in *Lonicera* where although the loculi are pluriovulate, only a few seeds are formed in the ovary. The sterility of particular ovules is not pre-determined. In *Symphoricarpus* the ovules of the pluriovulate loculi, which are similar in form to the fertile ovules, are definitely sterile. The megaspores are not arranged in a linear row, as in the fertile ovule, and the embryo-sacs are incomplete. In *Viburnum* the sterile ovules are very imperfect. The integument and raphe are considerably reduced, and the sporogenous tissue develops abnormally. The ovules in *Sambucus* are represented only by a few cells. The Hamamelidaceæ also show stages in reduction in the number of ovules, but the stages are not similar in the two families.

3. The vascular structure of the flower exhibits a definite advance upon that of *Aralia* in the direction of economy. Instead of the double peripheral series of bundles which exists in *Aralia*, only a single series is present. By a further economical advance the peripheral bundles, which in *Leycesteria* are numerically equal to the sum of the petals and stamens, are reduced to one-half the number in *Viburnum*, arriving at a similar phase in the evolution of the vascular system of the flower to that attained by the Compositæ.

4. The Caprifoliaceæ mark an advance upon the typical Araliaceæ in the direction of progressive loss of carpellary autonomy. The styles are united, except in *Sambucus* and *Viburnum*. Again, the synthetic development of the vascular system has led to the disappearance in the body of the ovary of a distinct series of bundles corresponding to the inner peripheral series of dorsal and lateral carpellary bundles that exists in *Aralia*, *Acanthopanax*, and *Hedera*. This series is represented in the superior portion of the ovary of *Sambucus* and *Viburnum* by strands which connect the ovarian bundles with the stylar prolongations of the axial (marginal) bundles. But the connecting strands are absent in *Leycesteria* and *Lonicera*, so that the final traces of the dorsal bundles have disappeared.

5. The ovules of the Caprifoliaceæ are similar in structure, and take up a tangential position in the loculus. This position is unaffected by abortion. In *Symphoricarpus*, however, the lowermost sterile ovule in each pluriovulate loculus is radially situated, the raphe being abaxial.

6. The morphology of the terminal seed in the Caprifoliaceæ is rendered somewhat obscure, owing to abortion and sterilization in the ovary. The seed is axially suspended in *Sambucus*, and is in this respect analogous to the lowermost ovules in the pluriovulate loculi of *Symphoricarpus*. The seed, in *Viburnum*, has through abortion become displaced from the axial position which it originally occupied to a parietal position. Since rudimentary ovules occur immediately above the placental area of the seed, the latter also appears to correspond to the lowermost member of a series, as in *Sambucus*. The seed produced from the single ovule of the uniovulate loculus in *Symphoricarpus* may correspond to the lowermost ovule of the pluriovulate loculi; but, if so, the fact is not evident, since the parietal portion of the uniovulate carpels, perhaps owing to a sudden mutation, has

become entirely obsolete. It is clear that the terminal ovules of the Caprifoliaceæ have not all originated in the same manner, but they are either axially situated or of axial origin, whereas those of the Hamamelidaceæ and of *Aralia*, *Acanthopanax*, and *Hedera* are situated parietally.

7. The vascular structure of the single axially-suspended ovule in the genera with uniovulate loculi is similar to that of a pair of ovules in the pluriovulate loculi—two bundles enter the ovule and join to form one in the raphe. But in *Aralia*, *Acanthopanax*, and *Hedera*, and in the Hamamelidaceæ, where the terminal fertile ovule is parietally suspended, only a single bundle enters the ovule.

8. It is evident that the ovaries of several genera of Caprifoliaceæ have reached their present stage of construction in different ways, and in all probability from more than one prototype. *Leycesteria* and *Diervilla* present strong resemblances—both genera possess a tubular corolla with an irregular limb, the loculi of the ovary are in each case pluriovulate and the fruit polyspermous—nevertheless, the ovaries are structurally different. In *Diervilla* the placentæ are adpressed throughout the greater portion of the ovary; in *Leycesteria* they are congenitally united in the lower portion. Now, according to published descriptions, ovaries of both the above-mentioned types occur in the flower of the species of the Hamamelid, *Rhodoleia*. Hence it is not improbable that the structures obtaining in *Diervilla* and *Leycesteria* originated from prototypic ovaries fluctuating like those of *Rhodoleia* in the degree of centripetal development of the carpels. But it would be unwise to consider the prototypes necessarily identical, since the loculi in *Leycesteria* contain biseriate rows of ovules, whereas those of *Diervilla* may contain multiseriate rows. The latter condition recalls that of *Polyosma*, a genus included among the Saxifragaceæ in Engler's System.

The remaining Lonicereæ, with the exception of *Lonicera* itself and *Triosteum*, possess dimorphic carpels. *Abelia* and *Linnæa* differ in form and habit, but the ovaries are structurally similar; the same is the case with regard to *Symphoricarpus* and *Dipelta*. The ovaries of *Symphoricarpus* and *Triosteum* are structurally dissimilar, and must be regarded as having originated independently from an ovary constructed like that of *Leycesteria*.

The seriate rudimentary ovules of *Viburnum* and the biseriate rudiments present in *Sambucus* indicate that the ovaries in both genera were originally pluriovulate, whilst the structural characteristics of the ovary itself suggest that each has passed through the *Leycesteria* stage of construction. Nevertheless, the Sambuceæ have long been recognized as forming a distinct subsection of the Caprifoliaceæ, distinguished from the Lonicereæ, which possess congenitally united styles and a tubular corolla, by their rotate corolla and free styles. Indeed, Höck established a separate family for *Sambucus*—the Sambucaceæ. Moreover, from a study of the ovary in *Sambucus* and *Viburnum*, it seems clear that the process of abortion has been in each case a different one and dissimilar to the processes that have affected the construction of the ovary of the Lonicereæ. Hence the actual origin of the Sambuceæ remains obscure, and it is by no means certain whether the descent of either *Sambucus* or *Viburnum* could be legitimately traced to prototypic forms of the Lonicereæ.

4. CORNACEÆ.

Nine genera of Cornaceæ have been studied:—*Cornus*, *Marlea*, *Aucuba*, *Garrya*, *Helwingia*, *Corokia*, *Melanophylla*, *Griselinia*, and *Nyssa*.

Each genus is described separately, and the points are taken in the following order:—

Morphology of the flower and ovule.

Vascular structure.

Interpretations and comparisons.

(*a*) Cornus.

Morphology of the Flower and Ovule.

The genus *Cornus* was made the type of a new family, the Corneæ, by De Candolle *, and is characterized by possessing polypetalous, epigynous flowers with an inferior, bilocular ovary (rarely trilocular, according to Bentham and Hooker), surmounted by alternating tetramerous whorls of sepals, petals, and stamens. The genus *Benthamia*, established by Lindley † in 1833, which produces flowers of the *Cornus* type grouped to form a globular capitulum, is now regarded as a subgenus of *Cornus*, since the kind of inflorescence no longer forms a distinctive character.

The writer has devoted special attention to the following points:—Variability in the ovary, the structure of the style, the insertion of the ovules, and the structure of the nucellus.

The flowers of several species of *Cornus*, including *C. mas*, *C. sanguinea*, *C. Amomum*, *C. alba*, have been examined, but the ovaries have proved to be bilocular without exception. Benjamin Clarke ‡, however, records that he found several loculi in cultivated specimens of *C. sanguinea*. Thus he states:—"I have found, when cultivated in a nursery, the number of petals and stamens frequently increased to five, six, seven, or more—the greatest increase observed being eight petals and ten stamens, the ovary of the flower being four-celled; the carpels, however, sometimes increased to seven without any further increase of the petals and stamens."

The ovary of *Cornus*, which is terminated by a single style, might not be strictly bicarpellary, for several instances have been recorded in other families where the loculi and the styles present in the ovary belong to different carpels. Or, again, the style might be composed of the styles of four carpels. Now the structure of the style in *C. mas* does not afford a clue as to its composition. The stylar canal is ribbon-shaped and opens out eventually into the loculi. Clarke, however, observed important structural peculiarities in the styles of *C. alba* and *C. sanguinea*. He found that the canal in the upper part of the style is four-lobed—the lobes

* De Candolle, Prodromus, iv. 271.

† J. Lindley in Bot. Reg. t. 1579.

‡ B. Clarke in Hooker's Kew Journ. Bot. ii. (1850) 130.

alternating with the four-rayed stigma. This fact led to the expectation that either two or four units enter into the composition of the style. He then discovered that the lobes of the canal in *C. alba* and *C. sanguinea* are not orientated alike, being situated, in the latter species, opposite stamens instead of petals. In both species, the lobed canal passes into a ribbon-shaped canal, which is homologous with that in *C. mas*. Clarke's observations led him to the conclusion that the style is composed of the styles of two carpels, that two of the canal lobes are marginal and two sutural, and that the anomalous orientation in *C. sanguinea* is due to the imbricate disposition of the congenitally united styles. The writer's observations are in complete accord with those made by Clarke. Clarke also found in the case of a flower with a trilocular ovary that the number of canal lobes was increased by two—one marginal and one sutural—for each additional loculus.

The development of the ovary takes place in the manner described by Payer *—the projection is first of all flask-shaped; later, a basal ridge develops which divides the single cavity into two. The ovules arise from this ridge or septum, one on either side. The ovular mamelon grows downwards. During the downward growth the nucellus differentiates at the tip and is first directed towards the septum; later, it bends away from the septum, and turns obliquely upwards so that it assumes a tangential position. At the same time it is invested by a single integument.

The development of the ovular mamelon and differentiation of the nucellus were observed in *C. alba* and *sanguinea*. The structure of the young nucellus is shown in Pl. 29. fig. 67. Pl. 29. fig. 65 represents a vertical section through the ovule of *Benthamia*, in which the nucellus and an early stage in the growth of the single integument are evident. The nucellus resembles a sporangium, since the archesporial cells are much alike, but the sporangial appearance is partly due to viewing the nucellus in an oblique plane, for in fig. 66 (*Benthamia*) and fig. 67 (*C. sanguinea*) the cells are clearly arranged in rows and, in the latter case, one row (*ax*) is more noticeable than the rest. A complete series of preparations leading up to the fully-formed embryo-sac has not been obtained. The embryo-sac, however, appears to be formed in the normal manner from one cell of a row of four. A formation of parietal tissue has not been observed.

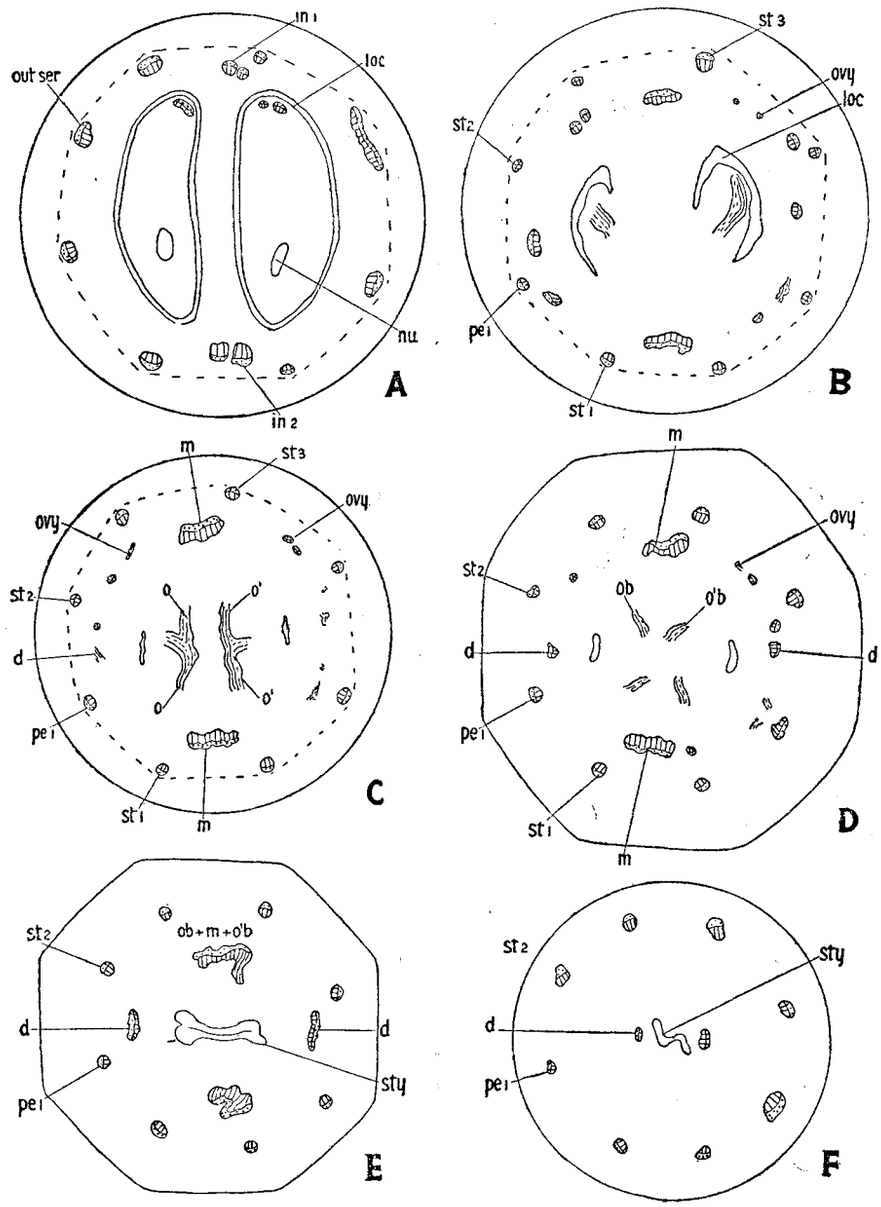
Vascular Structure.

The vascular tissue of the pedicel, in mature flowers of *C. sanguinea*, separates into an outer series (*out ser*) of eight and two inner bundles (*in*), all of which traverse the wall of the ovary (Text-fig. 5, A). Of the outer series, alternate bundles (*st*) extend towards the stamens and the remainder (*pe*) towards the petals B–F. Small inner branches, *ovy* (B, C), arise from the outer bundles before the latter emerge from the ovary—of which some unite to form the "dorsal" bundles, *d* (E, F), present in the style. The bundles *st* 1 and *st* 3 (A, B) opposite the inner bundles (*in*) do not branch.

* J. B. Payer, Traité d'organogénie comparée de la fleur (1854–1857), 418.

The inner bundles (*in* 1, *in* 2) are situated one at each end of the septum. Each divides into three (C, *o*, *m*, *o'*), the opposite lateral branches (*o*) unite and extend towards

Text-fig. 5.



Diagrams illustrating the course of the vascular tissue in *Cornus sanguinea*. (For abbreviations see p. 308.)

ovules on either side. The median branches (*m*) are joined by small branches; *o b* and *o' b* from *o* and *o'* respectively (D) pass into the style, one on each side of the canal (E), but soon die out, leaving only "dorsal" bundles present there (F).

Comparison with the Caprifoliaceæ and Hamamelidaceæ.

Kunth *, influenced by the resemblance between *Cornus* and *Viburnum*, placed the Corneæ, typified by *Cornus*, in the Caprifoliaceæ. But the Corneæ were soon afterwards separated from the latter to form a new family, the Corneæ (De Candolle †, Endlicher ‡) or Cornaceæ (Lindley §). Lindley considered that their habit and general characters, and especially their polypetaly, justified this removal. Bentham and Hooker note that the polypetalous condition is the only real distinctive character. It is, in the writer's opinion, a valuable one, for the Caprifoliaceæ are definitely gamopetalous, notwithstanding the fact that the corolla is highly variable in different genera.

In variance with Kunth, Lindley and Oliver ‖ are of opinion that the Corneæ more nearly approach the Hamamelidaceæ. Oliver considers even that the latter family may not improbably be regarded as a section of the former. Oliver is guided by general morphological resemblances, such as arrangement of the leaves, the form of inflorescence (capitate in *Benthamia* and *Nyssa capitata*), disposition of the stamens, the "inferior, bicarpellary and bilocular ovary," the ovules solitary and pendulous, etc. But the facts regarding the embryology of the Hamamelidaceæ revealed in Shoemaker's ¶ paper on *Hamamelis*, and those deduced from the study of the ovule in the Cornaceæ, are against the approximation of these families: in the Hamamelidaceæ, the nucellus is bulky, it is invested by two integuments and an extensive parietal tissue is formed, as in the Saxifragaceæ; whereas, in *Cornus*, the nucellus is small, without or with very little parietal tissue and invested by a single integument.

The writer finds a close correspondence in the floral organization between *Cornus* and the Sambuceæ, and *Cornus* and *Sambucus* may be profitably compared. The whorls in *S. canadensis* are pentamerous, those in *Cornus* tetramerous with the exception of the ovary. In both genera, the loculi are uniovulate, the ovules terminal, axially borne and tangentially orientated; the nucellus is very similar and invested by a single integument: with regard to the vascular structure, a single series of bundles is present in the ovary, dorsal branches pass into the style, and the vascular connections of the ovule are similar. Now the variability in the number of units contributing to the ovary in *Sambucus* is accompanied by a corresponding variability in the number of loculi, axial bundles, and styles, and the writer has expressed the opinion that the dorsal portions of the carpels have become definitely incorporated as an integral and invariable portion of the ovary-wall. Hence the ovary is not strictly bi-, tri-, or quadri-carpellary in bi-, tri-, or quadrilocular ovaries. Passing to *Cornus*, the presence of an additional unit, as shown by Clarke, is asserted by the appearance of an extra loculus, a peripheral ovular bundle and two additional lobes to the stylar canal, the structure of the ovary-wall remaining unchanged, as in *Sambucus*; so that it does not seem unreasonable to interpret the organization in terms of that of *Sambucus*, nor to consider the ovary bicarpellary

* Kunth, Nov. Gen. et Sp. iii. 430.

† A. de Candolle, Prodr. iv. 271.

‡ S. Endlicher, Gen. Pl. (1836) 798.

§ J. Lindley, Veg. King. 2nd ed. (1847) 782.

‖ D. Oliver in Trans. Linn. Soc., Bot. xxiii. (1860) 83.

¶ D. N. Shoemaker in Bot. Gaz. xxxix, (1905) 262.

by reduction from a quadricarpellary form, just as the ovary of *Sambucus nigra* may be considered bi-, tri-, or quadricarpellary by reduction from the symmetrical condition in *S. canadensis*. In the Hamamelidaceæ, the ovary is bicarpellary in the hypogynous state, and the bicarpellary condition is constant along the line of advance pursued by the flower in this family in the direction of epigyny.

If sympetaly does indeed constitute a real barrier between *Cornus* and the Sambuceæ, one is struck by the parallelism evident in the construction of the ovary, lessened only a little in importance by the occurrence of ovular rudiments and free styles in *Sambucus*.

(*b*) Marlea and Alangium.

Morphology of the Flower and Ovule.

The flowers of *Marlea* are hermaphrodite, and consist of an inferior ovary surmounted by isomerous whorls of from four to eight sepals, petals, and stamens—usually six, according to Clarke *, in *M. begonifolia*, seven in flowers of *M. platanifolia* growing at Kew, in 1910.

The flowers of *Alangium* resemble those of *Marlea*, except that the stamens may be equal to, or twice or four times as many as the petals. The ovary is unilocular.

