XIX.—Contributions towards a Knowledge of the Anatomy of the Lower Dicotyledons. II. The Anatomy of the Stem of the Berberidaceæ.

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Introductory.

The present paper is the second of a series of investigations into the anatomy of the lower Dicotyledons (1), aiming at the accumulation of anatomical data which, it is hoped, may prove of service in elucidating the phylogeny of the complex of orders usually regarded as situated somewhere near the base of the Angiosperm phylum. The continuance of the War has again materially retarded these investigations, and has also rendered it almost impossible to obtain material from abroad that would, doubtless, have been available in peace time. We are greatly indebted for substantial assistance in this relation more especially to Sir David Prain, F.R.S., Director of the Royal Botanic Gardens, Kew, and to Sir Frederick Moore, F.R.S., Director of the Glasnevin Gardens, Dublin, and to them we tender our grateful thanks.

According to Prantl (2), the order Berberidaceæ includes eight genera—Podophyllum, Jeffersonia, Diphylleia, Achlys, Nandina, Epimedium, Leontice, and Berberis (including Mahonia). To these Lotsy (3) adds Hydrastis and Glaucidium, which Prantl places among the Ranunculaceæ. The Lardizabalaceæ are included in the Berberidaceæ by Solereder (4), as also by Bentham and Hooker (5), while Berberidopsis, sometimes placed in Berberidaceæ, is included in Flacourtiaceæ by other authors. In the following pages seven of the eight genera of Berberidaceæ, as enumerated by Prantl, and representatives of four genera of the Lardizabalaceæ, viz. Lardizabala, Stauntonia, Akebia, and Decaisnea are discussed.

For detailed treatment the common Barberry, *Berberis vulgaris*, L., has been selected, and its anatomy is compared with that of several other species of the genus. This has provided a basis on which to found a discussion of the other genera referred to, and has suggested certain general remarks on the relationships of the various types dealt with, both to each other and to members of other orders.

The Anatomy of the Stem of Berberis.

Berberis vulgaris is a shrub with small simple leaves, with solitary spines formed by prolongation of the mid-ribs. Occasionally two additional spines are developed as marginal outgrowths towards the apex of each leaf. The flowers are yellow and trimerous, suggesting an affinity with Monocotyledons.

The most prominent feature shown in a transverse section of the stem is the deeply-seated ring of cork cells with remarkably large lumina. The tissues are arranged in the following sequence (figs. 1, 2):—

1. An epidermis of regular rectangular cells with cuticle and numerous stomata.

2. One or two layers of thin-walled cells with intercellular spaces. In older stems these cells persist in that condition, but in other cases they are crushed by the growth of tissues more centrally placed.

3. These cells are bounded internally by a ring of sclerotic tissue three or four layers thick. In very young stems this ring is not quite continuous, but is interrupted by thin-walled cells, usually in the interfascicular regions, agreeing in this respect with the similar ring found in the Papaveraceæ (1). In older stems the sclerotic ring increases considerably in thickness and complete continuity is established, though later it is again segmented into patches as a result of the tension set up by the growth of the internal tissues and as a preliminary to being cast off by the cork.

The individual fibres are long, and their endings are either truncate, oblique, or tapering. They all show simple pits. Occasionally this tissue, by hypertrophy, produces ridges, although other species show this to a much greater extent than *B. vulgaris*. SOLEREDER considers this ring as belonging to the outer pericycle.

4. Immediately within this sclerotic band is the deeply-seated cork, which at first consists of one layer of regular, large, thin-walled cells with remarkably wide lumina. These cells are two, three, or more layers deep in older stems.

5. Next follows a region of cortical cells, the outer being small and compact, the inner larger and having intercellular spaces. All are thin-walled and have protoplasmic contents. In the medullary ray region, "berberin" is present in the form of yellowish-green granules, and often the whole cell contents are impregnated with it; some cells in this region contain also klinorhombic crystals of calcium oxalate, which almost completely fill the cell lumina (fig. 3). Berberin is an isoquinoline alkaloid, insoluble in water, and hence can be best seen in sections of fresh material mounted in water. Spirit in which Berberis material has been preserved becomes yellowish-brown owing to the dissolved "berberin," which remains as a resinous deposit on evaporation. Further research is at present being carried out on the chemical composition and reactions of this substance.