The ovary of *Marlea*, according to Bentham and Hooker †, may contain from one to three loculi, or it may be unilocular in the upper and trilocular in the lower portion. Wangerin ‡ states that it consists of two carpels and may be either uni- or bilocular; he records a second smaller sterile loculus in *M. barbatum*. The writer has found only one-celled ovaries in *M. platanifolia*. Clarke § recorded an occasional increase in the number of carpels in *M. begonifolia* when growing under confined circumstances, "in one instance there were two additional imperfect cells separating the original cell and in another three fully formed fertile carpels." The ovary of *Marlea* terminates in a single style. The canal and the stigma are four-lobed in *M. begonifolia*, leading to the expectation that the style is made up of two or four units. Clarke compared the style with that of *Cornus alba* and interpreted it accordingly.

Bentham ‖ and Hooker state that the ovules are suspended from a central column in *Marlea*—that is, axially. Clarke's ¶ original figures of *M. begonifolia* confirm this statement.

The ovular mamelon, in the very young flower of *M. platanifolia*, almost entirely occupies the exceedingly small loculus. The mamelon grows downwards and the nucellus develops from it obliquely. The mature ovule is tangentially orientated in multilocular ovaries of *M. begonifolia*, from Clarke's ** figures. Harms and Wangerin

* B. Clarke in Hook. Kew Journ. Bot. ii. (1850) 131.

† Bentham et Hooker, Gen. Pl. i. pt. iii. 949.

‡ W. Wangerin in Das Pflanzenreich, 41 Heft, Alangiaceæ, 1.

‖ Bentham et Hooker, Gen. Pl. ii. 949.

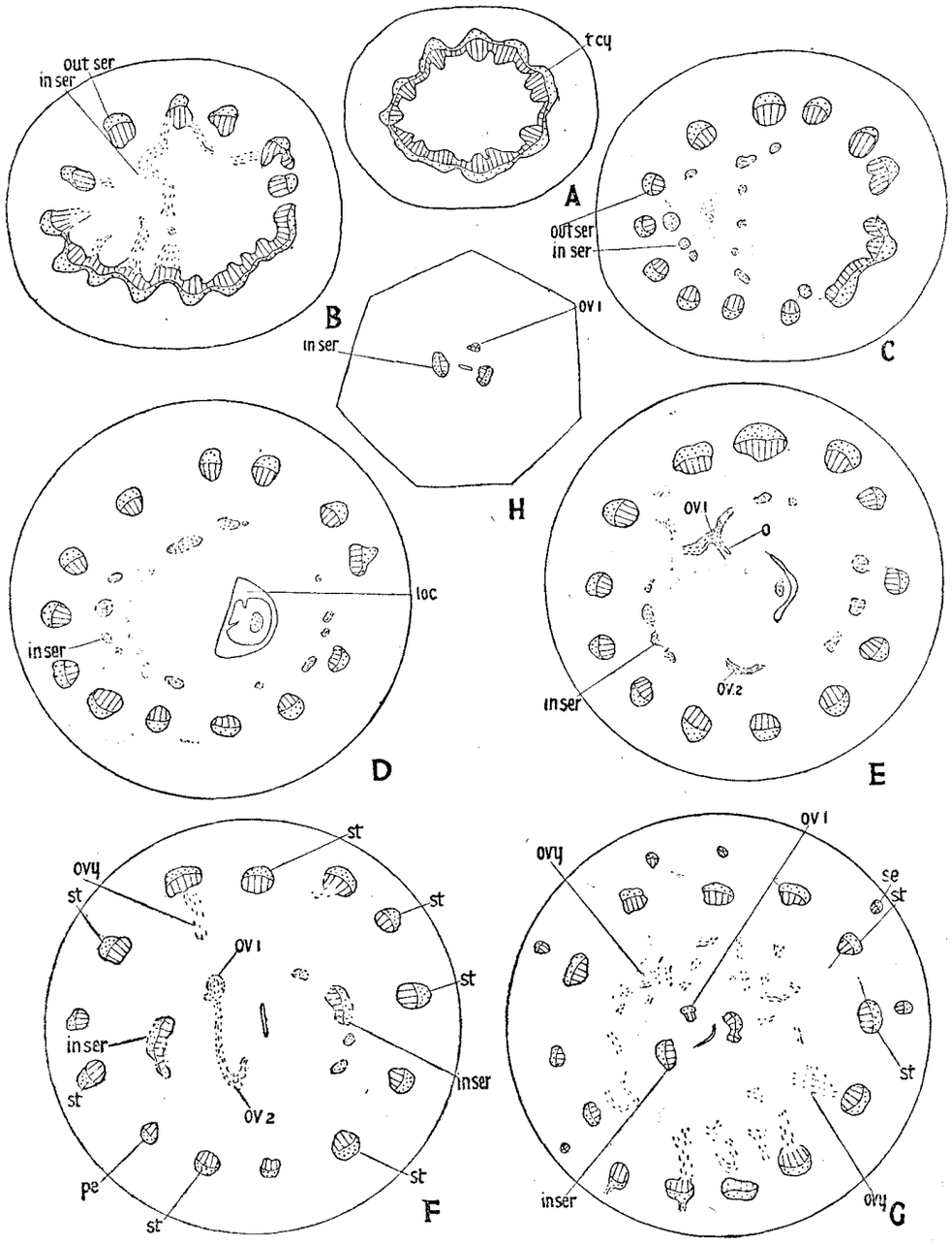
** B. Clarke, *l. c.* pl. 5. A. figs. 8, 9.

§ B. Clarke, *l. c.* 130.

¶ B. Clarke, *l. c.* pl. 5. A. figs. 2, 8, 9.

state that two integuments are present and two are figured in 'Die Pflanzenfamilien' and 'Das Pflanzenreich' respectively. The writer has only observed the primordium

Text-fig. 6.



Diagrams showing the course of the vascular tissue in *Marlea platanifolia*. (For abbreviations see p. 308.)

of one integument, but the question cannot be definitely settled until slightly older flowers have been examined.

Vascular Structure.

The sections examined were obtained from very young flowers. The following description relates to the series through the oldest flower obtained prior to the upgrowth of the integument.

The toral vascular cylinder separates to form an outer series of fourteen bundles, which extend upward in the ovary-wall toward the petals and stamens (Text-fig. 6, A–G, *st* and *pe*), and an inner series of fine strands (B–E, *in ser*).

The bundles of the outer series branch before leaving the ovary to form series of inwardly extending strands (G, *ovy*). The latter behave in an irregular manner, but could not be traced into the style, and clearly correspond to the middle ring of bundles—equivalent to dorsal and lateral carpellary bundles—present in *Davidia*.

The bundles of the inner series are feebly differentiated, and extend as far as the point of insertion of the ovule (E, *in ser*): some originate directly from the toral cylinder (B, *in ser*), passing internally as far as the axis of the flower, then outward and upward in the ovary-wall; the rest arise from the outer bundles at a higher level (C, D).

The connection with the ovule could not be definitely settled. A small branch, *o*, could be traced from *ov* 1 (E), so that it is possible that branches from *ov* 1 and *ov* 2 unite to form the ovular bundle. Higher up in the series (F) the bundles *ov* 1 and *ov* 2 are still evident and *ov* 1 is present in the style (H). The remaining bundles of this series aggregate into two (F) which extend into the style (H). The bundles of the inner series are clearly concerned with supplying the ovule with nutriment, and appear to correspond with the innermost or septal bundles of *Davidia*. Clarke's * view of the bicarpellary condition of *Marlea* partly depended upon tracing the dorsal ribs of the carpels into the style, but it is now evident that the so-called dorsal ribs are merely collections of small ovular strands.

The axial extension of certain branches of the inner series at the base of the single loculus in *M. platanifolia* is curious, but *M. begonifolia* is often bilocular, and it is not improbable that the branches which are infralocular in *M. platanifolia* pursue a septal or axial course in bilocular forms of *M. begonifolia*.

Nature and Origin of the Flower.

The position of *Alangium* and *Marlea*, in the systems of different authorities, oscillates between the Combretaceæ and Cornaceæ. De Candolle †, who was followed by Lindley ‡, and for a time by Endlicher §, established these genera in a separate family, the Alangieæ, on the Combretacean side—an arrangement that, at the time, seemed consistent with the occurrence of multiseriate stamens and a unilocular ovary in both the Alangieæ and Combretaceæ.

* B. Clarke in Hook. Kew Journ. ii. (1850) 129.

† A. P. De Candolle, Prodr. iii. 203.

‡ J. Lindley, Veg. King. 2nd ed. 719 (1847).

§ S. Endlicher, Gen. Pl. 1184.

Baillon *, who was undoubtedly influenced by his researches † on the organogeny of the flower in the Amentiferæ, postulated a closer affinity. He had discovered that the ovary in *Quercus*, *Betula*, and *Castanea*, which is at first unilocular, becomes ultimately multilocular, owing to the slow inward or centripetal growth of the parietal placentæ, and compared the development of the ovary in *Castanea* with that in *Terminalia*, a genus of Combretaceæ. Moreover, Payer ‡, in describing the growth of the terminal placentæ in the latter family, had already demonstrated their parietal and centripetal nature. Baillon, accordingly and not unwisely, conceived the origin of the bilocular ovary in *Marlea* from the unilocular *Alangium*, supposing that the tendency towards centripetal development exhibited by the Combretaceæ had advanced further in *Alangium* and *Marlea*. He then inferred that a close affinity existed between the Combretaceæ and the Alangieæ, and literally swept the Alangieæ into the Combretaceæ.

Endlicher §, in 1847, discarded the idea of Combretacean affinity and transferred the Alangieæ to the Cornaceæ. Clarke ‖, in 1850, from his comparative study of *Marlea* and *Cornus*, advocated a very close affinity with the latter genus, stating that there is but little left to distinguish the Alangieæ and Cornaceæ. The view of Cornacean affinity held almost general acceptance until the advent of Wangerin's paper ¶; with this, the balance again inclines to the Combretaceæ. Engler at first accepted the opinions of Harms **, but later †† brings the Alangiaceæ into juxtaposition with the Nyssaceæ between the Rhizophoraceæ and Combretaceæ in the Myrtifloræ.

The facts accruing from this investigation do not, in the writer's opinion, favour one side more than the other. Baillon's hypothesis is plainly untenable for the following reasons:—Only one placenta is present in the ovary when unilocular, not two; the ovary-wall is much thicker on one side than on the other, leading to the expectation that a loculus has failed to develop; and, finally, the infra-locular vascular tissue, under the circumstances already discussed by the writer, suggests an originally axial or septal extension. The evidence, on the contrary, shows conclusively that the ovary is reduced.

Although *Marlea* agrees with *Cornus* in the placentation and orientation of the ovule, the resemblance between them is less close than Clarke supposed, and even the styles possess distinctive characters; the vascular systems, too, are dissimilar.

A thorough comparison cannot be made until the structure of the ovule and nucellus in *Marlea* is better understood.

* H. Baillon in Adansonia, xii. (Castaneacées), 1-20.

† H. Baillon in Adansonia, xi. (Corylées), 163.

‡ J. B. Payer, Traité d'organogénie comparée de la fleur (1854-1857).

§ S. Endlicher, Gen. Suppl. iv. part iii. 17 (1847).

‖ B. Clarke in Hook. Kew Journ. ii. (1850) 132.

¶ W. Wangerin in Das Pflanzenreich, 41 Heft, 6 (1910).

** Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8.

†† A. Engler, Syll. der Pfl. ed. VI. 179 (1909).

(*c*) Aucuba.

Morphology of the Flower and Ovule.

The plants are unisexual, and the bracteate flowers are borne in compound cymose racemes with branches arranged decussately. The female inflorescence bears a number of minute rudimentary, as well as perfect flowers. The male flower consists of alternating tetramerous whorls of sepals, petals, and stamens, the female of a unilocular ovary with alternating epigynous tetramerous whorls of sepals and petals. A few hermaphrodite flowers bearing two or three stamens were found on the female plants of *A. himalaica* growing at Kew in 1910. The ovary terminates in a style with an oblique stigma, which points towards the placental side of the ovary. Payer and Eichler state that the placenta is directed away from the bract; Baillon, that it may be directed away from the bract, towards it, or laterally; the writer finds that it may occupy any one of the four antepetalous or alternipetalous positions. Hence the orientation of the ovary relative to the perianth is variable. The development of the flower has been accurately described by Payer—its primordium resembles an incomplete circular ridge (this becomes circular with an oblique opening); as growth proceeds, the mamelon becomes ovoid enclosing a cavity—the loculus,—and the narrow orifice forms eventually the slit-shaped stylar canal. The placenta, which is terminal and bilobed in transverse sections of mature ovaries, arises as a well-defined bulge from the ovary-wall. The single descending ovule develops at the end of this protuberance. The ovaries are very rarely biovulate. One biovulate ovary was found in *A. japonica*—the additional ovule developed from a placenta on the opposite wall of the loculus, but the ovary remained unilocular; the stigma was unequally bilobed. Two out of twenty ovaries were biovulate in *A. himalaica*; the stigmas were irregularly lobed—perhaps an abnormal feature, since a capitate stigma is figured in Hooker's * illustrations of this species.

The earliest stages in the development of the ovule, prior to the differentiation of the nucellus, are shown, in vertical section, in Text-fig. 13, F, G. The pivot-cells at the point where the mamelon bends away from the ovary-wall are indicated at *p*. In G the portion of the mamelon below the pivot-cells shown in F has elongated considerably, owing to cell-division, and three regions of special merismatic activity are to be observed. The lowermost of these is localised at *un int*, which is the primordium of the lower rim of the integument; the next is confined to the primordium of the nucellus, *nu*; the third and uppermost, *up int*, extends from the upper edge of the nucellus to the pivot-cells on the adplacental side of the ovule. Here the cells are providing for horizontal extension. The next stage (D) shows the ovule after considerable growth has taken place; the chalazal region is now clearly defined and the nucellus has turned through an angle of 45°. This has been accomplished by the longitudinal elongation of the abplacental (*ab*) end of the ovule during chalazal differentiation, whilst the adplacental (*ad*) side has undergone less longitudinal, but

* J. D. Hooker, Illustr. Himal. Plants, 12.

more horizontal, extension. The under-margin of the integument has now enclosed and extended beyond the lower end of the nucellus, and its upper concave end forms the floor of the micropyle. The upper portion of the integument, which Baillon styles an obturator, is of considerable bulk and of an unusual type. It invests the upper surface of the nucellus and forms the roof of the micropyle. It consists of cells arranged in curved rows (*intr*), clearly shown in D, E, that have originated from the short rows shown in G. This curvature is due to the growth-changes, which cause the rotation of the nucellus. The nucellus is entirely free from the integument. Subsequent growth-changes place the axis of the nucellus towards the vertical, and are more concerned with the development of the lower portion of the ovule.

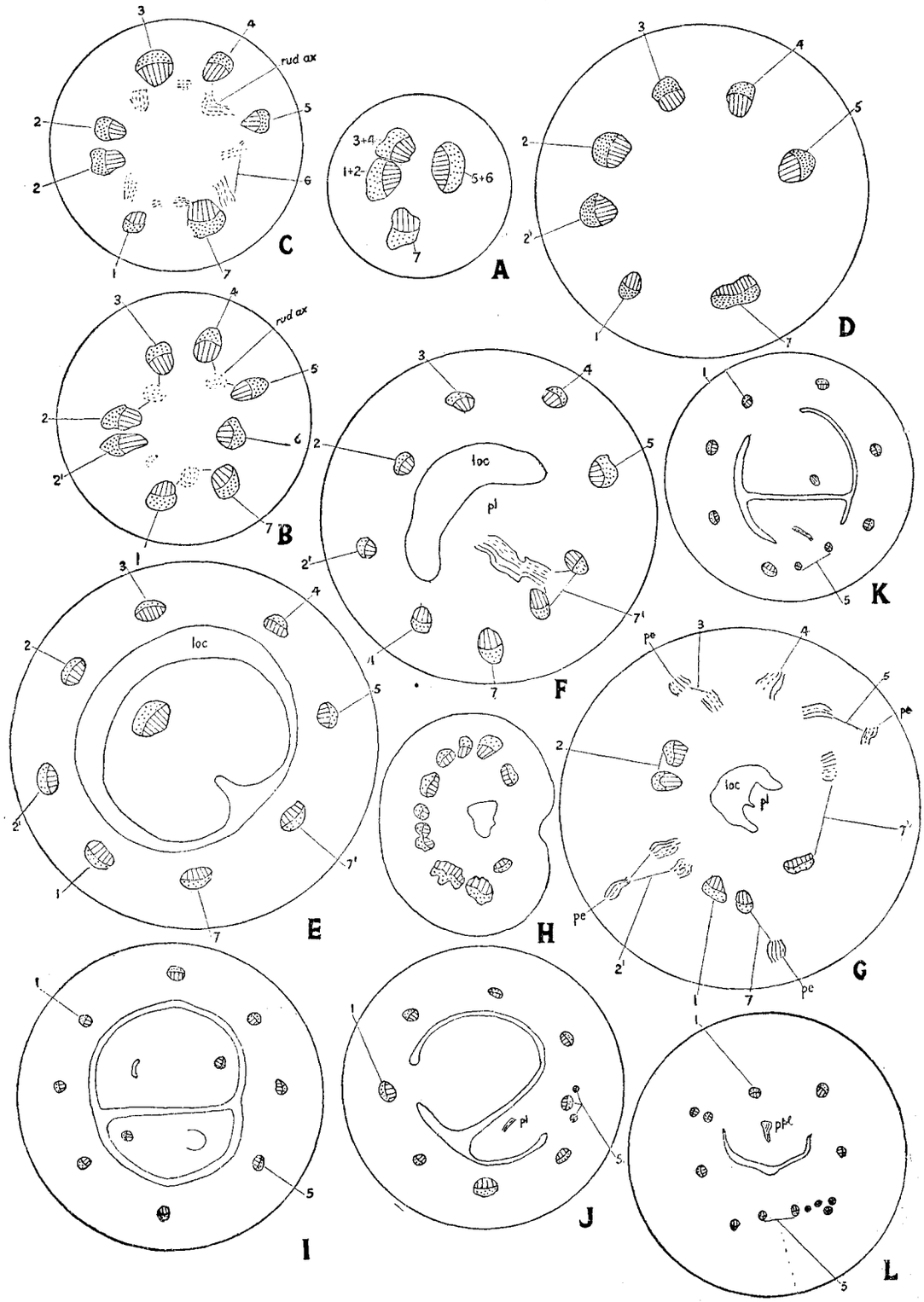
A complete series of stages in the development of the nucellus has been obtained. When the ovule has reached the stage shown in G, the nucellus already consists of several short axial rows of cells. From Pl. 29, fig. 69 it is evident that the primary archesporial cells have divided to form primary parietal and sporogenous cells. In one row further divisions have ensued, resulting in the formation of three parietal and two sporogenous cells. The next stage was obtained in *A. himalaica*, where a linear row of four megaspores and a definite layer of parietal tissue had been formed. The embryo-sac, in the case shown in fig. 70 (*A. japonica*), will evidently be formed from the lowermost member of the linear row, being relatively deep-seated. Sometimes more than one megaspore prepares to germinate, as in fig. 71 (*A. japonica*), megaspores of adjacent rows; and in fig. 72 (*A. himalaica*) a second megaspore is situated near the embryo-sac, which, in this case, appears to be the third cell of the row. During the formation of the megaspores, the nucellus increases in bulk by division of the cells forming the axial rows. The epidermal cells also undergo division (fig. 70). The embryo-sac develops in the normal manner.

Vascular Structure.

A reconstruction of the vascular system of the flower of *A. japonica* was made in wax from serial transverse sections of a particular flower. The vascular system of this flower will now be described, and can be best followed by diagrams of transverse sections (Text-fig. 7). Three bundles of different sizes are present in the pedicel (A): of these the largest (A, 1, 2, 3, 4) divides first to form two and ultimately five bundles (B, 1, 2′, 2, 3, 4); another (A, 5–6) divides once—one branch forms a principal bundle (B, 5), the other (B, 6) extends towards the axis a little and divides into two small branches (C), which extend outward again and join the principal bundles (C, 5, 7) on either side; the third (A, 7) forms two principal bundles (D, E, 7, 7′). Rudimentary axial branches are formed from the other bundles evident in the pedicel (B, C, *rud. ax.*)

The principal bundles extend as far as the point of insertion of the ovule without branching (F), and then each divides to form two or three smaller branches (G); four of these leave the ovary—one to each petal (G, *pe*),—the remainder form first an arc-shaped group (H) and higher up a single bundle in the style.

Text-fig. 7.



Diagrams showing the course of the vascular tissue in the female flower of *Aucuba*; A–H, uniovulate ovary; I–L, biovulate ovary. (For abbreviations see p. 308.)

The ovular bundle is directly connected with a principal bundle; and the latter divides into three, of which the median extends into the ovule (F). In another flower, branches from the adjacent principal bundles unite to form the ovular bundle.

The diagrams I, J, K, L are drawn from sections of a biovulate ovary. The ovular bundles originate from the principal bundles 1 and 5 (I, J).

The Nature and Origin of the Flower.

Aucuba was first of all placed among the "genera Corneis affinia" of Endlicher's System *, but later included among the Corneæ †, under a subfamily, the Aucubeæ. It has remained closely associated with *Cornus* in subsequent systems.

Diverse interpretations have been made of the nature and origin of the unilocular ovary. Baillon ‡ argued the probable derivation of the ovary of *Cornus* (bilocular) from that of *Aucuba* by the centripetal ingrowth of parietal placentæ, pointing out that the ovary of *Garrya* formed a connecting-link between the two. This argument would imply that the ovary is polymerous, consisting of carpels united by their margins.

According to Eichler §, on the other hand, the ovary is monomerous. Wangerin ‖ considers it to be monomerous by reduction:—"Der underständige Fruchtknoten wird hier von einen einzigen Karpellblatt gebildet" and "*Cornus* bildet das Zentrum dieser Gruppe, von dem sich *Aucuba* hinsichtlich der Reduktion in Gynæciums am weitesten entfernt."

Now the ovary of *Aucuba* could be easily synthesized from carpels which become united by their margins, and, if this were so, Baillon's hypothesis would carry weight, since the carpels retain the potentiality for centripetal ingrowth. But the vascular evidence at present turns the scale in favour of a different explanation. The rudimentary branches at the base of the loculus recall the similarly situated infra-locular branches in *Marlea platanifolia*. It was suggested in this case that the infra-locular branches extend as axial or septal bundles in septate forms of *Marlea begonifolia*. Hence, in the case of *Aucuba*, it seems not unreasonable to suppose that the curious infra-locular rudiments represent an axial or septal system that existed in the primitive flower. If this were so, the ovary was probably quadrilocular and hence tetramerous. The primitive ovary of *Aucuba* may be likened to that of *Viburnum*, the effect brought about by abortion, however, being different in the two cases. It was deduced for *Viburnum*, from the peculiar floral morphology and vascular structure, that the parietally placed ovule was originally axially suspended—the abortion of septa being evidently accompanied by the displacement of the axially borne ovule and axial vascular tissue to a peripheral position. But anomalies of the kind described for *Viburnum* do not occur in *Aucuba*, so we may conjecture that the axially suspended ovules present in the primitive *Aucuba* disappeared with the septa, leaving only a single parietally borne ovule in the ovary. In

* S. Endlicher, Gen. Pl. 798.

† S. Endlicher, Gen. Pl. Suppl. iv. part 3. 18.

‡ H. Baillon in Bull. Soc. Linn. Paris (1877) 139.

§ Eichler, Blütendiagr. ii. (1878) 415.

‖ W. Wangerin in Engl. Bot. Jahrb. xxxviii. Heft 2 (1906) 6, 50.

biovulate ovaries, the ovules from their situation belong to different carpels, but the manifestations of the second unit are confined to the additional ovule and a small additional stigmatic lobe. Here, again, as in *Sambucus*, the dorsal portions of the carpels have become a permanent portion of the ovary-wall and are non-variable. The entity of the carpel is almost completely lost, so that the disappearance of the septa must be regarded as only modifying the polymerous condition of the ovary; the ovary is not reduced to a single carpel.

The polymeric hypothesis outlined above receives contributory support from the evidence that has been deduced from studying the course taken by the vascular tissue in the flower. The principal bundles are clearly composite—that is to say, they exist or existed in relation to more than one organ, as they do, for instance, in *Viburnum*. Thus, in the upper part of the ovary, the bundles connected with the petals branch. These branches are comparable to the carpellary bundles, which traverse the style in *Sambucus* and *Cornus*; whilst the remaining alternate bundles occupy the site of stemonal bundles, although stamens are absent (when a stamen, normally present, is absent, as in *Aralia*, *Davidia*, and *Helwingia*, the corresponding bundle is absent also). Hence each of the eight bundles, in *Aucuba*, is partly of carpellary origin. If the carpellary element in each is alternately of "ventral" and "dorsal" origin, in correspondence with the bundles of *Garrya*, this would indicate a tetramerous ovary. But, on the other hand, the carpellary elements might have originated from a single carpel of the type found in *Davidia* and the Araliaceæ, having several bundles. The evidence afforded by biovulate ovaries, however, is opposed to the latter possibility, since the appearance of an additional unit is not accompanied by a corresponding increase in the number of carpellary branches in the style—an increase which, according to Benjamin Clarke, happens with the manifestation of an additional unit in *Cornus*.

If these speculations are correct, the flower was originally hermaphrodite and the ovary polymerous—multilocular in its lower, unilocular in its upper portion, as in *Leycesteria*. By analogy with the Caprifoliaceæ and Hamamelidaceæ, but perhaps prior to the attainment of epigyny, the loculi were pluriovulate—the ovules in the lower portion axially, those in the upper portion parietally borne. Then the septa disappeared and the ovules were numerically reduced, leaving only a single parietally suspended ovule analogous to the single fertile ovule present in the loculi of *Aralia* and *Hamamelis*.

Now it is evident, from the facts that have been enumerated for both *Cornus* and *Aucuba*, that considerable differences exist between them. First, the ovule of *Cornus* is suspended axially—a situation that is constant for the Caprifoliaceæ with terminal ovules; whereas, in *Aucuba*, it is borne upon a parietal placenta—a placentation apparently constant for the terminal ovules of the Hamamelidaceæ. This difference is one of fact, and does not depend upon the hypothesis of origin outlined above. Secondly, the nucellus in *Aucuba* exhibits distinctive characters, and in its primary bulk, definite "calotte" epidermal cap, and subsequent girth-extension, owing to cell-multiplication, is closely comparable to that of the Rosaceæ.

(*d*) Garrya.

Morphology of the Flower and Ovule.

The plants of *Garrya* are dicœcious. Both the male and female inflorescences are catkin-like. The flowers are situated in the axils of decussate bracts, either singly as in *G. Fadyenii* and the majority of the species, or in groups of three as in *G. elliptica*. The bracts are free in *G. laurifolia*, free and foliaceous in *G. ovata*, but connate at their bases and foliaceous toward the lower end of the inflorescence in *G. Wrightii*.

The male flower of *G. elliptica* consists of an outer whorl of perianth leaves, an inner whorl of four stamens which alternate with the perianth divisions and centrally situated rudiments of an ovary. Payer*, who studied the development of the flower in *G. elliptica*, states that two whorls of perianth leaves are present:—"Le périanth est double et composé: l'externe d'un petit bourrelet à quatre dents dont deux sont latérales et un peu plus grande que les deux autres situées, l'une en avant et l'autre en arrière; l'interne, de quatre divisions alternes libres entre elles jusqu'à la base." Similar observations were made by Baillon†, who also described the development of the flower in this species. Harms‡ discovered a small tooth-like process alternating with the perianth divisions—also in *G. elliptica*,—which he identified as a rudimentary calyx leaf. But Wangerin §, from a study of several species, points out that the projections observed by Harms are homologous with bracts. The writer has not reinvestigated the development, but is unable to detect the presence of a second whorl in the mature flowers of *G. elliptica*.

Bentham and Hooker ‖, in 'Genera Plantarum,' and De Candolle, in 'Prodromus,' note that the stamens are opposite the calyx lobes in some species of *Garrya*. "Stamina calycis lobis in aliis speciebus alternata, in aliis certe opposita." The information is evidently derived from Bentham's ¶ description of the new Mexican species, *G. laurifolia* and *G. ovata*, in 'Plantæ Hartwegianæ':—"Stamina in utraque specie laciniis perigonii opposita, sic etiam ut videtur *G. elliptica*." But no reference to opposite stamens occurs in Harms's diagnosis nor in Wangerin's monograph on the Cornaceæ. For this reason it became eminently desirable to settle the point definitely. Accordingly, Dr. Rendle very kindly allowed the writer to examine specimens of the male flowers of *G. laurifolia* (one of the species in question) from the Herbarium of the British Museum of Natural History. Two portions were dissected. Each consisted of a terminal flower and the lateral axillary flowers situated immediately below. In both specimens the uppermost bracts were small and resembled the perianth segments. Owing to this circumstance, one of the terminal flowers (Pl. 28. fig. 22) appeared to consist of an outer whorl of six perianth segments and an inner whorl of four stamens; of the latter, two were opposite the perianth-like bracts (*br*). The other terminal flower (fig. 24) consisted

* J. B. Payer, 'Leçons sur les Familles naturelles des Plantes' (1860–1865) 124.

† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 139. ‡ Harms in Ber. Deutsch. Bot. Gesell. xv. (1897) 19.

§ W. Wangerin in Engl. Bot. Jahrb. xxxviii. Beibl. n. 86 (1906) 52–53.

‖ Bentham et Hooker, Gen. Pl. i. 951. ¶ G. Bentham, Plant. Hartwegianæ, 14.

of an outer whorl of five leaves and an inner of three single and one branched stamens (*st*), so that it simulated a pentamerous flower. One of the stamens (*st*) was situated opposite the bract. But the lateral flowers (fig. 25) of both specimens resembled those of *G. elliptica*—the stamens were alternate with the perianth segments. Bentham seems to have fallen into error through examining the terminal flowers of the inflorescence.

The male inflorescence of *G. Thuretii*, a hybrid between *G. elliptica* (male) and *G. Fadyenii* (female), called in error *G. Macfaydiana* by Carrière, discovered by M. Gustave Thuret at Antibes about 1862, combines the characters of both parents This point was overlooked by Carrière * in his descriptions published in the 'Revue Horticole,' of 1869 and 1879, and subsequently by Baillon †, who states that the male flowers resemble those of *G. elliptica*. The material upon which the following observations are founded was gathered at Kew from plants obtained from France about the year 1896. The "flowers" occur singly in the axil of each bract, agreeing thereby with the female parent, but each stalk bears in reality three, more or less congenitally-united flower-heads, so that there is a marked correspondence with the male parent. There were from four to six perianth leaves in the specimens examined, and in some cases two or three were congenitally united to form a lobed structure. The stamens varied in number from four to twelve: the outer were usually of normal size, the inner smaller and often rudimentary.

The female flower consists of a bicarpellary ovary terminated by two, almost free, styles and surmounted in *G. elliptica* by a pair of minute folioles, which are situated almost at right angles to the styles. Lindley ‡ regarded the folioles as a calyx and they are described as such by Harms § in 'Die Pflanzenfamilien.' Baillon ‖, on the other hand, points out that the terminal flowers of the inflorescence often bear on the sides of the ovary near mid-height two bracts which alternate with the two preceding normally orientated ones; for this reason he considers that the supposed sepals are nothing more than displaced bracts. Wangerin ¶ investigated the matter in greater detail, and his original figures show a complete series in the displacement of bracts, thus:—The folioles are absent in *G. gracilis* (Wang., fig. 5, D); they are situated at about one-third the height of the ovary in *G. Wrightii* (Wang., fig. 4, D); they are depicted higher up still in *G. laurifolia* (Wang., fig. 2, D), and terminal in *G. Fremontii* (Wang., fig. 2, C). Having examined herbarium specimens of several species of *Garrya*, notably *G. Veitchii* and *G. laurifolia*, the writer is able to confirm Wangerin's observations.

The development of the female flower of the hybrid, *G. Thuretii*, was described by Baillon ** as follows:—"Sa fleur femelle est-elle representée au début par un mamelon plein qui occupe l'aiselle d'une bractée de l'inflorescence. Bientôt sur ce mamelon se montre, à droite et à gauche, une feuille carpellaire. Toutes deux s'elèvent en devenant connées et constituent la cavité de l'ovaire, que leurs sommets couronnent ensuite en

* E. A. Carrière in Revue Hort. 1869, 17, and 1879, 154.

† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 139.

‡ J. Lindley, Veg. King. 2nd ed. 295 (1847).

§ Harms in Engl. u. Prantl, Nat. Pfl., Teil iii. Abt. 8, 256.

‖ H. Baillon, *l. c.*

¶ W. Wangerin in Das Pflanzenr. Heft 41 (1910), Garryaceæ, 1–17.

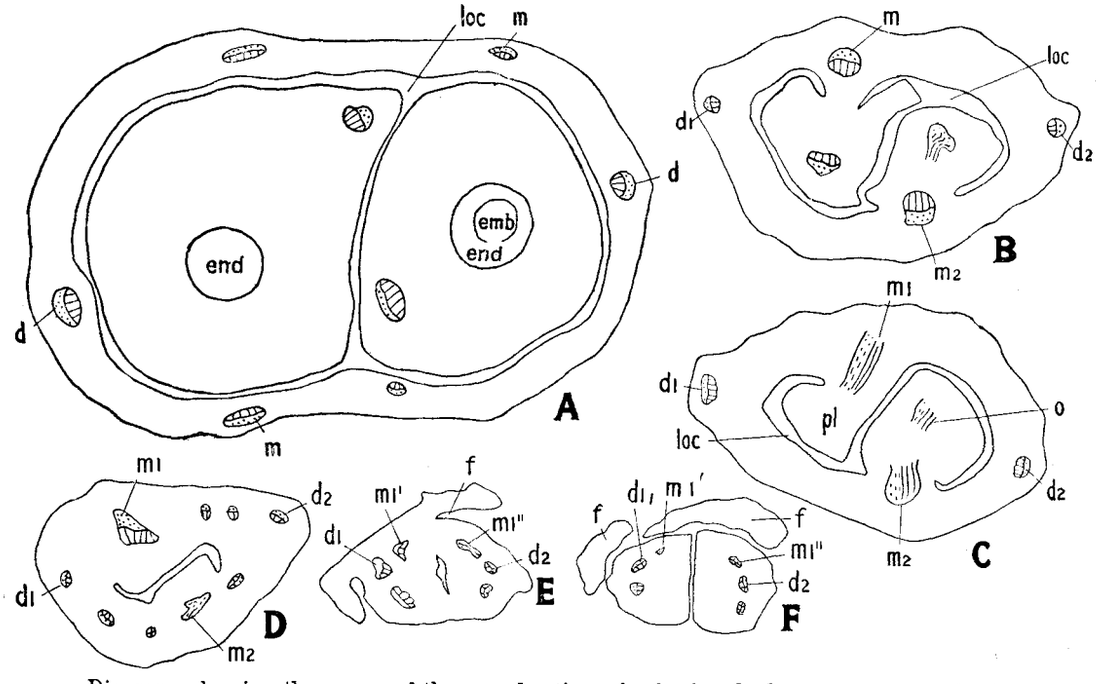
** H. Baillon, *l. c.* 140.

divergeant de deux branches stylaires latérales." The parietal placentæ are terminal and situated opposite one to the other. They are orientated laterally, not antero-posteriorly as described by Baillon, but they may occupy either position in the species with singly situated flowers, according as the single flower represents a median or a lateral member of the axillary groups of three present in *G. elliptica*. The styles should rest normally at right angles to the placentæ, but they are slightly twisted from this position in *G. elliptica*. They rest in the plane of the placentæ in *G. Veitchii* and *G. longifolia*.

A single descending ovule with "dorsal" raphe develops from each placenta. It becomes ultimately tangentially orientated. The nucellus is invested by a single integument.

The writer has been unable to follow the development of the nucellus, owing to the lack of suitable flowers. The first material examined consisted of fruits of the hybrid, *G. Thuretii*. Later, fertile fruits of *G. elliptica* were obtained. Finally, some flowers of this species were examined and the ovules removed and microtomed. These were in an advanced stage of development. The embryo-sacs were considerably elongated and sterile, having escaped fertilization. The basal part of the nucellus consisted of about five rows of cells; so that, in all probability, the young nucellus is comparable in bulk to that of *Cornus*.

Text-fig. 8.



Diagrams showing the course of the vascular tissue in the female flower of *Garrya elliptica*. A, young fruit; B–F, flower. (For abbreviations see p. 308.)

Vascular Structure.

The vascular tissue of the pedicel consists of two opposite simple bundles (*d*) and two groups of small strands, which alternate with the former. The small bundles of each

group unite to form one (*m*), so that four (*d* 1, *d* 2, *m* 1, *m* 2) traverse the ovary-wall (Text-fig. 8, B). Each of the bundles *m* forms an ovular branch *o* (C), and then extending upward divides to form two (E, *m'*, *m''*), which become the opposite marginal bundles of the free styles (F); *d* 1 and *d* 2 become the median bundles of the corresponding styles (F).

The ovary corresponds closely to that of *Hamamelis* and other Hamamelidaceæ, consisting of two carpels with their respective traces, the adjacent marginal bundles being congenitally united.

Nature and Origin of the Flower.

Notwithstanding his interpretation of the morphology of *Garrya*, Lindley * found some difficulty in assigning it a systematic position. He first selected the "Urtical Alliance," but later decided in favour of the Helwingiaceæ, then recently established by Decaisne, and accordingly associated the monotypic family Garryaceæ with the Helwingiaceæ to form the alliance or cohort Garryales. Both families agree, writes Lindley, in possessing an epigynous calyx and a minute embryo embedded in copious endosperm.

Garrya, bearing the hall-mark of epigyny, is henceforth compared with epigynous forms, even by Baillon, who sceptically regarded Lindley's calyx. Baillon † included *Garrya* in his Cornaceæ. He supposed that the ovary, from an evolutionary point of view, is intermediate in structure between those of *Aucuba* and *Cornus*. This *Aucuba-Garrya-Cornus* series of his is analogous to that which he believed could be traced between the Combretaceæ and bilocular forms of *Marlea*.

It is now evident that the true nature of the flower has long been masked, owing to the vagaries of bracts. Bracts are inserted on the ovary-wall in several species, and in the common species, *G. elliptica*, reach an epigynous position. In *G. Fadyenii*, where the folioles do not exist, the perianth was supposed to have disappeared; thus Endlicher ‡ states, "perigonii in floribus pistilligeris vestigium nullum." Bracts, again, caused Bentham to err when he described opposite stamens in *G. laurifolia*: the stamens are alternate with the perianth segments. Finally, the close proximity of a pair of bracts to the perianth segments in the male flower led Harms astray, who believed that they represented a calyx.