According to SOLEREDER, the fibrous ring, the cork, and the cortical region just mentioned form a composite pericycle.

No endodermis is differentiated, for ordinary cells of the cortex abut directly on the vascular bundles.

In the young stem the vascular bundles are distinct, the interfascicular regions being composed of sclerotic tissue; but later the bundles, together with the broad primary medullary rays, form a complete ring of lignified tissue (fig. 1).

The phloem consists of very small elements arranged in radial rows. In older stems it shows sieve tubes with bevelled ends occupied by sieve plates and callus, with slime strings across the plugs from segment to segment; but no grouping of sieve plates into areas is observable. This may be due to the very small size of the sieve tubes, which also prevents the definite location of plates on the lateral walls, though they appear to be present. Some of the sieve tubes are accompanied by companion cells, although this is by no means an invariable rule. Phloem parenchyma is abundant, and the cells show intercellular communications. Lignified fibres with deep simple pits are also present. They are short and spindle-shaped, and in cross section show strongly thickened walls and small lumina, thus differing from the pericycle fibres, which are much wider and have walls less strongly lignified. These bast fibres are formed in tangential rows in the inner secondary phloem and border the lamellæ into which the phloem is divided as growth proceeds, thus recalling the alternating bands of Vitis, though they are developed to a much less extent. A few scattered fibres are also found in the outer primary phloem, but no stone cells are present.

Crystals and "berberin" granules are found in the medullary ray region of the bast, as above mentioned. The bast fibres are not continued across these regions.

In the early stages the xylem elements are regular and similar in size and shape, with wide lumina, some showing remains of protoplasmic contents. Later the lignification becomes more pronounced, the lumina decrease, and the arrangement in radial rows becomes more obvious. Comparatively large polygonal vessels are distinguishable in the protoxylem and in groups towards the centre of each vascular bundle. In the protoxylem the first formed vessels are spirally thickened, the innermost spirals being right-handed and later ones left-handed, as pointed out by DE BARY (6). The other vessels possess bordered pits with slit-like apertures (fig. 5), the slits lying at right angles to the axis of the vessel; many have faint spiral thickenings in addition to pits, similar to those recorded for Romneya (Papaveraceæ) (1) and for Dendromecon by LÉGER (7). Most of the xylem consists of prosenchymatous fibres with simple pits on all their walls and often containing starch, particularly in the winter condition. These fibres always occupy the regions abutting on the medullary rays. SANIO (8) says that septate fibrous cells are found only in the first annual ring. This does not seem to be invariably true, although the septa are not so frequent in the fibres of the second and subsequent years. Comparatively few tracheids are present, and these have bordered pits accompanied by spiral thickenings, as in Taxus. There seems to be little difference between the pitted fibres and the pitted tracheids. Spiral tracheids resembling fibres are also present.

The predominance of stereome and the reduction in the number of conductive elements is to be correlated with the xerophytic character of the plant. The small amount of leaf surface, and the consequent reduction in transpiration, the necessity for protecting the cell contents from the intense insolation to which Berberis is subjected in its native habitats (Asia, South and Central America), may also be associated with the predominance of sclerosis and the large development of wood fibres.

Broad primary medullary rays persist, and consist of markedly sclerotic cells which, in transverse section, closely resemble the xylem elements, but are often larger than the adjacent xylem fibres. The rays are three or four cells wide, and the cells have rounded ends. They are elongated radially, the radial diameter being in many cases almost twice the tangential one. All the walls show numerous simple pits, and most of the cells are well filled with starch grains during the winter. No secondary rays are produced. The contents of the medullary ray regions of the cortex have been previously described.

The medulla is heterogeneous; the cells near the protoxylems are smaller than the rest and have well-thickened walls. They show nuclei when young, and starch grains in the winter condition at all ages. Numerous simple pits occur on all their walls. The central cells are larger and become polygonal by mutual pressure; they are thin-walled and devoid of contents.

The petioles are slender and wiry. In the main portion of the petiole there are four vascular bundles surrounded by sclerenchyma, but these unite as the lamina is approached. In the basal region there are only three vascular bundles, which later on divide into four. As the petiole expands into the lamina the vascular bundles again rearrange themselves into three bundles.

Other Species of Berberis.