The loss of the epigynous *calyx* or *perianth*, which had been considered homologous with the perianth of Cornaceæ, involves a total reconsideration of the whole problem.

Wangerin, influenced by the amentaceous inflorescence, dicœcism, apetalous and hypogynous flowers, compares *Garrya* with *Salix*, *Betula*, *Juglans*, and *Myrica*, and removes it from the Cornaceæ to the restored Garryaceæ. This family, in Engler's revised Syllabus, is re-established in the Garryales, now situated between the Salicales and Myricales. Both Wangerin and Engler seem to have regarded certain characters as of little consequence—for instance, the basal "orthotropous" ovules of *Juglans* and

* J. Lindley, Veg. King. 2nd ed. 295.

† H. Baillon, Histoire des Plantes, vii. 82.

‡ S. Endlicher, Gen. Pl. Suppl. ii. 30.

Myrica and the exalbuminous seeds of *Salix*, *Juglans*, *Betula*, and *Myrica*. The ovules of *Garrya* are anatropous, and the seeds contain copious endosperm.

Again, since the embryology of *Garrya* is not yet understood, it would be wise to reserve a final judgment until a more thorough comparison with the Amentiferæ could be made, the embryology in the latter group being already known from the work of Benson and others.

Now genera with amentaceous inflorescences and diœcious, apetalous, hypogynous flowers occur also among *albuminous* families with *anatropous* ovules, and their ovaries are comparable in many cases to those of *Garrya*. Thus the resemblance to the Hamamelidaceæ is comparatively close. The structure of the ovule forms the only considerable difference. *Garrya*, in many features, is not unlike *Scepa*, now incorporated with *Aporosa*, a genus of the Phyllantheæ; but the Phyllantheæ are defined as possessing ovules with a ventral raphe, which is not the case in *Garrya*. Lastly, *Garrya* may be favourably compared with *Forstiera*, a genus of Oleaceæ.

(*e*) Helwingia.

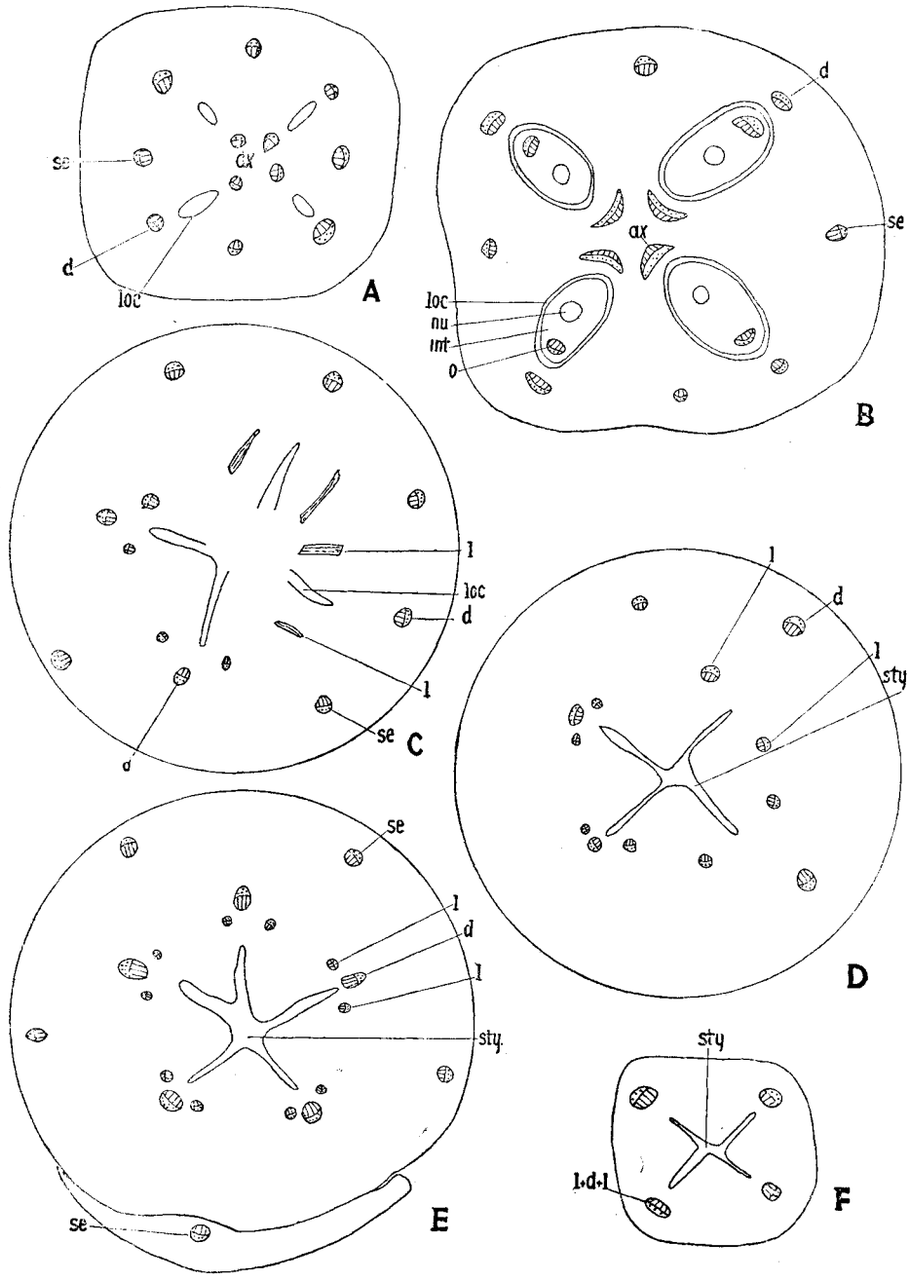
Morphology of the Flower and Ovule.

The flowers are unisexual and seated upon the midrib of a foliose bract. The male inflorescence consists of a group of separate pedicellate flowers, found to be either trimerous or tetramerous, both kinds being present in the same inflorescence. Each flower possesses a polyphyllous perianth and a single whorl of stamens, which alternate with the perianth leaves. The female inflorescence comprises a single, minutely pedicellate, epigynous flower, which bears at its base a small foliole. The flower consists of an inferior polycarpellary ovary terminated by free styles and surmounted by a single whorl of perianth leaves, resembling those of the male flowers, which alternate with the stigmas. Stamens, or the rudiments thereof, are entirely absent. Both whorls are usually tetra- or pentamerous, but in one exceptional case a pentamerous ovary was surmounted by a tetramerous perianth. The ovary is multilocular, each loculus containing a single, terminal, axially suspended, descending, anatropous ovule with abaxial raphe. The ovule is radially orientated, and since the nucellus of the mature ovule rests between the axial portion of the ovary and the abaxial raphe, the orientation is the inverse of that characteristic of the Araliaceæ, where the ovules are also radially orientated.

Owing to its radial orientation, vertical sections of the ovule are easily obtained. Such a section of the youngest ovule found is shown in Pl. 29. fig. 73. The integument shows no sign of dual origin. The nucellus approximates closely to the condition in *Lilium*, and consists of three short axial rows made up each of two or three cells. Pl. 29. fig. 73 shows a single enlarged subepidermal archesporial cell, of which the subsequent development has not been traced. The nucellus soon assumes the vertical position, owing to the activity of meristem at its base, and by the time the embryo-sac is formed the ovule has elongated considerably (Text-fig. 13, B).

This elongation is due to the activity of the lower cells of the nucellus, which, owing to the continuous formation of transverse partitions, give rise to vertical tiers of cells, so

Text-fig. 9.



Diagrams of transverse sections showing the course of the vascular tissue in the female flower of *Helwingia ruscifolia*. (For abbreviations see p. 308.)

that the nucellus expands longitudinally and provides for subsequent extension. Meanwhile, the lower rim of the integument increases by cell-division to form oblique rows (*int*), whilst the upper rim obtains only a small extension; hence the integument,

as a separate organ, forms only a small portion of the ovule, as in *Davidia*. Its boundary, *l*, is indicated in Text-fig. 13, B. The embryo-sac, as shown in Pl. 29. fig. 74, is immediately subjacent to the epidermis of the nucellus. Only one epidermal cell is shown in the figure, and no trace of a cap formed from sterile megaspores nor traces of parietal tissue are evident. The embryo-sac itself exhibits no noteworthy departure from the normal.

Vascular Structure.

The vascular tissue of the pedicel in the female flower separates into a peripheral and an axial (*ax*) series of bundles (Text-fig. 9, A). There are ten outer and five inner bundles in pentamerous flowers, but the number in each series varies with the carpels; in the case of the exceptional flower noted above (*Helwingia*, text, p. 278), the bundle corresponding to the missing sepal was absent. The bundles of the outer series opposite the loculi (B, *d*) take an upward course, without branching, into the style (F) and stylar lobes—one into each, corresponding to dorsal carpellary bundles; those alternating with the loculi (B, *se*) extend upward also without branching and enter the sepals.

The bundles of the axial series (B, *ax*) are opposite the loculi. Each one extends axially as far as the corresponding placenta, forms three branches of which the median becomes the ovular bundle, whilst the lateral branches (C, E, *l*) pass outwards, and ultimately join the corresponding dorsal bundle (F).

Two interpretations of the vascular structure may be presented, and until more extended investigations have been made claim equal attention. The first is suggested by a comparison with *Aralia* and *Nyssa*. As in *Aralia*, the traces are free, and when the number of carpels and perianth segments deviates from the normal the traces vary correspondingly. A transition from hermaphrodite to female flowers occurs in *Nyssa*, when both the stamens and stemonal traces disappear; so *Helwingia*, by analogy with *Nyssa*, may have lost both stamens and petals, together with their traces, when epigynous. The second and perhaps a more tempting solution is to suppose, by analogy with *Garrya*, that the flower was already apetalous and unisexual in its hypogynous state, in which case petal and stemonal traces have never existed in the ovary-wall.

Morphology of the Perianth.

Lindley * compares the perianth with the supposed calyx of *Garrya*. Bentham and Hooker †, on the contrary, hold that it is homologous with the corolla of *Meryta*, a genus of the Araliaceæ. Both genera are placed side by side in the Araliaceæ for the following reasons:—(1) The perianth leaves alternate with the stamens in both genera, and the æstivation is valvate; (2) in *Meryta* both calyx and corolla are present in the male flower, although the calyx is absent in the female flower. Bentham and Hooker deduce that the calyx, already obsolete in the female flower of *Meryta*, has entirely disappeared

* J. Lindley, Veg. King. 2nd ed. 295 (1847).

† G. Bentham et J. D. Hooker, Gen. Pl. i. (1867) 940.

in *Helwingia*. Now Bentham and Hooker state that the Cornaceæ and Araliaceæ are to be distinguished by the type of ovule prevailing in the family; so they were evidently unaware that the ovule, in *Helwingia*, does not conform to the Aralian type, with ventral raphe, and hence could not belong to the latter family. If, then, the genera are not closely related, the arguments bearing on the homology of the perianth diminish in value.

Another solution of the puzzle presents itself, however. It will be observed that the perianth leaves alternate with stamens in the male flower, corresponding in position to petals; but in the female flower they alternate with the stigmas, and might represent sepals. Now if the perianths of the male and female flowers are homologous, it is conceivable that some anomaly exists with regard to the stamens. If it were supposed that the flower was primitively ob- or diplostemonous, but has lost the inner or outer whorl of stamens, as the case may be, then the perianth segments could be interpreted as sepals and the orientation of the whorls in both the male and female flowers could be explained. Among Cornaceæ a double whorl of stamens has been recorded in *Nyssa sessiliflora*.

Comparison between Helwingia *and* Cornus.

Morren and Decaisne* established *Helwingia* in a new family, the Helwingiaceæ. This arrangement was subsequently criticised by Baillon†, who states that Decaisne was misled by artificial characters. Baillon points out that the female flower is constructed very like the flower of *Cornus*, and the ovules of both genera are of the same type. He considered that Bentham and Hooker, in placing *Helwingia* among the Araliaceæ, were led astray owing to the numerous agreements in character and organization between *Helwingia* and *Meryta*.

Now the ovules of *Cornus* (with dorsal raphe) are orientated tangentially—an orientation that appears to be constant for the Caprifoliaceæ; whereas those of *Helwingia* (with dorsal raphe) are radially orientated, and the position taken up in the loculus seems to be the outcome or result of a genetic difference in the ovule, as explained by the writer in a previous paper. Hence the ovules of the two genera are not necessarily homologous, as considered by Baillon.

Again, the vascular systems do not correspond. That of *Helwingia*, owing to the existence of separate perianth and dorsal carpellary bundles, agrees more nearly with the Aralian type. The vascular supply to the ovule is different in the two cases. In *Helwingia* each axial bundle divides to form three, of which the median enters the ovule; in *Cornus*, lateral branches from a pair of opposite peripheral bundles unite to form the ovular trace. These details show that the resemblances between the two genera are not so real as Baillon supposed, and that he himself was influenced by structural parallelisms.

* Morren et Decaisne in Bull. Acad. Brux. v. (1836) 169.

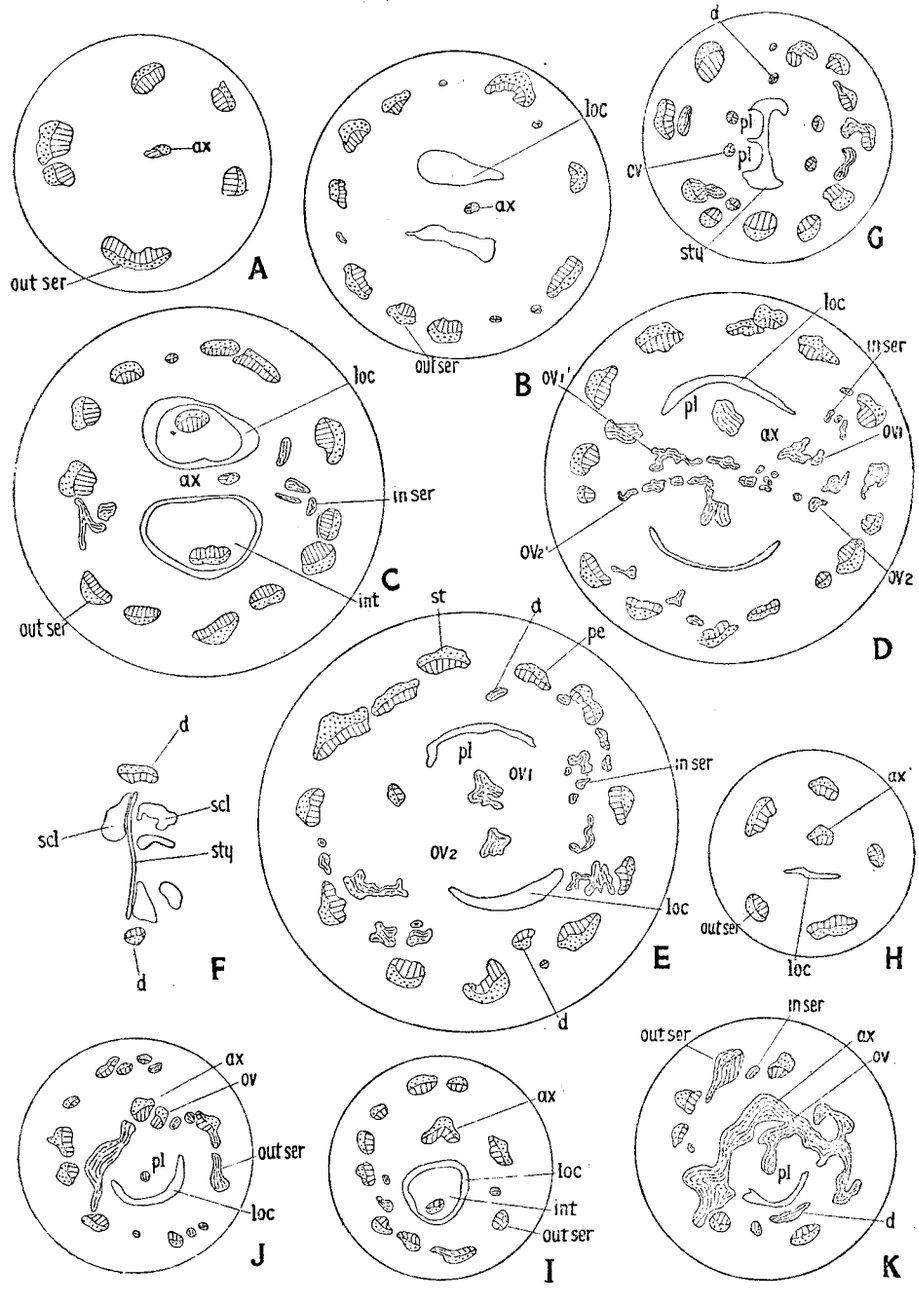
† H. Baillon in Bull. Soc. Linn. Paris, i. (1877) 137.

(*f*) Corokia.

Morphology of the Flower and Ovule.

The flowers of *Corokia Cotoneaster* are hermaphrodite, with epigynous pentamerous whorls of sepals, petals, and stamens. The ovary is usually unilocular, sometimes

Text-fig. 10.



Diagrams showing the course of the vascular tissue in the flower of *Corokia Cotoneaster*.
(For abbreviations see p. 308.)

bilocular. The style consists of two congenitally united units in bilocular forms. The

stylar canal is cross-shaped (in bilocular forms), and upon tracing it downwards the longer arm passes into communication with the loculi and the shorter arm is distinctly sutural. The canal is sometimes three-lobed in unilocular ovaries.

The terminal ovules in bilocular ovaries are axially suspended, one in each loculus; but traces of parietal placentæ, absent in *Cornus*, exist immediately above the point of insertion of the ovules (Text-fig. 10, G, *pl*). The ovules are radially orientated, as in *Helwingia*. The orientation is not disturbed in relation to the absence of the septum.

Vascular Structure.

Several hand-cut series and one by the microtome were prepared through unilocular ovaries, whilst two series by hand and one by the microtome were taken through bilocular ovaries. The last-mentioned microtomed series will now be described. Six peripheral bundles (*out ser*) and one centrally-situated or axial bundle were present below the loculus (Text-fig. 10, A). The peripheral bundles, branching and anastomosing, increase upward to form an outer series of twelve bundles which are the traces of six petals and six stamens, and some small inner branches (B–E). The majority of the inner branches arise from the bundles near the septum on either side (D). They extend into the septum, and strands from opposite sides (*ov* 1, *ov* 1′, and *ov* 2, *ov* 2′) augmented by the axial bundle (*ax*) unite to form the ovular trace. Two bundles extend upward from this level, but soon die out (E). In another flower four bundles were present at a corresponding level, one in each placenta (G, *ov*). Two of the above-mentioned inner branches (E, *d*) extend upward and occupy a dorsal position in the style (F).

In unilocular ovaries, the "axial" bundle is situated near the side of the loculus (H, I). It extends upwards and is joined by inner branches corresponding to those marked *ov* in D, so that an irregular arc or collar of vascular tissue is formed (J, K) from which the ovular trace arises.

The change to the unilocular condition is accompanied by the displacement of the axial bundle, and by the diversion of the vascular tissue pertaining to the absent ovule to the present ovule.

Comparison with Cornus.

Corokia was described by A. Cunningham * in 1839. Endlicher † at first placed it near the Rhamnaceæ, but later ‡ transferred it to the Cornaceæ, and it remains in this family in the systems of Bentham and Hooker, Baillon, Harms, and Wangerin. *Corokia*, however, differs from *Cornus* in the following details:—(1) the presence of parietal placentæ immediately above the situation of the ovule; (2) the existence of an axial bundle; (3) the method of vascular supply to the ovule, and (4) orientation of the ovule. Hence the structural agreement is not quite so close as hitherto supposed.

* A. Cunningham in Ann. Nat. Hist. iii. (1839) 249.

† S. Endlicher, Gen. Pl. 1103 (1840).

‡ S. Endlicher, Gen. Pl. Suppl. iv. pt. 3, 18 (1850).

(*g*) Melanophylla.

This genus was first described by Baker * in 1886. Two species—*M. alnifolia* and *M. aucubifolia*—were recorded. According to Baker's description, the flowers are hermaphrodite with alternate pentamerous whorls of sepals, petals, and stamens. The ovary is bi- rarely trilocular and the styles bi- or trifid. The loculi are uniovulate, Baker † described a new species, *M. crenata*, in 1896 with illustrations. Figures from specimens of this species in the Herbarium Boissier are given by Wangerin ‡ in 'Das Pflanzenreich.' Only one loculus is shown in both Baker's and Wangerin's illustrations.

Baker, in 1886, states that two species of *Melanophylla* are comprised in Humblot's collection from the north-east portion of the island of Madagascar. Now in 'Plantes de Madagascar' §, a new species, *M. Humbloti*, is figured which is evidently one of those mentioned by Baker. This species is not recorded in 'Das Pflanzenreich' and no written description seems to have been published, but it is mentioned in Palacký's ‖ 'Plantarum Madagascariensium.' According to the figures of *M. Humbloti* the stigmas, which are tongue-shaped, are not recurved as in Baker's species—the calyx is depicted with a waved rim and not with definite segments as in *M. crenata*, and there are slight differences in the ovary and the stamens. Only one loculus and one ovule are figured.

Wangerin associates *Melanophylla* with *Griselinia* to form a new tribe of Cornoideæ, the Griselineæ.

(*h*) Griselinia.

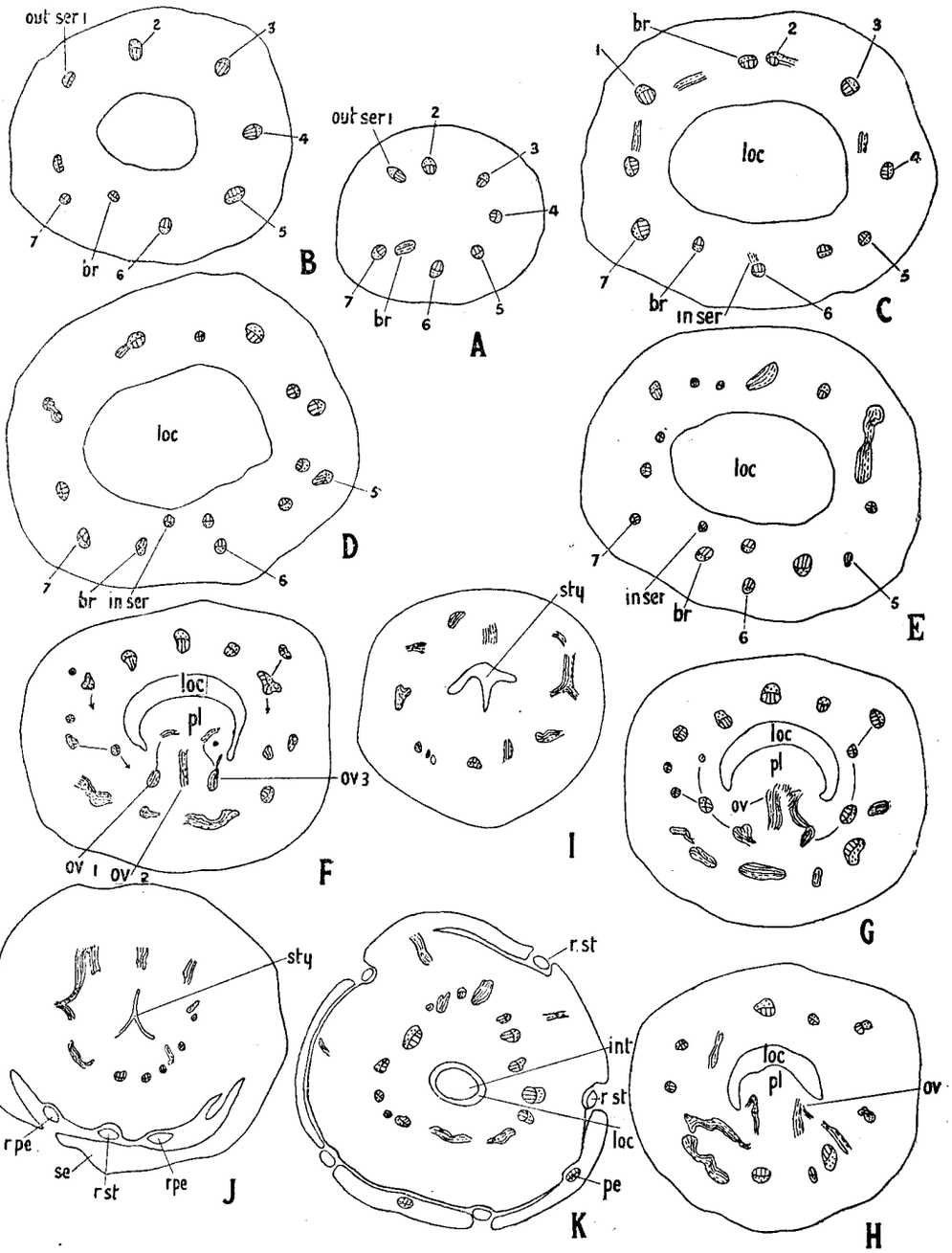
Morphology of the Flower and Ovule.

The plants and flowers of *Griselinia* are unisexual. The male flowers of *G. littoralis* and *G. lucida* consist of sepals, petals, and stamens in alternating pentamerous whorls, which surround a flat circular disc with five or six grooves radiating outward from the centre. Ovarian rudiments are absent. The female flowers are epigynous, and surmounted by sepals and petals in *G. littoralis* and by sepals only in *G. lucida*. The petals are imbricate. Stamens are absent in all the species. Bentham & Hooker ¶ and Wangerin ** state that there are no rudiments of stamens, and none have hitherto been recorded. The writer finds not only rudiments of stamens in *G. littoralis* and *G. lucida*, but rudiments of the absent petals in *G. lucida*. These are very minute, but they can be observed with the aid of a good pocket-lens. Text-fig. 11, K, represents a transverse section of *G. littoralis*; here the positions of the petals are denoted by

* J. G. Baker in Journ. Linn. Soc., Bot. xxi. (1886) 352.
† J. G. Baker in Hook. Ic. Pl. xxv. (1896) pl. 2499.
‡ W. Wangerin in Das Pflanzenr. Heft 41, 100.
§ H. Baillon in 'Plantes de Madagascar,' Atlas, iii. pl. 400 (1896).
‖ Palacký in Plant. Madagasc. fasc. iv. (1906) 50.
¶ G. Bentham et J. D. Hooker, Gen. Pl. i. 951.
** W. Wangerin in *l. c.* 95.

pe, and the rudiments, five in number, occur just within the sepals, occupying the position of stamens (*r st*). The rudiments of stamens and petals in *G. lucida* are

Text-fig. 11.



Diagrams showing the course of the vascular tissue in the flower of *Griselinia*: A–J, *G. lucida*; K, *G. littoralis*.
(For abbreviations see p. 308.)

shown in J. The ovary is terminated by three styles. It is unilocular or bilocular according to Bentham and Hooker*. Wangerin† describes only one loculus. The

* G. Bentham et J. D. Hooker, Gen. Pl. i. 951.

† W. Wangerin in Das Pflanzenr. Heft 41, 95.

writer finds no bilocular ovaries in his material of *G. lucida*. The ovular mamelon grows downwards and develops into an ovule of the abaxial type. The orientation in bilocular ovaries has, of course, not been observed. The nucellus, which is comparatively long, is of very small bulk—a median section shows three rows of cells within the nucellar epidermis; it is invested by a single integument (Pl. 29. figs. 75, 76).

Vascular Structure.

Serial sections of the flowers of both *G. lucida* and *G. littoralis* were prepared. In *G. lucida* six or seven bundles were present at the base of the ovary (Text-fig. 11, A). These branch to form a single series, consisting of a variable number of bundles—twelve or more—in the ovary-wall (B–F). Some of the smaller bundles extend inward, and in the neighbourhood of the placenta anastomose, presenting in thick sections the appearance of an incomplete vascular collar (F–I); from this "collar" as many as five separate bundles, of which three (*ov* 1, *ov* 2, *ov* 3) are shown (F), extend into the "placenta" and unite there to form the single ovular bundle. Since the petals and stamens are absent in this species, there are no outgoing branches to these organs, and all the principal bundles, together with a few which proceed from the "collar," extend into the basal portion of the style (I, J), diminishing in number until only a few remain. The vascular structure is similar in *G. littoralis* (petals present), except that the bundles are more numerous—nine at the base of the loculus and sixteen higher up in one specimen.

The vascular structure in the neighbourhood of the placenta recalls the somewhat similar collar-like arrangement of vascular tissue in the reduced unilocular ovary of *Corokia*. In *Griselinia*, however, branches from every part of the ovary-wall contribute to the bundles entering the "placenta."

Nature of the Ovary.

Baillon considered the ovary of *Griselinia* to be incompletely tricarpellary, the body of the ovary consisting of the lower portion of one carpel. But the peculiar vascular structure justifies a modification of this view. When we consider the cases already discussed, it is found that where the terminal ovule is by origin axially situated the vascular tissue presents an anomaly, but where it is parietally situated by origin the conditions are not the same and the vascular tissue need not necessarily be diverted from the normal course. Thus, in *Viburnum*, the ovary was primitively septate, but, owing to the loss of the septa, the vascular tissue that had originally an axial extension became diverted to a peripheral position. Again, in *Corokia*, where in bilocular forms the ovules are suspended from the septum, the absence of a loculus disturbs the normal disposition of the vascular tissue in relation to the ovule. But in *Aucuba*, also originally septate, where the ovule is suspended from a parietal placenta and comparable to the parietally situated ovules in the Combretaceæ, no vascular anomaly exists in relation to the position occupied by the ovule. Now, in *Griselinia*, the placenta is abnormally large, and the numerous branches contributing to the ovular trace arise from bundles

extending in all parts of the ovary-wall, and appear to have been diverted from the original disposition. Hence not only can we deduce that the ovary was primitively septate, but also that the ovule was axially placed.

Now, abortion, in *Viburnum*, originally tricarpellary, has conduced to the special development of the body of one carpel, a fact that is evident from the asymmetrical disposition of the vascular tissue in the flower and from the arrested loculi. But, in *Griselinia*, as also in *Corokia* and *Aucuba*, the original course taken by the floral vascular tissue does not appear to have been affected by abortion. Hence the conclusion is reached that the septa disappeared without a special enlargement of the lower portion of any one carpel.

The writer's interpretation of the floral structure may be summarized briefly as follows:—The flower was primitively hermaphrodite, and became unisexual after the attainment of epigyny; it exhibits an apetalous tendency, definitely expressed in *G. lucida*, the ovary was originally tricarpellary and trilocular, and the loculi, by analogy with the Caprifoliaceæ, were at first pluriovulate. Subsequent abortion resulted in the disappearance of the septa, but did not induce the special enlargement of the lower portion of any one carpel, as in *Viburnum*; concurrently, the ovules were numerically reduced to one, the equivalent of an axially suspended ovule in the primitive ovary. If Baker's record of bi- and trilocular ovaries in *Melanophylla* be correct, we may conceive that *Griselinia* has proceeded a stage further than *Melanophylla* in the direction of abortion.

(*i*) Nyssa.

Morphology of the Flower and Ovule.

The flowers of *Nyssa* are hermaphrodite or unisexual. The male flowers consist of sepals, petals, and stamens, which vary from five to an indefinite number. According to Bentham and Hooker *, ovarian rudiments are absent or a subulate process exists in the centre of the disc. The female flowers consist of an inferior ovary surmounted by a calyx—petals are absent or minute and there are no rudiments of stamens—and terminated by one or two styles. The flowers of *N. sylvatica*, growing at Kew, which the writer examined, proved to be either hermaphrodite or female. The hermaphrodite flowers possessed one, two, or three stamens, so that a complete series existed between the two kinds.

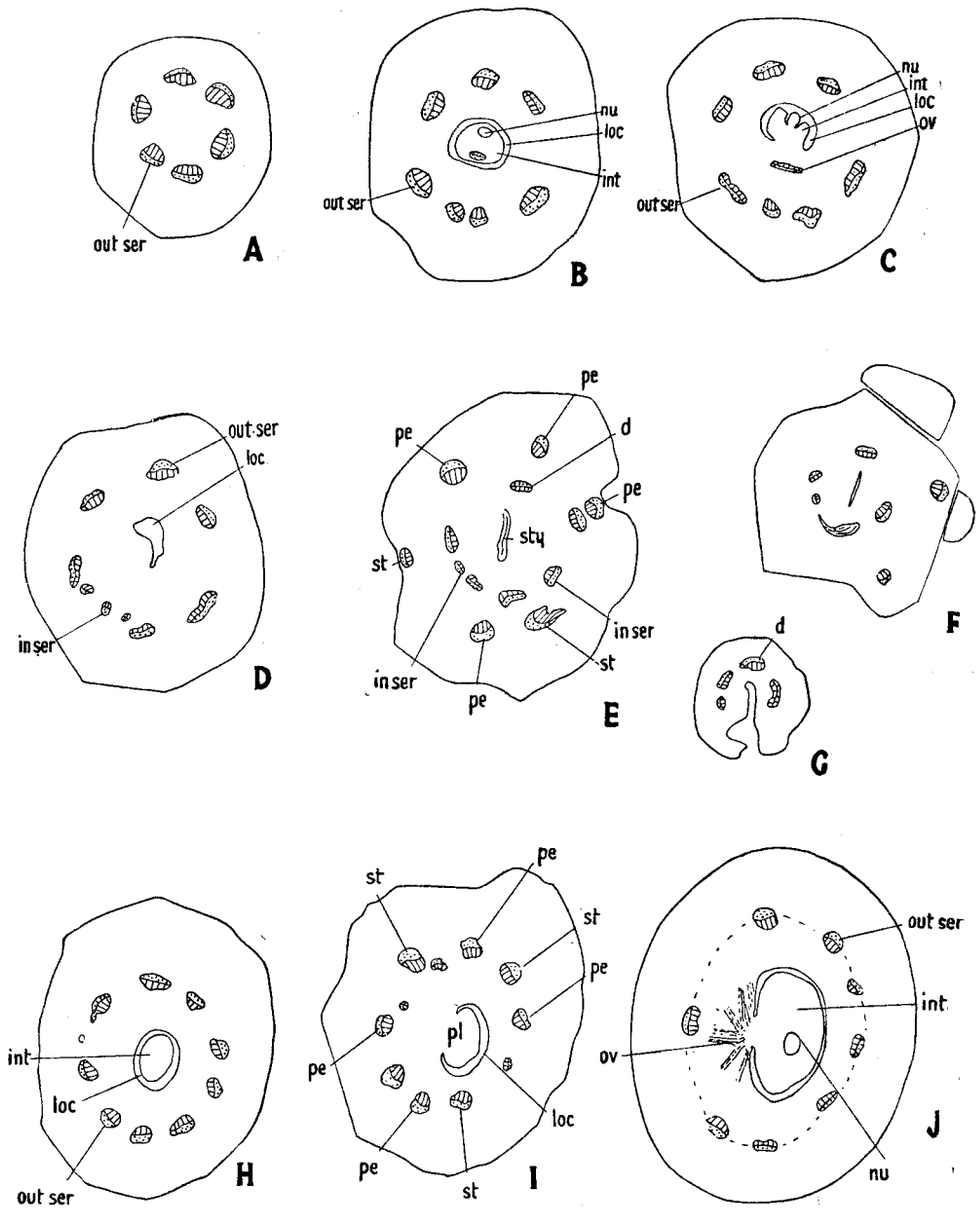
Bentham and Hooker † state that the ovary is unilocular, but Baillon ‡ records that it may be sometimes bilocular. The writer has observed only unilocular ovaries in *N. sylvatica*. The ovule is terminal in mature ovaries, but this is not strictly so in very young flowers; in one particular case measurements were made with the aid of a series of sections, each ·015 mm. thick; the height of the loculus was 0·24 mm.; the total length of the ovule 0·165 mm. The ovule was attached to the ovary-wall at a point

* G. Bentham et J. D. Hooker, Gen. Pl. i. (1867) 952.

† G. Bentham et J. D. Hooker, *l. c.* ‡ H. Baillon, 'Histoire des Plantes,' vi. 267.

about 0·08 mm. from its own summit and the top of the loculus. It is of the adaxial type and comparable to that of *Davidia*. Wangerin states that two integuments are present, but the writer finds only one (Pl. 29. fig. 77). The nucellus is of small bulk

Text-fig. 12.



Diagrams showing the course of the vascular tissue in the flower of *Nyssa sylvatica*. A–G, one flower; H, I, another flower; J, fruit. (For abbreviations s. e p. 308.)

and comparable to that of *Davidia*, but its further development has not been followed, owing to the lack of suitable material.

* W. Wangerin in Das Pflanzenreich, Heft 41, p. 9.

Vascular Structure.

Serial sections through very young flowers and hand-sections of sterile "fruits" were prepared from only one species—*N. sylvatica.*

In one flower six bundles were present in the lower portion of the ovary (Text-fig. 12, A), these extended upward toward four petals, *pe*, and two stamens, *st* (B–E); in another, nine bundles occurred (H), but only seven of these supplied stamens (three) and petals (I).

An inner series of fine branches originates from the cylinder of bundles near the point of attachment of the ovules (D, E) and extends into the style (F). The branch *d* occupies a dorsal position in the style, but the flowers were too young to show the vascular connections of the ovule, hence the nature of the remaining branches could not be determined. From sections of fruits it appears that two or three strands unite to form the ovular bundle (J).

Owing to the variability in the flower in the genus, a comparison needs to be made with the remaining species before the significance of the vascular peculiarities can be adequately discussed.

Comparisons.

Endlicher* placed *Nyssa* in a new family, the Nyssaceæ, near the Santalaceæ. Baillon† transferred it to the Combretaceæ for reasons similar to those which influenced him in attaching *Alangium* to this family. But the occasional presence of two styles, one of which is rudimentary in *N. sylvatica*, and the recorded case of a second incomplete loculus indicate that the ovary is unilocular by abortion. Bentham & Hooker‡ and Harms§ include *Nyssa* among the Cornaceæ, but it differs from *Cornus* in possessing the Aralian type of ovule, in its variable flowers, imbricate corolla, free styles, and reduced ovary. Wangerin‖ separates it from the Cornaceæ on the ground that the ovule is bitegumentary, but since the ovule possesses only one integument this criterion fails.