Most of the species of Berberis exhibit features similar to those described for *Berberis vulgaris*, among which the following structural variations may be noted. Spines occur on the stems of some species. They are outgrowths from single epidermal cells, and are present in *B. Yunnanensis*, Franch., *B. stenophylla* × hort., *B. angulosa*, Wall., *B. Wallichiana*, DC., *B. empetrifolia*, Lam., and *B. Darwinii*, Hook. (fig. 6). In the last-mentioned species they are much longer, are curved, and have transverse partitions.

The sub-epidermal parenchyma in *B. aristata*, DC., *B. stenophylla* × hort., *B. empetrifolia,* Lam., and *B. aquifolium*, Pursh., shows foldings in the cell walls as described for *Corydalis racemosa* (1), but in the present instances the folding appears to be caused by the pressure of internal tissues acting in opposition to the resistance offered by the epidermis. In the older stems the compression increases until these cells are cast off along with the other tissues external to the deeply-seated cork.

The sclerotic pericycle in some cases is increased so much as to form ridges in the stem, *e.g.* in *B. angulosa*, Wall. (fig. 8), and *B. Yunnanensis*, Franch.

The spines so characteristic of the Berberidaceæ consist mainly of sclerenchymatous fibres and are obviously modified leaves, as shown by their position at the nodes and by their structure. The sheath of sclerenchyma almost entirely encloses two cavities filled with loosely arranged thin-walled cells and one or more vascular bundles (fig. 9). Stomata are found only on the incurved surface, where they are abundant. The sclerotic fibres are continuous throughout the spine to the tip, which is formed solely of fibres covered by epidermis.

The inner layers of the heterogeneous pericycle, which consist of thin-walled parenchyma, are often so loosely arranged as to produce conspicuous cavities crossed by cellular bridges (fig. 10). In some species these layers are increased locally, contributing to the production of the stem ridges.

Resin ducts are present in the phloem in some cases. In transverse section they appear to consist of single large cells with lignified walls showing oval pits (fig. 11).

In the young stem of *B. Jamesoni*, Lindl., vessels and tracheids with comparatively large lumina predominate, but as the stem increases in age and girth lignified fibres are developed bordering the medullary rays, as in *B. vulgaris*.

According to HABERLANDT (11), "medullary rays always abut directly against xylem parenchyma on their flanks as well as on their upper and lower borders." This suggests that the prosenchymatous fibres which always border the medullary rays may be parenchyma cells modified to give additional support to the stem (fig. 12). They are well supplied with simple pits, while some show septa and many contain starch grains.

Several species show oval bordered pits longer than those of *B. vulgaris*, *e.g.* *B. Sieboldii*, Miq. Others show bordered pits in conjunction with faint reticulate markings, *e.g.* *B. Wallichiana*, DC., and *B. Yunnanensis*, Franch. The former also shows loose reticulate markings in vessels without pits.

A few species show a slight development of normal xylem parenchyma, *e.g.* *B. stenophylla* × hort., *B. Jamesoni*, Lindl., *B. Sieboldii*, Miq. The parenchyma when present always surrounds the larger vessels in the protoxylem regions, and is usually lignified and similar to the xylem fibres in transverse section.

In *B. angulosa*, Wall., the greater portion of the wood consists of tracheids with round bordered pits resembling those of Pinus, but smaller in size.

SOLEREDER states that scalariform markings occur occasionally in Berberis; no such thickenings were found in any of the species of Berberis examined, though they are to be found in Podophyllum and Diphylleia.

There is very little variation in the medullary rays; most of them closely resemble those of *B. vulgaris*. The ray cells are well lignified, thus rendering them hardly distinguishable from the surrounding xylem. They vary in width from two to eight cells, the widest being found in *B. Wallichiana*, DC., where they have very abrupt endings. In the very few cases where secondary rays have been found, they are by no means uniform in their occurrence, a transverse section showing perhaps only three or four secondary rays to a large number of primary ones. The presence of secondary rays is always associated with wide bundles and narrow primary rays.

The pith in the majority of cases is heterogeneous, as in *B. vulgaris*, L. Many species show solitary klinorhombic crystals of calcium oxalate in addition to starch in the peripheral cells, *e.g. B. aquifolium*, Pursh., *B. stenophylla* × hort., *B. Jamesoni*, Lindl., *B. empetrifolia*, Lam., *B. Darwinii*, Hook.