Nyssa approaches *Aralia* in the form of ovule (adaxial). But the ovules of *Aralia* are parietally borne, whereas the ovular bundles of *Nyssa*, by analogy with *Griselinia*, might indicate that the ovule was originally axially suspended. A closer structural agreement exists between *Nyssa* and *Davidia*, both genera possessing polygamous flowers, free styles, and numerous stamens.

SUMMARY.

1. The following details of floral morphology are recorded:—
   - *a.* The occasional occurrence of hermaphrodite flowers in *Aucuba himalaica.*
   - *b.* Biovulate ovaries in *A. japonica* and *himalaica.*
   - *c.* Anomalous flowers in the hybrid *Garrya Thuretii*—these consist of three congenitally united flower-heads borne upon one "pedicel," thus combining

* S. Endlicher, Gen. Pl. 328.

‡ Bentham et Hooker, Gen. Pl. i. 952.

‖ W. Wangerin in Das Planzenr. Heft 41, 9.

† H. Baillon, Bull. Soc. Linn. Paris, i. (1877) 271.

§ Harms in Engl. u. Prantl, Nat. Pfl. Teil iii. Abt. 8, 257.

the characters of both parents, viz., *G. elliptica* in which the flowers occur in axillary trimerous groups, and *G. Fadyenii* in which they are situated singly in the axil of each bract.

d. Rudiments of a single whorl of stamens in the female flowers of *Griselinia littoralis* and *lucida* and of the absent petals in *G. lucida*.

e. Rudimentary terminal parietal placentæ in *Corokia Cotoneaster*.

2. The terminal ovules are suspended axially in *Davidia*, *Cornus*, *Helwingia*, and in bilocular forms of *Marlea* and *Corokia*; probably axially by origin in *Nyssa* and *Griselinia*, and parietally borne in *Aucuba* and *Garrya*.

3. The ovule exhibits considerable variety in organization :—

a. It is in *Nyssa* and *Davidia* of the dorsal type (raphe ventral or adaxial) with radial orientation ; of the ventral type in *Helwingia* and *Corokia* (raphe dorsal or abaxial) with radial orientation, but the inverse of the former ; and of the ventral type with tangential orientation in bilocular forms of *Cornus* and *Marlea*.

b. The nucellus in the genera investigated (including *Davidia* and *Nyssa* deseribed as bitegumentary by Harms and Wangerin) becomes invested with a single integument.

c. The integument is completely free from the nucellus in *Aucuba* and *Griselinia*, but in the specialized ovules of *Davidia* and *Helwingia* is only found as a separate organ towards the summit of the nucellus.

d. The nucellus consists of about seven axial rows of cells in *Aucuba*; four or five in *Cornus*, *Davidia*, *Griselinia*, and *Garrya*; and three in *Helwingia*, where it approximates to the condition obtaining in *Lilium* and *Inula*.

e. The nucellus of *Aucuba*, in the formation of a definite layer of parietal tissue, a small epidermal cap, and in subsequent bulk-extension owing to cell-division, approaches the type described by Péchoutre for the Rosaceæ.

f. The germination of more than one megaspore, already recorded by the writer for *Davidia*, occurs also, but not to the same extent, in *Aucuba*.

4. The floral vascular systems of the Cornaceæ do not conform to one type as in the Caprifoliaceæ. It is in *Cornus* of the Caprifoliacean type. The systems of *Griselinia*, *Nyssa*, and *Helwingia* exhibit Araliacean tendencies; those of *Davidia* and *Marlea* are transitional in character between that found in *Aralia* and the synthetic systems of *Cornus* and the Caprifoliaceæ. The stage of economical advance reached by *Viburnum* has not been attained.

a. Infra-locular extensions of vascular tissue occur in *Aucuba* and unilocular forms of *Marlea*.

b. The ovular trace is anomalous in *Griselinia*, *Nyssa*, and unilocular forms of *Corokia*.

c. Branches from the ovular trace traverse the peripheral region of the integument in *Davidia* and *Corokia*.

5. The flowers of certain genera admit of the following interpretation:—

a. Cornus: The ovary is bilocular by reduction from a quadricarpellary primitive type. It is analogous to that of *Sambucus*.

b. Alangium: The ovary is unilocular by reduction from the bilocular type found in *Marlea begonifolia*, and reduced from a form primitively polycarpellary.

c. Aucuba: The flowers have become unisexual since the attainment of epigyny. The ovary was primitively quadricarpellary and quadrilocular. The septa subsequently disappeared, but the lower portion of the carpels remained unmodified. The ovules, originally numerous, became numerically reduced until only a single parietally suspended one remained.

d. Garrya: The flower is hypogynous as already noted by Wangerin.

e. Griselinia: The flowers have become unisexual since the attainment of epigyny, and a tendency towards apetaly finds its expression in *G. lucida*. The ovary was primitively tricarpellary and trilocular, at all events in its upper portion, but the septa disappeared, leaving the lower portion of the carpels unmodified, but involving the displacement of an ovule that was primarily axially situated.

6. Progressive abortion in the ovary reaches its limit in this family—the ovaries of *Davidia* and *Helwingia* are multilocular, the change from the bi- to the unilocular condition can be traced in *Corokia*, and the ovaries of *Aucuba*, *Nyssa*, *Alangium*, and *Griselinia* are unilocular.

7. Progressive sterilization has proceeded still further than in the Hamamelidaceæ and Caprifoliaceæ, nearly all the genera have reached the level of the extreme cases in these families, and the ovary or loculus is absolutely uniovulate.

8. The general series that has been traced in the direction of the loss of carpellary autonomy culminates in *Aucuba*, where, owing to the absence of septa and to the parietal situation of the ovule, the gynæcium appears to consist of a single carpel.

9. Both the Cornaceæ of Harms and the Cornaceæ of Wangerin are heterotypic, but this fact is masked, owing to parallel development and convergent organization.

5. FINAL DISCUSSION.

THE INTERPRETATION OF RESEMBLANCES AND DIFFERENCES.—Hitherto that which may be called the Principle of Resemblances has held amazing sway. Drawing first breath, as it were, in the days of Ray, virile before the birth of the 'Origin of Species,' it has evolved through the length of two centuries, and reached its zenith as presented by Adolf Engler in 'Die Natürlichen Pflanzenfamilien' just over twenty years ago. Almost on the eve of the publication of Engler's mighty work, a new era in botanical history had dawned. In 1889, De Vries's 'Intracelluläre Pangenesis' had been given to the world, an essay which Bateson * declares "remarkable as a clear foreshadowing of that conception of *unit-characters* which is destined to play so large a part in the development of genetics," to be swiftly followed by 'Die Mutationstheorie' †; whilst the year 1900 brought with it the triple rediscovery of Gregor Mendel.

* W. Bateson, Mendel's Principles of Heredity,' 5 (1913).

† H. De Vries, 'Die Mutationstheorie' (1901–3).

As the incidence of the 'Origin of Species' shed transcendent light upon the mystery of the Natural System in 1859, so the work of these great protagonists in experimental evolution, and the expositions emanating from the schools of experiment and thought founded by them, cannot fail in time to illuminate Systematic Botany and inaugurate a new phase in the evolution of the idea of the Natural System.

De Vries by a rigid analysis of *Œnothera* separated numerous diverse forms breeding true, some exhibiting comparatively great differences. The Mutation theory postulates the evolution of forms progressively divergent. Hence it is conceivable that forms—for instance, genera grouped in different families—are in some cases comparatively closely related. Again, the characters exhibited by De Vries's mutant Œnotheras are paralleled in other mutating races—for example, giantism in *Œnothera gigas* also occurs in *Lathyrus odoratus* (Bateson, 1909), *Pisum sativum* (Mendel), and in *Primula sinensis* (Keeble, 1912). Facts of this kind serve to redirect attention to the importance of the doctrines of parallel development and convergence in relation to floral evolution, especially since the surviving natural races trend in the direction of synthetic and economic advance. Convergence in reproductive characters may occur even more frequently than has yet been contemplated, so that like forms, such as genera in the same family, may be less closely related than others are that differ more pronouncedly. Hence the Principle of Resemblances must now be qualified by a greater regard for the significance of differences, even if it be not shaken to its foundation by the doctrine of convergence and the existence of insidious parallelisms.

Before proceeding to attempt to solve the phylogenies of the families considered here, it will be convenient to review the evolutionary processes that have been discussed in relation to the results obtained by the experimentalists. But the prospect is by no means encouraging, since De Vries* writes: "The great lines of evolution of whole families and even of genera and of many larger species obviously lie outside the limits of experimental observation. They are the outcome of the history of the ancestors of the present types, and a repetition of their history is far beyond human powers."

The carpels in *Davidia* vary from five to ten, with a mean number of six or seven; they vary in number in the forms of *Hedera Helix*; and, in *Sambucus*, species are characterized by five, and a range of from two to four with a mean of three respectively.

Mutation in the carpels has not yet been specially mentioned as occurring in the races produced by experiment.

Syncarpy supervenes upon apocarpy, and the advance towards syncarpy is accompanied or followed by that towards perigyny and epigyny, but here again there is as yet little direct experimental evidence.

The most fascinating phenomena are those attendant upon sterilization. A vast number of instances are known in which sterility is probably due to seasonal conditions, or to diversion or poorness of the nutrient supply, including the very numerous cases where only few of very many flowers develop in the inflorescence. *Davidia*, where all the ovules in the ovary may be fertile or sterile, may be included in this category. Thence we pass to numerous other cases in which it is doubtful whether sterility has

* H. De Vries, 'Species and Varieties' (1905) p. 223.

become definitely fixed or not: as in *Lonicera*, where the majority of the ovules habitually abort; in *Polyosma*, where, according to Blume, only one of the numerous ovules forms a seed; in *Liquidambar*, where the lowermost ovules are stated to be always sterile; in *Aralia* and *Corylopsis*, where one of a pair, and in *Quisqualis*, where one of three ovules is sterile. And, finally, cases occur, exemplified by *Symphoricarpus*, where the sterility of particular ovules is no longer a matter of circumstance, having become fixed and hereditary.

Sterilization proceeding to an extreme leads to unisexuality; thus in the Hamamelidaceæ series exist between forms in which the ovary may or may not be sterile, to others with definitely polygamous flowers and others where the unisexual condition is attained; in *Nyssa*, series can be traced between hermaphrodite and female flowers owing to the loss of stamens; in *Griselinia*, *Aucuba*, and *Garrya* rudiments of the absent sex are retained, but the last traces have disappeared in *Helwingia* and in the male flowers of *Davidia*.

A great deal of light has been thrown on the series just enumerated by the results obtained in the experimental fields of enquiry. De Vries *, by his analysis of ever-sporting varieties, was able to show how profoundly the environment affects development. Here the primordium of the flower in Polycephalic Poppies was influenced by changed conditions applied within the fifth or sixth week after the beginning of germination, and fewer anomalous stamens were produced than under normal conditions, whilst the occurrence of polycotyly and polycephaly in polycotylous and polycephalous half-races did not become definitely fixed during cultivation and selection. The phenomena concerned variability, not mutability. He † also found that the development of the anther and pollen in *Œ. scintillans* was dependent on external conditions to a high degree. De Vries's ‡ *Œnothera* mutants show clearly grades of sterility. Some are rich in pollen, whilst *scintillans* is poor; others form many seeds, some few, as in *elliptica*, whilst in *brevistylis* many plants set no seed at all, but he believes the degree of fertility in many mutants will ultimately be found to follow Quetelet's law of fluctuating variability. Finally, with regard to sex sterility, unisexuality is exhibited by ever-sporting varieties, mutants, and Mendelian hybrids. R. P. Gregory § records that no stamens occur in one of the double forms thrown off by *Primula sinensis*; and E. R. Saunders ‖ has shown that the gynœcium in double Petunias is more or less deformed and when fertilized yields no seed, whilst double ¶ stocks are always sterile and are always obtained from seed set from ever-sporting singles. De Vries ** obtained a male sterile mutant, *Œnothera lata*. Lastly, Bateson ††, Punnett, and Saunders, working with Sweet Pea, and Salaman ‡‡, with Potato, have isolated male-sterile Mendelian forms.

* H. De Vries, 'Species and Varieties' (1905) 369, and 'Mutation Theory,' ii. (1910) 343, 450.

† H. De Vries, 'Mutation Theory,' i. (1910) 383.

‡ H. De Vries, *l. c.*, *scintillans*, 383; *elliptica*, 396; *brevistylis*, 316.

§ R. P. Gregory in Journ. Gen. i. (1911) 90.

‖ E. R. Saunders in Journ. Gen. i. (1911) 63.

¶ E. R. Saunders in Journ. Gen. i. (1911) 304.

** H. De Vries, *l. c.* 409.

†† Bateson, Punnett, & Saunders in Rept. Govt. Com. Roy. Soc. iv. 16.

‡‡ Redcliffe N. Salaman, in Journ. Linn. Soc., Bot. xxxix. (1910) 301.

The facts that the number of chromosomes may vary in mutants, as recorded by Gates* (1907) and later by Anna M. Lutz † (1907) for *Œnothera*, and that giantism is accompanied by increase in cell-size as first shown by Gates ‡ (*Œnothera*), and later by Keeble § (*Primula*), show the depth as well as breadth of the new aspect of things. It is hardly possible, therefore, to exclude the ovule from the possibilities of mutation. The change and grades of change from orthotropy to anatropy, the origin of the single and double integument, and even the change from many to few axial rows may yield in turn to patient and persistent experimental endeavour.

We are now able to conceive the origin of mutants in floral characters. Mutants might arise, for example, from apocarpous forms bearing some few and some many carpels. These could in time produce new species. If both the floral and vegetative organization alter considerably during the continuance of mutation, forms would arise exhibiting still greater divergence. But the advent of syncarpy and epigyny again and again in different families, and the frequent occurrence of sterilization in both Monocotyledons and Dicotyledons, culminating time after time in the evolution of uniovulate ovaries, whilst increasing enormously the tale of floral diversity, nevertheless contribute toward the evolution of synthetic and convergent structures.

Origins.—The interpretation of phylogenies must be influenced by views of origin, and the origin of new forms, as postulated by the Mutation Theory, is to render the recognition of affinities more problematic than ever. It is the custom to sort plants into divisions and groups according to this or that bias, and to construct a phylogenetic twig or branch of the great tree of descent; but the Mutation Theory brings home to us that that which is actually accomplished in Systematic Botany is the aggregation or linking of species, genera, and even families, as the case may be, that have attained a similar level in evolution, a similar resultant effect of racial experiences. These aggregations may or may not be related. The Compositæ, for example, form a homogeneous group consisting of genera in the same phase of synthetic and economic development; but is it certain that the members of the family are bound by the bonds of relationship, and are traceable to a single progenitor?

A general device in Comparative Morphology is to seek for clues to an interpretation of the origin of a structure from morphological series, and thence deduce a concept of affinity. But spacial series may not necessarily coincide with series in time, as exemplified by the sterilization series in the Caprifoliaceæ and De Vries's Œnotheras, where one form has not passed into another form, but each one has originated separately. Some points, however, carefully chosen, may establish unlooked-for differences. Thus the situation of the sole surviving seed is constantly parietal in the Hamamelidaceæ and axial in the Caprifoliaceæ. Hence in the Cornaceæ, where genera occur with either the parietally or axially borne seed, there is a strong bias towards the use of this character as an indicator of different origins. Again, the tangentially and radially orientated

* R. R. Gates in Bot. Gaz. xliii. (1907) 81–114.

† Anna M. Lutz, Science, xxvi. (1907) 151.

‡ R. R. Gates in Arch. f. Zell. iii. (1909) 525–552.

§ F. Keeble in Journ. Gen. ii. (1912) 163.

ovule, as exemplified by *Cornus* and *Helwingia* respectively, may prove a useful character, the sympathetic development of the ovary in relation to the form of ovule having evidently evolved independently in each genus during the period of abortion through which the ovary has conceivably passed.

PHYLOGENY OF THE HAMAMELIDACEÆ.—Robert Brown* considered that the Hamamelidaceæ possessed affinities with Bruniaceæ on the one hand and the Cornaceæ on the other. Affinity with the Bruniaceæ and Saxifragaceæ is more nearly consistent with well-balanced modern opinion.

Lindley† placed *Altingia* and *Liquidambar* between the Betulaceæ and Salicaceæ. Hallier‡, in 1905, reverts to this affinity, conceiving the descent of the Betulaceæ from the Hamamelidaceæ. This plausible supposition is not supported by the embryology, and the endosperm as a crucial character has been too lightly regarded. L. S. Gibbs§ suggests that the Alsinoideæ illustrate an intermediate stage in the development of the exalbuminous seed by a progressive reduction in the functions of the nucellus; and Péchoutre's‖ investigations point to a similar tendency in the Rosaceæ. But even if the evolution of the exalbuminous seed has occurred in several families, it scarcely follows, especially when the embryology is different, that the Betulaceæ are virtually exalbuminous Hamamelidoideæ. The families are probably convergent, with separate and distinct lines of origin.

The Hamamelidaceæ, whilst exhibiting diverse characters of floral organization, form nevertheless a fairly homogeneous group. It is difficult to subdivide the family into well-defined sections, and every criterion hitherto used has failed. The characters are in harmony with Saxifragacean characteristics, and the Hamamelidaceæ pass presumably into a pro-Saxifragacean plexus forming an older line originating perhaps from more than one progenitor.

PHYLOGENY OF THE CAPRIFOLIACEÆ.—The Caprifoliaceæ are remarkable, owing to a singular correspondence in several important and deep-seated characters—the epigynous ovary, the biseriate ovules, the evolution of an axially suspended seed owing to abortion, and the tangentially orientated and similarly organized ovule. Here, again, the characters that have been adopted to separate the genera into groups or even families have proved futile, except in the case of *Adoxa*.

Diervilla temptingly recalls *Polyosma*, but the resemblance reveals divergencies from the Caprifoliaceæ rather than a possible prototype; the differences, however, are not incompatible with affinity on the Saxifragacean side.

Lindley¶ suggested a possible connection between *Sambucus* and *Hydrangea*, partly

* Robert Brown, 'Characters and Descriptions of Three new Species of Plants' (London, 1818).

† J. Lindley, Veg. King. 2nd ed. (1847) 253.

‡ Hans Hallier in New Phyt. iv. (1905) 151.

§ L. S. Gibbs in Ann. Bot. xxi. (1907) 51.

‖ F. Péchoutre in Ann. Sci. Nat., Bot. 8me sér. xvi. (1902) 156.

¶ J. Lindley, Veg. King. 767.

influenced by the sterile ray-florets in both genera. Here, although the reasons given may now be thought unsound, and the differences between the types compared are greater than in the former case, a second reasonable line of descent on the Saxifragacean side may be contemplated.

The organization of the ovary of *Leycesteria* is not far removed from that of *Pyrus*, whilst biseriate ovules are found in *Spiræa*, but the structure of the ovule is not compatible with direct descent on the Rosacean side. *Leycesteria* perchance originated from an issue of the pro-Rosacean plexus, in which the ovule itself progressed and the biseriate rows, reduced in *Pyrus*, were retained.

Phylogeny of the Cornaceæ.—The Cornaceæ of both Harms and Wangerin are polyphyletic, and the family consists chiefly of outlying forms, representatives of stocks that have become obsolete.

There is no warrant from recent discoveries for the recession of *Garrya* to the vicinage of the orthotropal cohorts. *Garrya* is more reasonably linked by slender and far distant threads to the Bruniaceæ and Hamamelidaceæ.

Aucuba is probably a scion from pro-Rosacean stock. Here the descending form of ovule found in *Pyrus* and *Prunus* has become specialized, and the ovary considerably reduced.

It is curious that, whilst this morphological analysis dissociates *Garrya* and *Aucuba*, the most successful reciprocal effects in cross-grafting have been obtained with these genera. Owing to the kindness of Sir Harry Veitch, the private records of a long series of experiments, records of successes and failures in cross-grafting, have been placed at the writer's disposal. Here, whilst the successful grafts are nearly always between genera of the same family, it must be admitted that failures between nearly related genera are numerous. In one case alone a graft succeeded, and that only for a time, in which genera of different families were used—the reciprocal grafting of *Ilex Perneyii* and *Buxus balearica*. But genera from different families were infrequently chosen for experiment. The following reciprocal grafts failed:—*Cornus* and *Aucuba*, *Griselinia* and *Aucuba*, *Sambucus* and *Viburnum*, *Loropetalum* and *Hamamelis*, *Distylium* and *Sycopsis*, *Nyssa* and *Aucuba*, *Aralia* and *Hedera*.

Helwingia is difficult to relate. It may be, perhaps, regarded as an epigynous representative of a parallel line to the Sapindaceæ.

Davidia and *Nyssa* are isolated forms abutting on the Araliaceæ, but scions from different progenitors belonging to a pro-Araliacean stock. Here obtains a specialized form of the Rosacean ascending ovule; so that this plexus might extend through issues now extinct into the primitive Rosaceæ.

Alangiaceæ still await a keen scrutiny of the ovule, and leave the respective claims of the Cornaceæ, Combretaceæ, and *Polyosma* unsatisfied. *Alangium* appears to be a reduced analogue of *Davidia*, possessing the Cornean type of ovule.

Corokia and *Griselinia* are provisionally regarded as outlying forms to *Cornus* that have had an independent origin.

Vascular Structure of the Flower in Angiosperms.—Since Van Tieghem's * memoir of 1868, when the vascular systems of several evolutionary types of both monocotyledonous and dicotyledonous flowers were examined, this subject has progressed very little beyond the purely descriptive stage. Hence the leading features of economical advance may be outlined here. The simplest trace of a single carpel consists of a median or dorsal and two marginal or ventral bundles. In the Hellebore, where the carpels are united at their bases, bivalent traces occur in the basal portion. Pronounced cases of syncarpy reveal two series of bundles in the ovary-wall—the outer homologous with dorsal, the inner with marginal bundles, and in *Geranium longipes* the marginal bundles coalesce in pairs. The vascular changes which supervene with perigyny and epigyny vary in different families. In *Aralia* the stemonal and perianthic traces, now included in the ovary-wall, form a third and outermost series of bundles. The two outer series, distinct in *Aralia*, have become synthesized to form one in *Castanea*, several genera of Cornaceæ, and the epigynous Sympetalæ. The amalgamation is incomplete in *Davidia* and *Marlea*. Another mode of origin of the single outer series is indicated in the Hamamelidaceæ, where the single series of bundles, evident as far as the insertion of the perigynous ridge, might have a further upward extension as the ovary becomes inferior.

The last traces of the dorsal carpellary bundles may disappear, as in *Lonicera* and *Leycesteria*, but here the bundles passing to stamens and petals are perhaps not strictly homologous with stemonal and petal traces respectively.

By a further economical advance the bundles in the single series, which in *Cornus*, *Leycesteria*, and many other genera are equal to the sum of the petals and stamens, are in *Viburnum*, the Campanulaceæ, and Compositæ reduced to one-half the number.

Lines of asymmetrical development are exemplified by *Viburnum*, a precursor of the irregular vascular systems which prevail in the Valerianaceæ.

No phylogenetic significance can be attached to a particular form of vascular system; but vascular details may afford a clue in support of an interpretation of origin, as in *Viburnum*, *Aucuba*, etc., but they should always be used with the utmost reserve.

The Ovule in Angiosperms.—Mirbel † wrote in 1829: "On peut dire qu'à cette première époque tous les ovules sont orthotropes."

The orthotropous ovule is primitive to the anatropous types.

The ovule, in *Juglans regia*, according to Benson and Welsford ‡, is not strictly orthotropous, but exhibits "one mode of the phylogenetic origin of the orthotropous basal ovule from an anatropous parietal type." Benson and Welsford describe two types of flower: in one there are two opposite basal parietal placentæ, of which one bears a single erect ovule and the other is barren; in the other, the ovule is apparently borne by the two placentæ and becomes basal and orthotropous. Now, in the first case, the

* Ph. Van Tieghem in Ann. Sci. Nat., Bot. 5me ser. ix. (1868) 127-226, t. 9-12.

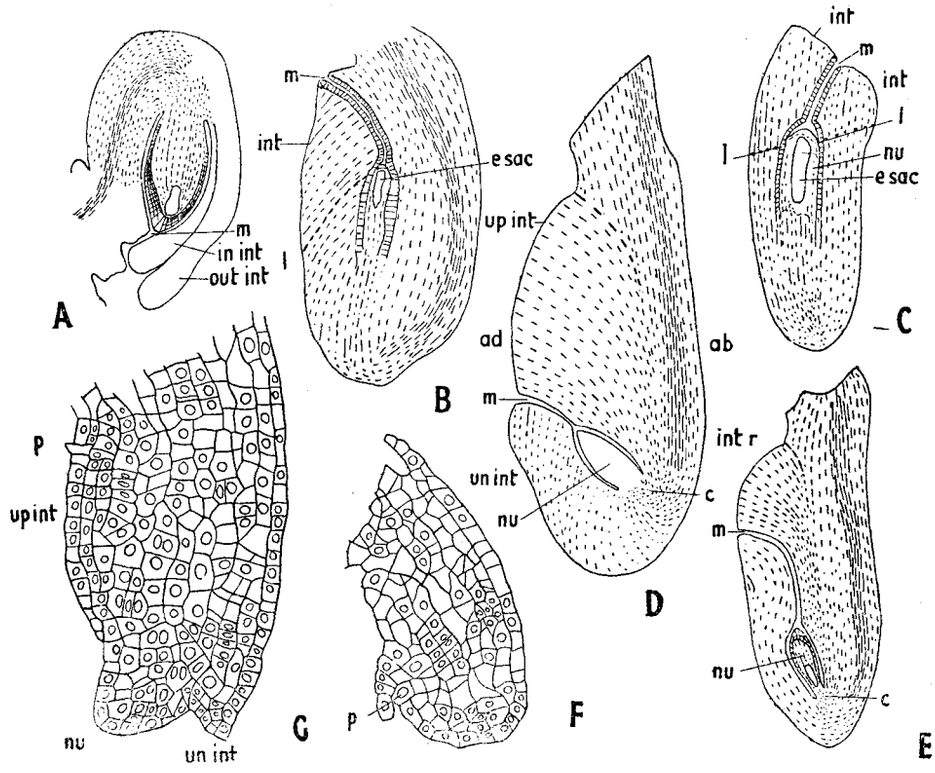
† Mirbel in Mém. de l'Acad. des Sciences, ix. (1830) 611.

‡ Benson and Welsford in Ann. Bot. xxiii. (1909) 629.

ovule, being erect, is only slightly anatropous and hence can be regarded as exhibiting the very earliest stage in the evolution of the anatropous ovule.

The stage in evolution evident in *Juglans* is followed by the complete inversion of the nucellus, owing to the curvature of the raphe as in the Cactaceæ and Saxifragaceæ, and further by the congenital union of the raphe and integument as exemplified by the Rosaceæ. This phase of evolutionary advance is characterized by the separation of several anatropal types. Two types obtain in the Rosaceæ: one "ascending," with the nucellus directed upwards as in *Cerasus juliana*; the other, "descending," with the

Text-fig. 13.



Diagrams illustrating the structure of the ovule.

A, *Pyrus Malus*; B, *Helwingia ruscifolia*; C, *Davidia involucrata*; D–G, *Aucuba japonica*.

ad=adplacental side; *ab*=abplacental side; *c*=chalaza; *e.sac*=embryo-sac; *int*=integument; *int.r*=cell-rows of integument; *in.int*=inner integument; *out.int*=outer integument; *up.int*=upper margin of integument: *un.int*=lower margin of integument; *l*=limit of integument; *m*=micropyle; *n*=nucellus; *p*=pivot cell.

nucellus directed downwards, as in *Cratægus Oxyacantha* and *Pyrus Malus* (Text-fig. 13, A). The former type is not far removed from the "dorsal" ovule which prevails throughout whole families, such as the Araliaceæ, whilst the ventral ovule in Cornaceæ (Text-fig. 13, E, *Aucuba*; B, *Helwingia*) is conceivably an advance upon the "descending" type. Specialized forms of the "dorsal" and "ventral" ovule are found in *Davidia* and *Helwingia* respectively (Text-fig. 13, C and B), where the integument (*int*) exists as a separate organ for only a short distance below the summit of the nucellus —to the line marked *l* in the figures.

The line of anatropal advance and specialization is accompanied by the transition from the bi- to the uni-tegumentary condition.

Benson *, in 1894, found all stages from two completely free integuments in Fagaceæ, to two more or less fused in Casuarinaceæ and Corylaceæ. Péchoutre †, in 1902, demonstrated a similar series in Rosaceæ and both the uni- and bi-tegumentary condition in one genus, *Spiræa*.

A third series occurs in the Ranunculaceæ, whilst one or two integuments characterizes the Dilleniaceæ and Ochnaceæ. A single integument is found, for example, in the Triuridales, Ceratophyllaceæ, Empetraceæ, Aquifoliaceæ, Cochlospermaceæ, Loasaceæ, Umbelliflorae, and prevails almost exclusively in nearly all the cohorts of the Sympetalæ.

A third line of advance lies in the direction of the reduction in bulk of the nucellus. The axile rows are numerous in the Rosaceæ, few in the Araliaceæ, and reach their minimum development in *Lilium*, *Helwingia*, and *Inula*.

Ovular Connections.—Where each loculus contains several series of ovules, as in the Saxifragaceæ, the main placental bundles branch repeatedly throughout their course on their outer side; branches of the second and third order arise from these and the ultimate branchlets supply the ovules—one to each. Transitional vascular stages, accompanying the change from the multiseriate to the biseriate arrangement, have not been studied; but when the ovules are in two series, as in *Leycesteria*, the system is reduced, each main bivalent axial bundle produces short branches on either side, supplying ovules in the right- and left-hand loculus respectively—one branch to each ovule. When the ovules in the double series are reduced to a terminal pair, rendering each loculus biovulate, the branches are also reduced to two as in *Aralia* and the Hamamelidaceæ. The further change from the biovulate to the uniovulate loculus involves several instances. Thus the change from *Aralia* or *Corylopsis*, where one of a pair of ovules is sterile, to *Hamamelis*, where one placenta of each pair is barren, is accompanied by the abortion of the branch pertaining to the barren placenta and the ovule receives a single bundle. But where the single ovule is axially borne, the ovular trace is frequently double, receiving a vascular supply equivalent to that of a pair of axially borne ovules. In *Davidia*, the branches uniting to form the ovular trace arise from several small bundles extending in the right- and left-hand septa and pertain to the right- and left-hand sides of the carpel; in *Cornus*, the branches arise from bivalent peripheral bundles; and in *Helwingia*, where the median branch from an axial bundle forms the ovular trace, the axial bundle represents two united marginal bundles of the same carpel, so that the median branch may be considered bivalent.

In more advanced stages of reduction, where the septa disappear and the ovary becomes uniovulate, various anomalies occur, such as have been described in detail for *Viburnum*, *Corokia*, *Griselinia*, and *Nyssa*.

It is highly probable that a parallel series of stages will be found leading towards

* M. Benson in Trans. Linn. Soc., Bot. 2nd ser. iii. (1894) 409–424, t. 67–72.

† F. Péchoutre in Ann. Sci. Nat., Bot. 8me sér. xvi. (1902) 88.

genera where the ovule in the uniovulate loculus or ovary is basal. In the case of *Juglans regia*, already cited, the ovule, when parietally borne, is supplied by the bundle in the corresponding placenta, as in *Aralia*; but when basal (axially situated), bundles from both placentæ are contributory as in *Cornus*.

Ovular Vascular System.—Integumentary vascular tissue has been known since 1829, when Mirbel * described and figured the vascular systems of the ovules of *Myrica pensylvanica*, *Corylus Avellana*, *Juglans regia*, and *Quercus Robur*, and states:—"On voit fréquemment à la superficie de la Primine des nervures tantôt simples tantôt ramifiées qui partent de la chalaze et se dirigent vers l'Exostome." A. Gris †, in 1861, figured integumentary bundles in *Ricinus communis*; Van Tieghem ‡, in 1872, indicates several examples selected from different families, and Le Monnier §, in the same year, described and figured the nervation in many seeds. The vascular system in *Myrica*, *Juglans*, and certain Amentiferæ was rediscovered by E. M. Kershaw ‖ in 1909.

Balfour ¶ suggested that in non-vascular seeds the integument forms the water-supply of the ovule.

L. S. Gibbs ** subsequently showed that the outer integument in the Alsinoideæ actually performs this function.

The writer †† explained that in *Davidia* the ovular bundle branches and forms a considerable system in the young seed, and the "integument" with its vascular system is organized as an elaborate reservoir during the accumulation of an abundant endosperm.

The water problem has to be solved in connection with seed-development from ovules of numerous types, and it is clear that a similar device is adopted time and again in phylogeny, early or late in ovular development according to special needs. Hence the possession of a vascular supply is scarcely of considerable phylogenetic importance, as suggested by E. M. Kershaw.

Phylogeny of Angiosperms.—The author of each great system has in turn realized that his classification is far from perfect and contains speculative groups difficult to define. Hence the finding that two families of Angiosperms are polyphyletic, in itself, merely corrects or modifies a fragment of Engler's system, and, indeed, Engler has already recognized the polyphyletic nature of his original Cornaceæ by adopting Wangerin's not satisfactorily established arrangement in 'Das Pflanzenreich.' But the facts that have influenced the writer to deduce polyphyletic origin for these families are derived from an investigation in detail as yet unattempted, except perhaps in the

* Mirbel in Mém. de l'Acad. des Sciences, ix. (1830) 632.

† A. Gris in Ann. Sci. Nat., Bot. 4me sér. xv. (1861) 5–9, t. 2.

‡ Ph. van Tieghem in Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 228–232.

§ G. Le Monnier in Ann. Sci. Nat., Bot. 5me sér. xvi. (1872) 233–305, t. 9–12.

‖ E. M. Kershaw in Ann. Bot. xviii. (1909) 353, 692.

¶ I. B. Balfour in Proc. Brit. Assoc. Adv. Sci., Bot. Sect. (1901).

** L. S. Gibbs in Ann. Bot. xxi. (1907) 25–55, t. 5, 6.

†† A. S. Horne in Trans. Linn. Soc., 2nd ser. Bot. vii. (1909) 315.

case of very few families, and he claims polyphyly for at least three genera of the Caprifoliaceæ and eight of the Cornaceæ, although in the latter family some genera have remained closely associated for a considerable period. Now very many families comprise a certain number of obscure forms, and subsequent analysis may determine not only that these cannot be included in any existing family, being the sole representatives of extinct lines, but even the apparently stable members of the family may show evidence of parallel development and convergence.

Allowance must also be made in phylogenetic systems for cases where differently organized forms may possess probable affinity, such as, for instance, *Polyosma* and *Diervilla*, but the suggested origin of one from the other must be compatible in all respects with morphological structure and evolutionary methods established by experiment; thus, relatives of *Polyosma* should possess the power of advance towards the condition in *Diervilla*, both with respect to gamopetaly and the number and nature of the ovules.

It is a long-established custom to regard certain characters as more constant and dependable than others, conceiving that the ovule, for example, would be less liable to change than more superficial characters. According to De Vries's view of indiscriminate mutation, however, the ovule would be equally liable to change, but since mutation is a rare phenomenon, difficult to perceive. Even then, however, the ovule would pass through relatively fewer mutations than the floral organization, so that a certain form of ovule might remain constant for a considerable range of floral and vegetative change. Hallier reverts to an indiscriminate use of characters without due regard to relative value; thus *Garrya* is retained in the Cornaceæ owing to the discovery of aucubin by Hérissey and Lebas* in this genus, although a criterion of this kind is of doubtful value unless supported by considerable research. Hallier† has attempted that which cannot be accomplished from the evidence yet accumulated, and the inevitable result of this finds expression in the extreme instability of his system.

Knowledge of the phylogeny of Angiosperms can only be truly advanced by the detailed morphological and experimental investigation of many more families, and then, but not till then, can Engler's system be replaced by a greater scheme more nearly approximating to natural relationships. In such a scheme the barrier between the Polypetalæ and Sympetalæ will doubtless be removed, and the various families, upon reconstruction, will be arranged in plexuses according to their probable origin and relationship. It is possible to forecast the lines upon which this will be attempted, but the effort lies beyond the scope of this present work.

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* Hérissey and Lebas in Bot. Centralbl. cxvii. (1911) 176.

† H. Hallier in Beihefte Bot. Centralbl. xxiii. 2 (1908) 81, and Arch. Néerl. d. Sci. Ex. et Nat. sér. 3, Bd. i. 146 (1912).

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EXPLANATION OF THE PLATES.

PLATE 28.

Fig. 1. *Cornus Amomum.* Young flower.
Fig. 2. *C. Amomum.* Young flower with two petals removed.
Fig. 3. *C. alba.* Fruit.
Fig. 4. *Marlea platanifolia.* Portion of a very young inflorescence with flowers in a stage prior to the development of the ovarian cavity.
Fig. 5. *M. platanifolia.* Single flower older than 4, ovary still undeveloped.
Fig. 6. *M. platanifolia.* Portion of a flower slightly older than 5.
Fig. 7. *M. platanifolia.* Flower slightly older than 6, with some of the petals and stamens removed.
Fig. 8. *Aucuba himalaica.* Normal flower.
Fig. 9. *A. himalaica.* Flower with six petals.
Fig. 10. *A. himalaica.* Flower with five petals and one stamen.
Fig. 11. *A. himalaica.* Flowers with petals removed showing bilobed style.
Fig. 12. *A. himalaica.* Flower with petals removed showing three styles.
Fig. 13. *Garrya elliptica.* Female catkin, nat. size.
Fig. 14. *G. elliptica.* Female flower with one style bilobed.
Fig. 15. *G. elliptica.* Young fruit slightly enlarged.
Fig. 16. *G. elliptica.* Portion of male inflorescence.
Fig. 17. *G. elliptica.* Portion of male inflorescence, bracts removed.
Fig. 18. *G. elliptica.* Single flower.
Fig. 19. *G. Thuretii.* Portion of male inflorescence, showing one "flower" with four perianth-segments and nine stamens.
Fig. 20. *G. Thuretii.* Single "flower" with seven perianth-segments and seven stamens.
Fig. 21. *G. Thuretii.* Another "flower" with five perianth-segments and ten stamens
Fig. 22. *G. laurifolia.* A terminal male flower (*br*=bract).
Fig. 23. *G. laurifolia.* The same flower, different view.
Fig. 24. *G. laurifolia.* Terminal flower.
Fig. 25. *G. laurifolia.* Lateral flower.
Fig. 26. *Helwingia ruscifolia.* Trimerous male flower.
Fig. 27. *H. ruscifolia.* Tetramerous male flower.