Some species show a pith sclerotic throughout, but here also the central cells are often larger than the peripheral ones, *e.g. B. Darwinii*, *B. angulosa*.

The general plan of structure of the stem in *Berberis* (*Mahonia*) *aquifolium*, Pursh., is the same as that of other species; a sclerotic pericycle and cork cells with wide lumina are present; the xylem shows the same predominance of lignified fibres and the same broad primary medullary rays. The bordered pits have round apertures, as in *B. angulosa*, in contrast to the slit-like pits most frequent in the genus. No lignified fibres occur in the bast. The pith is sclerotic throughout.

Summary of Anatomical Characters of Berberis.

1. There is a continuous sclerotic ring of pericycle fibres, similar to that present in the Flacourtiaceæ.

2. Cork cells with remarkably wide lumina occur, as in some Menispermaceæ.

3. Bast fibres occur in tangential rows in the secondary phloem, agreeing in form and arrangement with those of Lauraceæ and some Magnoliaceæ.

4. The xylem is composed chiefly of strongly lignified fibres with occasional thin transverse septa, as in Lauraceæ and Flacourtiaceæ.

5. The largest vessels and some of the tracheids exhibit bordered pits with slit-like apertures, while most species show a combination of bordered pits and spiral thickenings.

6. Very little parenchyma occurs in the xylem, in which particular it again agrees with that of the Menispermaceæ.

7. Broad lignified primary medullary rays are characteristic of the genus, with only very occasional secondary rays. In the Menispermaceæ the rays are similar in all respects, save that some cells in the broad rays may not be lignified.

8. The pith is usually heterogeneous, though in some species the cells are sclerotic throughout. Heterogeneous pith also occurs in Magnoliaceæ, some Lauraceæ, and Menispermaceæ.

9. The phloem consists of sieve tubes, companion cells, phloem parenchyma, and bast fibres; the two former occur principally in the primary phloem, while the secondary phloem consists mainly of parenchyma and bast fibres.

10. Spines occur both as epidermal outgrowths from the stem and as modified leaves.

The Epimedeæ include Epimedium, Vancouveria, and Nandina, and doubtfully also Jeffersonia and Achlys. With the exception of Nandina, none of the genera investigated are woody.

Nandina domestica, Thunb., is a Japanese shrub. In the young stem there are distinct ridges formed by the development of sclerenchyma, especially in the neighbourhood of the vascular bundles. The vascular bundles are well separated by small cells which afterwards form medullary rays, 5–8 cells in width, in the older stages. The ridges gradually disappear owing to the development of sclerenchyma levelling up the depressions. The four or five large vascular bundles have rather smaller ones alternating with them, but all traces of this distinction disappear in older stems.

When in the young state the phloem areas are distinctly rounded in section and are destitute of lignified fibres. The xylem consists mainly of vessels with wide lumina, together with a few parenchymatous cells, while simple pitted fibres border the medullary rays, as in Berberis. The vessels show a variety of markings: spiral in the protoxylem, in other parts reticulate; slit-like pits merging into reticulate and bordered pits with slit-like apertures. Occasionally tracheids with bordered pits are also present.

When young most of the pith consists of thin-walled cells, but later it becomes entirely sclerotic. The pith is relatively large, comprising about 80 per cent. of the area in the transverse section of an old stem. Some of the cells are elongated and show simple pits; they appear to act as storage organs. Some near the periphery show peculiar forked endings.

Vancouveria hexandra, C. Morr. and Dec.—The species possesses an underground stem or rhizome in addition to the normal aerial stem.

The aerial region in the young state has a slightly cutinised epidermis followed by two or three rows of cells which are elongated longitudinally and show no intercellular spaces. Next follow three or four rows of small sclerotic fibrous cells forming a distinct ring, but merging into larger thin-walled cortical parenchyma, as a rule devoid of contents. Through this tissue run widely separated vascular bundles. In the young condition more than half of the bundle is composed of phloem without fibres. The xylem consists entirely of spiral and pitted vessels with comparatively wide lumina, while the protoxylem is flanked by small sclerotic cells in older stems.