Fig. 28. *H. ruscifolia.* Young female inflorescence.
Fig. 29. *H. ruscifolia.* Young female flower.
Fig. 30. *H. ruscifolia.* Mature flower, pentamerous.
Fig. 31. *H. ruscifolia.* Flower with four perianth-leaves and five carpels.
Fig. 32. *H. ruscifolia.* Tetramerous flower.
Fig. 33. *Corokia Cotoneaster.* Young flower.
Fig. 34. *C. Cotoneaster.* Mature flower.
Fig. 35. *Griselinia lucida.* Young male flower.
Fig. 36. *G. lucida.* Hexamerous male flower, side view.
Fig. 37. *G. lucida.* Hexamerous male flower, viewed from above.
Fig. 38. *G. littoralis.* Male flower, closed.
Fig. 39. *G. littoralis.* Male flower, open.
Fig. 40. *G. lucida.* Very young female flower, highly magnified.
Fig. 41. *G. lucida.* An older stage.
Fig. 42. *G. lucida.* Mature flower.
Fig. 43. *G. lucida.* Fruit.
Fig. 44. *G. littoralis.* Young female flower.
Fig. 45. *G. littoralis.* Mature flower.
Fig. 46. *G. littoralis.* Young fruit.
Fig. 47. *G. littoralis.* Older fruit.
Fig. 48. *Nyssa sylvatica.* Portion of a young inflorescence.
Fig. 49. *N. sylvatica.* Young flower.
Fig. 50. *N. sylvatica.* Young flower with petals removed to show the single stamen present in this specimen.

PLATE 29.

[Abbreviations:—*arch.* = archesporium; *ant.* = antipodals; *ax.* = axial row; *e. sac.* = embryo-sac; *l.* = loculus; *int.* = integument; *m.* = micropyle; *m. sp.* = megaspore; *n. ep.* = epidermis of nucellus; *par.* = parietal tissue.]

Figs. 51–54. *Symphoricarpus racemosus.* Development of sporogenous tissue in sterile ovules. 51, primary archesporial cell; 52, two sporogenous cells; 53, four sporogenous cells; 54, one of four megaspores has germinated to form an incomplete embryo-sac. × 600 approx.

Figs. 55–57. *Viburnum Lantana.* Development of the megaspores in the incomplete ovules. 55, primary archesporial cell; 56, binucleate sporogenous cell; 57, quadrinucleate sporogenous cell. × 600 approx.

Figs. 58–60. *V. Lantana.* Further development of the sporogenous tissue in the incomplete ovules. 58, portion of multinucleate protoplasmic sac showing eight of the twelve nuclei; 59, nuclei approximated in pairs; 60, segmented protoplasmic sac. × 600 approx.

Fig. 61. *Sambucus nigra.* Vertical section through a young ovule, showing single integument and nucellus with primary archesporial cell. × 290 approx.

Fig. 62. *S. nigra.* Section through an ovular rudiment showing the enlarged subepidermal cells. × 590 approx.

Figs. 63–64. *S. nigra.* The nucleus in the enlarged cells has divided to form two or four daughter nuclei. × 590 approx.

Fig. 65. *Benthamia fragifera.* Vertical section of a young ovule showing an early stage in the upgrowth of the single integument. × 290 approx.

Fig. 66. *B. fragifera.* Vertical section of a young ovule, showing the nucellus with axial rows. × 290 approx.

Fig. 67. *Cornus sanguinea.* Showing the single integument and axial rows. ×290 approx.

Fig. 68. *Aucuba japonica.* Vertical section showing the earliest stage in the development of the ovular mamelon. ×600 approx.

Fig. 69. *A. japonica.* An early stage in the formation of parietal tissue. ×590 approx.

Fig. 70. *A. japonica.* Vertical section through the nucellus showing the enlarged embryo-sac-mother-cell. ×290 approx.

Fig. 71. *A. japonica.* Transverse section of the nucellus showing two megaspores belonging to different axial rows. ×290 approx.

Fig. 72. *A. himalaica.* Reconstruction from three vertical sections of the nucellus showing a complete embryo-sac and an enlarged megaspore. ×290 approx.

Fig. 73. *Helwingia ruscifolia.* Vertical section of a young ovule showing an early stage in the development of the single integument and the nucellus. ×580 approx.

Fig. 74. *H. ruscifolia.* Vertical section of the nucellus showing the embryo-sac. ×290 approx.

Fig. 75. *Griselinia lucida.* Vertical section of the nucellus at a very early stage. ×580 approx.

Fig. 76. *G. lucida.* A slightly older stage showing axial rows. ×580 approx.

Fig. 77. *Nyssa sylvatica.* Transverse section of a very young ovule showing the nucellus invested by a single integument. ×580 approx.

N.B.—Figs. 51–77 are semi-diagrammatic.

Plate 30.

[Abbreviations:—*a*, *b*, *c*, *d*, *e* = principal bundles; *ax.* = inner peripheral bundle (corresponds to axial bundle); *in. ser.* = dorsal and lateral carpellary branches; *ov.* 1, *ov.* 2, *ov.* 3 = placental branches from *ax.*; *pe.* = petal-bundle; *st.* = stemonal trace; *x*, *y* = auxiliary bundles; *x'*, *y'* = branches from *x*, *y* respectively.]

Fig. 78. Photograph of a reconstruction in wax of the vascular system of the flower of *Viburnum Lantana.* ×60 approx.

Abbreviations occurring in Text-figures 1–12.

a. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
a'. Fig. 3, ovular rudiment.
ax. Figs. 2, 3, 9 and 10, axial bundles.
b. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
b'. Fig. 3, ovular rudiment.
br. Fig. 4, bracteole; Fig. 11, branches from outer series.
c. Fig. 3, ovular rudiment; Fig. 4, principal bundle.
c'. Fig. 3, ovular rudiment.
d. Figs. 1, 8–10, dorsal carpellary bundle; Fig. 4, principal bundle; Fig. 5, dorsal bundle.
e. Fig. 4, principal bundle.
emb. Fig. 8, embryo.
end. Fig. 8, endosperm.
f. Fig. 8, epigynous foliole (bracteole).
in. ser. Figs. 1–12, inner series.
int. Figs. 9 and 10, integument.
l. Fig. 1, lateral carpellary bundle; Fig. 9, branches from axial bundles.

loc. Figs. 1, 5–12, loculus.

m. Fig. 1, septal or placental bundles; Fig. 8, marginal carpellary bundles.

nu. Figs. 5, 8, 9 and 12, nucellus.

o, o′. Figs. 5 and 6, branches concerned with ovular supply.

ob. Fig. 5, branch from *o*.

ob′. Fig. 5, branch from *o′*.

ovy. Fig. 5, inner branches ; Fig. 6, dorsal and lateral carpellary bundles.

out. ser. Figs. (etc.), outer series.

ov., *ov.* 1, *ov.* 2, etc. Figs. 2 and 3, series of ovules ; Fig. 4, placental branches from *ax* ; Fig. 10, 11, and 12, vascular tissue supplying the ovules.

pe. Fig. 1, perianth traces ; Figs. 2, 6, 7 and 10, petal bundles ; Fig. 11, petal.

pl. Figs. 1, 3, 4 and 10, placenta.

r. pe. Fig. 11, rudiments of petals.

r. st. Fig. 11, rudiments of stamens.

rud. ax. Fig. 7, rudimentary axial bundles.

se. Fig. 9, sepal bundle; Fig. 11, sepal.

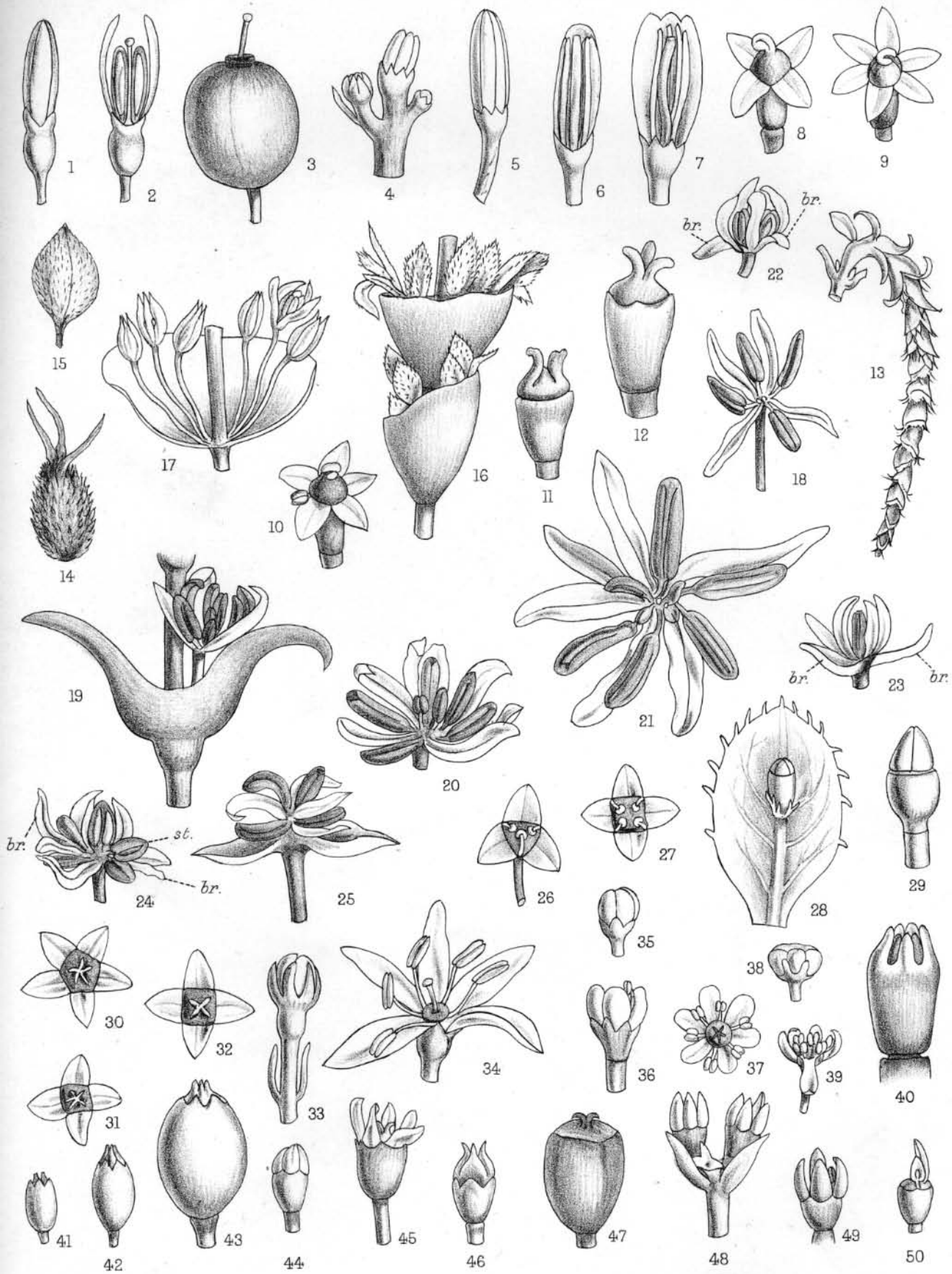
st. Figs. 1, 2, 4, 10 and 12, stemonal bundles.

sty. Figs. 5, 9–12, stylar canal.

t. cy. Fig. 6, toral cylinder.

xy. Fig. 4, auxiliary bundles.

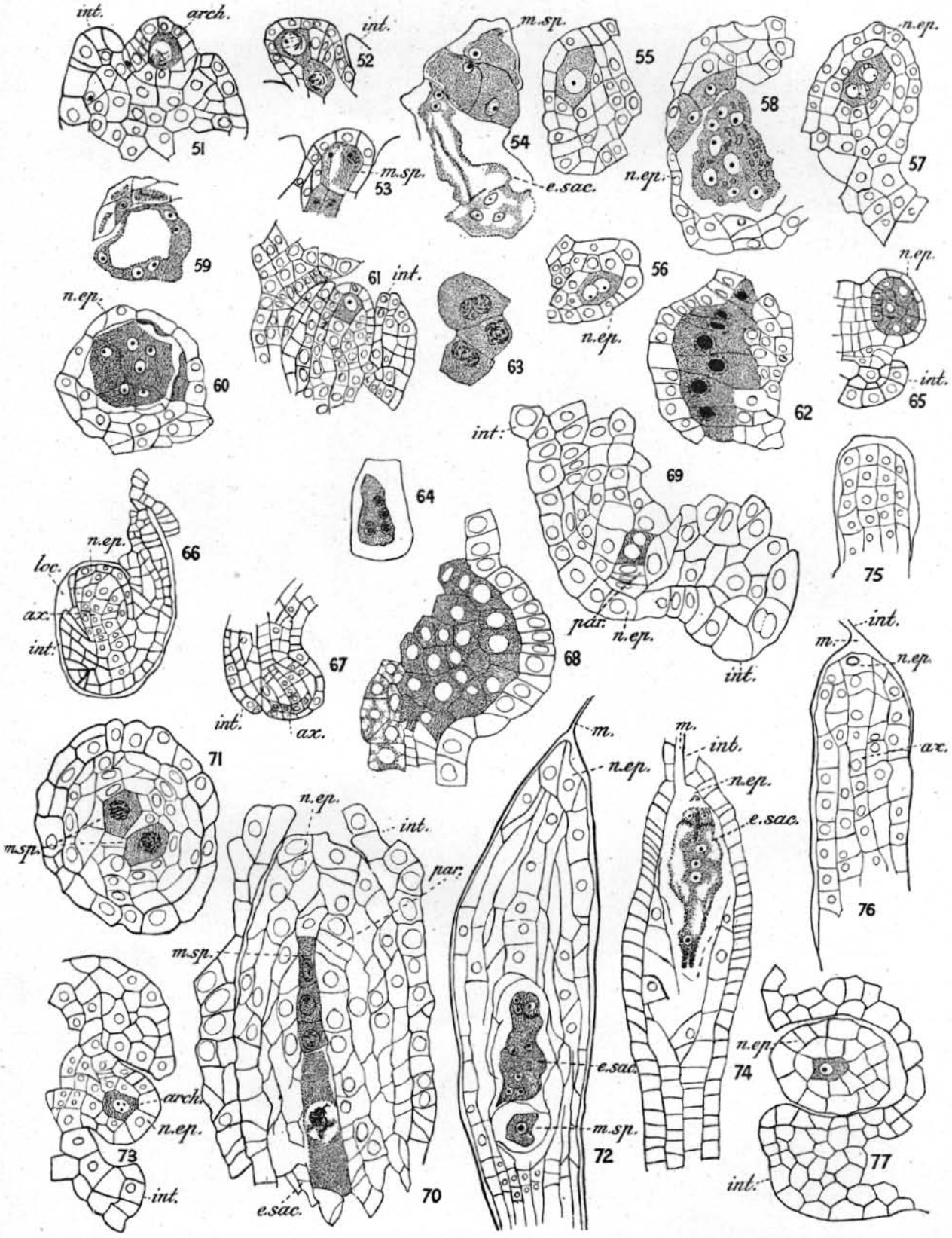
x′ y′. Fig. 4, branches from *xy*.

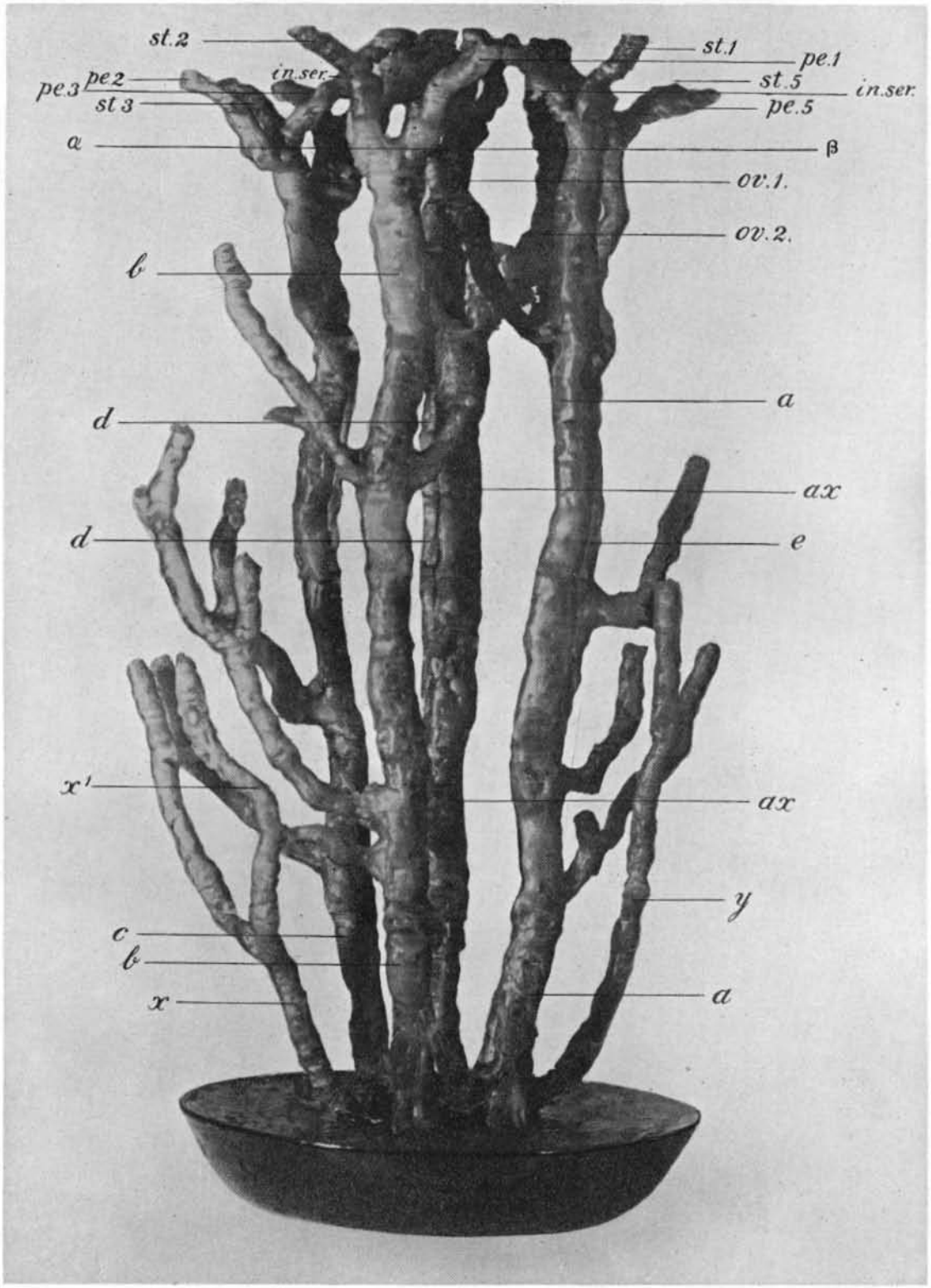


A. S. H. del.
J. N. Fitch lith.

West, Newman imp.

CORNACEAE.


int.
arch.
51
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52
m.sp.
53
m.sp.
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e.sac.
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n.ep.
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e.sac.
arch.
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73
int.
70
e.sac.
e.sac.
m.sp.
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74
77
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A. S. H. phot. Grout, sc. & imp

VASCULAR SYSTEM OF THE FLOWER OF *VIBURNUM LANTANA*