The xylem of the vascular bundles in the rhizomic region is so embedded in sclerotic tissue that together they form a complete ring of stereome, except in some old specimens where the continuity is interrupted and the internal and external parenchymatous areas are united by broad bands of non-sclerotic tissue. The phloem occurs in patches outside the stereome ring, and consists mainly of sieve tubes and companion cells. The sieve plates are in some cases transverse, in others oblique, while some show sieve plates on their external walls. No lignified fibres occur. The vessels occupying the centre of the bundles show various forms of lignification—spiral, reticulate, or bordered slits. On the lateral borders of these groups of vessels are thickened prosenchymatous fibres which occupy the whole of the interfascicular regions, thus completing the ring of mechanical tissue.

Outside the phloem areas are occasional sclerotic cells among the ordinary cortical cells, and beyond these lies a ring of slightly thickened cells corresponding to the sclerotic ring in the aerial stem. The rhizome thus contains two concentric rings of mechanical tissue—an inner one consisting of the xylem of the vascular bundles and sclerotic fibres, and an outer of sclerotic tissue only. The epidermal cells are thin-walled, and the sub-epidermal tissue consists of fairly large and irregular cells, many of which contain a brown deposit.

All the material examined was herbaceous and showed no signs of any development of cork.

Epimedium alpinum, L., shows a structure very similar to that of Vancouveria, but some of the vascular bundles are more peripheral, so that their phloems are embedded in the peripheral sclerotic ring. The medulla is markedly fistular. Many of the cortical cells are elongated with large oval pits in their walls, and hence are probably conductive.

In the rhizome the ring of mechanical tissue is incomplete, the bundles being separated by broad plates of parenchyma. In the aerial stem there are two rings of vascular bundles.

Epimedium sagittatum agrees with Vancouveria so far as the structure of the aerial stem is concerned.

Jeffersonia dubia, Benth. and Hook., and *Jeffersonia binata*, Bart., agree with the three previous genera in having their vascular bundles arranged in a ring, some of them partially embedded in the ring of sclerenchyma; in the structure of the xylem —having vessels with bordered slit-like pits, in having a lacunar cortex, and in having a phloem very rounded in section. In *Jeffersonia dubia* the sieve tubes are well developed, with well-marked callus plugs and faint canals across the callus, and the nodes on the median lamella. SOLEREDER says the arrangement of bundles in Jeffersonia is Monocotyledonous; but, apart from the fact that some bundles are smaller and rather nearer the periphery than others, the material we have examined presents no evidence in support of this statement.

The chief characters of stem anatomy of Epimedeæ may be summarised as follows:—

1. There is a continuous ring of sclerenchyma, pericyclic in origin.

2. The phloem bundles are very rounded in outline and have no fibres. The sieve tubes are larger than in Berberis, and in many cases show sieve plates on the lateral walls.

3. The xylem consists chiefly of vessels with fairly wide lumina. Those of the

protoxylem are spirally thickened, the others have reticulate or bordered slit-like apertures.

4. Prosenchymatous fibres occur only in Nandina and in the rhizome of Vancouveria; in the other genera xylem parenchyma replaces fibres.

5. Except in Nandina and in the rhizome of Vancouveria the bundles remain isolated, and the interfascicular tissue is unlignified.

6. The central parenchyma in Nandina becomes sclerotic, but in Vancouveria and Epimedium only the cells in close proximity to the protoxylem show sclerosis. In all save Nandina the cortex tends to become lacunar.

7. The vascular bundles are arranged in a ring, although developmentally constructed from two rings interlocking.

Achlys triphylla, DC.—In the aerial stem the bundles are irregularly arranged (fig. 13), and only a few are in contact with the ring of sclerotic tissue, which is similar in position to that in Vancouveria, Epimedium, and Jeffersonia. The smallest bundles are toward the periphery and the largest ones toward the centre, but no definite arrangement in rings is observable. The general appearance recalls the arrangement in Podophyllum rather than that in the Epimedeæ.

The xylem consists chiefly of spiral vessels without fibrous elements. The phloem is rounded in section and consists of sieve tubes with occasional companion cells. The sieve tubes show sieve areas on their lateral walls.

The bundles in the rhizome are arranged in two rings, as noted by TISCHLER (9). The main bundles form an inner ring, while the others, which consist chiefly of sclerenchyma, alternate with them and are nearer the periphery. The cork cells resemble those of Berberis; they have wide lumina, are deep-seated and of pericyclic origin. The xylem contains pitted vessels and tracheids. Pericyclic fibres do not occur in the rhizome.

The Podophylleæ include Podophyllum and Diphylleia, and also, according to LOTSY, Jeffersonia, Achlys, Hydrastis, and Glaucidium, although the two latter genera are placed by most systematists in the Ranunculaceæ. *Podophyllum Emodi*, Wall., very closely resemble *P. peltatum* in anatomical structure, as described by HOLM (10).

Stems of different ages show irregularly arranged bundles, widely separated from each other, the largest being central (fig. 14). With the exception of the cambium present in each bundle, the stem in section has the appearance of a normal Monocotyledon.

In the bud stage no sclerosis is present in the cells surrounding the bundles, but later a crescentic mass of sclerenchyma arises on the phloem side. Towards the periphery there is a ring of sclerenchyma in which the phloem of the outer bundles is embedded, as in Epimedium and Jeffersonia.

At first only a few of the xylem elements are lignified and show spiral markings, later formed units show annular and reticulate thickenings. Xylem parenchyma occurs but no fibres. The phloem appears to consist solely of sieve tubes with lateral plates and companion cells; as in *P. peltatum*, no fibres and no parenchyma are present.

The material examined was herbaceous and no cork was noticeable, although it is given by SOLEREDER as sub-epidermal in origin.

The rhizome shows a distinct ring of large bundles, with a few smaller ones outside in the cortex, but the arrangement is not as definite as in Achlys. There is no peripheral ring of pericyclic fibres such as is shown by the rhizome. In the main bundles the xylem consists of a few scalariform tracheids, wide vessels showing a variety of markings—spiral, loosely reticulate, long oval pits, and bordered slits,—and many parenchyma cells showing no lignification. The phloem is very little differentiated and consists of radially arranged elements, a few of which are sieve tubes, while most seem to be parenchymatous in their nature. The tissue bordering on both phloem and protoxylem consists of smaller cells which are slightly sclerotic, with simple pits in their walls. The central parenchyma cells, which are slightly elongated, contain resin.

The petiole resembles the aerial stem in having a ring of bundles towards the periphery and irregularly scattered bundles in the centre, formed from the bundles nearest the upper surface of the leaf.

Diphylleia cymosa, Michx., is very similar to Podophyllum in anatomical structure. In the aerial region there is the same ring of sclerenchyma towards the periphery and a ring of bundles with their phloems partly embedded in the sclerenchyma. The other vascular bundles are scattered irregularly, as in Podophyllum, and have sclerenchyma on the outer margins of their phloems. The phloem and xylem elements, as also the anatomy of the rhizome and petiole, agree with the description given for Podophyllum.

The chief characteristics of the stem of the Podophylleæ :—

1. The bundles are scattered, the larger being towards the centre, as in Monocotyledonous stems, while the outer and smaller bundles have their phloems embedded in a sclerotic ring.

2. In the aerial axes the main bundles are in the form of a ring with smaller ones more peripherally placed.

3. The xylem consists chiefly of vessels with annular, reticulate, and scalariform thickenings and long, oval bordered pits.

4. No prosenchymatous fibres were found, but unlignified parenchyma cells are present among the vessels.

5. The central parenchyma is practically homogeneous, although a few cells near the protoxylems are slightly sclerotic.

In comparing the stem anatomy of the Berberideæ, Epimedeæ, and Podophylleæ it may be noted—

1. That all three subdivisions are characterised by possessing a ring of pericyclic sclerotic fibres in their aerial stems.

2. That the remarkably wide-lumined cork cells which arise on the inner border of the composite pericyle are present in Berberideæ and in the aerial stems of some of the Podophylleæ, but are absent in the Epimedeæ and in the aerial stems of Podophylleæ, where the cork is normal in form and sub-epidermal in origin.

3. That in the aerial axes of Podophylleæ the bundles show a "scattered" arrangement, as in Monocotyledons, but that in the subterranean regions the chief bundles form a definite ring, while others are scattered in the cortex. In Epimedeæ they are arranged in a ring which appears to be formed by the interlocking of two rings of bundles. In Berberideæ the bundles exhibit the normal Dicotyledonous arrangement.

4. That bast fibres are present in tangential rows in the secondary phloem of Berberideæ, but are absent from the Epimedeæ and Podophylleæ.

5. That the rigid texture of the Berberideæ is produced by the relatively large amount of prosenchymatous fibres, not present in herbaceous Epimedeæ (though in the rhizomes of Nandina and Vancouveria), nor in the Podophylleæ; while unlignified parenchyma is present among the vessels of Epimedeæ and Podophylleæ, but not of Berberideæ.

6. That the vessels in all three groups possess bordered pits with slit-like apertures, their greatest diameter being always at right angles to the axis of the vessel. In the Berberideæ these are often accompanied by spiral or reticulate thickenings, but this combination does not occur in the Podophylleæ and Epimedeæ.

7. That broad primary medullary rays consisting of lignified cells link up the xylem of the vascular bundles into a complete stereome ring in some, whilst in others (except Nandina and Vancouveria rhizomes) the bundles are widely separated by undifferentiated parenchymatous cells.

8. That the central parenchyma is similar in all three groups, being composed usually of central thin-walled cells, with thick-walled cells towards the protoxylems. In both Berberideæ and Epimedeæ some species show uniformly sclerotic parenchyma. The Berberideæ alone show crystals in the central parenchyma.

9. That the sieve tubes in all genera have sieve plates on their bevelled ends, and occasionally on the lateral walls as well.

10. That the endodermis is not well marked, and that stone cells are conspicuously absent.

In stem anatomy *Hydrastis canadensis* does not resemble Podophyllum, for the vascular bundles are not scattered and the ring of sclerotic pericycle, which is invariably present in all the Berberidaceæ examined, is entirely absent. The anatomical characters suggest that this species is not closely allied to the Berberidaceæ.

The *Lardizabalaceæ* are regarded as a tribe of Berberidaceæ by Bentham and Hooker. They are included in that order also by Solereder, but separated from it by Engler and Prantl and by Lotsy. This order comprises Lardizabala, Stauntonia, Akebia, Decaisnea, Holbœllia, Parvatia, and Boquila.

Stems of the following have been examined, viz:—*Lardizabala biternata*, Ruiz and Pav., *Holbœllia latifolia*, Wall., *Akebia quinata*, Dec., and *Decaisnea Fargesii*, Franch. They all show marked differences from the Berberidaceæ, but many of these differences may be accounted for by their climbing habits. For instance, vessels of the xylem are much more numerous and have considerably larger lumina than any Berberidaceæ, while prosenchymatous fibres are very few, being replaced by xylem parenchyma which is often lignified and shows bordered pits with slit-like apertures. Thus the supporting tissue which predominates in woody Berberidaceæ is replaced in the Lardizabalaceæ by conductive elements. In common with many other climbers these plants show large sieve tubes. In Decaisnea the sieve plates occur on the bevelled ends, the polygonal sieve areas being separated by bands of cellulose, while sieve fields also occur on the lateral walls. Phloem fibres are absent, but on the external margins of the phloem areas are semi-lunar bands of sclerenchyma with very thick walls and packed with calcium oxalate crystals; they appear to be of pericyclic origin and correspond to the ring in Berberidaceæ. The ring in this case, however, is much more irregular since the sclerenchyma is formed in depressions in the interfascicular regions, producing the ridged appearance so characteristic of lianes.

The cork arises sub-epidermally and is normal in character.

Akebia shows a well-marked endodermis, the cells being thickened on three sides and thin-walled on the inner, which abuts on the parenchyma.

In many respects the Lardizabalaceæ appear to form a link between the Berberidaceae and the Menispermaceæ.

The Lardizabalaceæ and Menispermaceæ consist chiefly of climbing shrubs, whilst the Berberidaceæ are not climbers.

1. The cork in Lardizabalaceæ is sub-epidermal in origin, as also in some Berberidaceæ and Menispermaceæ.

2. The pericyclic sclerenchyma occurs in arcs outside the phloem bundles, and since the bundles are close together, the arcs of sclerenchyma unite more or less into a ring. In this respect the Lardizabalaceæ differ from the Berberidaceæ, where the ring is continuous, and resemble the Menispermaceæ, which do not possess a continuous ring but have sclerotic arcs round the vascular bundles connected by groups of stone cells.

3. Bast fibres are absent from the phloem of Lardizabalaceæ and Menispermaceæ, but present in woody Berberideæ.

4. The xylem of Menispermaceæ consists chiefly of vessels with large lumina, and this is true also of Lardizabalaceæ, whilst in Berberidaceæ prosenchymatous fibres predominate.

5. All three orders agree in having broad primary medullary rays. In all the non-herbaceous species of Berberidaceæ the medullary ray cells are well lignified. In some species of Lardizabalaceæ all the cells are strongly lignified, but in others

the cells in the centre of the rays are thin-walled, flanked by sclerotic cells. The Menispermaceæ agree with the Lardizabalaceæ in often having unlignified medullary rays.

Berberidopsis.—HALLIER describes Berberidopsis as a syncarpous Berberis with points in common with the Flacourtiaceæ, while ENGLER and PRANTL and BENTHAM and HOOKER place it definitely in the Flacourtiaceæ.

An examination of the stem structure of *Berberidopsis corallina*, Hook., presents the following characters (fig. 15):—

1. A thick cuticle is present on the epidermal cells.

2. The external cortex often contains stellate crystals of calcium oxalate.

3. The ring of sclerenchyma is very open and is interrupted in older stems. The cells are short and rectangular and have numerous simple pits in their thick walls (figs. 16, 17). These sclereides correspond to the stone cells in the cortex of young twigs of Acer and Æsculus, but in these two genera the sclereides accompany sclerenchymatous fibres, the latter being much more numerous, whereas in Berberidopsis the sclereides predominate and very few fibres occur. HABERLANDT (11) suggests that these sclereides are cortical parenchyma cells which have penetrated gaps produced in the mechanical cylinder of bast fibres as a result of tensions set up by the growth in thickness of the twigs. The cortical parenchyma cells afterwards become thick-walled and so restore the unity of the now composite mechanical cylinder. The varied shape and arrangement of the sclereides seem to support this view.

4. The cork arises sub-epidermally and is normal in character, the cells being rectangular.

5. The xylem contrasts markedly with that of Berberis, the elements are larger, and the main portion consists of large vessels which are slightly thickened and have very loose reticulations forming large irregular pits (fig. 18). Tracheids are present with oval bordered pits.

6. Most of the cortical cells are thin-walled, but a few near the protoxylems are sclerotic, and all of them show simple pits. The more peripheral cells often contain starch grains or crystals of calcium oxalate.

7. No bast fibres are present in the phloem. The information available as to the anatomy of the Flacourtiaceæ is at present very meagre, so that a detailed comparison with the Berberidaceæ is not possible. The following points of resemblance may, however, be noted:—

1. In the Flacourtiaceæ the sclerotic ring may be continuous, or in patches joined by bridges or broken up completely into islands.

2. In both the xylem shows wide reticulate thickenings.

3. The medullary rays are numerous and vary from one to four cells in width in both families, but in Berberidaceæ the rays are wider and less numerous.

Summary of the Anatomical Characters of the Berberidaceæ.

1. Scattered vascular bundles occur in the aerial stems of the Podophyllæ, the largest bundles being centrally placed. Save that cambium is present, the vascular anatomy closely resembles that seen in Monocotyledonous stems.

2. Bordered pits occur very frequently in the secondary wood, both in vessels and tracheids; the apertures vary in shape, some being circular, others more or less oval with slit-like apertures. Where circular bordered pits occur in tracheids they closely resemble those of Pinus, although both tracheids and pits are smaller than in the Coniferæ.

3. The combination of a double spiral thickening and bordered pits is of common occurrence in the woody species of the order; while bordered pits combined with reticulate thickenings occur in some (conf. Taxus).

4. The xylem parenchyma is as a rule unlignified. Some species show a few lignified cells among the vessels of the protoxylem, but in none are there continuous plates or areas of lignified parenchyma.

5. Lignified fibres are common in the phloem of the woody species.

6. The cork cells have remarkably wide lumina and are very deeply seated, arising from the inner layers of the pericycle. This is true only of woody species and of the rhizomes of some herbaceous forms.

7. There is a continuous ring of sclerotic fibres in the pericycle.

8. Sclereides are absent from the Berberidaceæ, unless Berberidopsis be included in the order.

9. In some woody species spines are present, either epidermocortical or foliar in origin.

10. No endodermis is distinguishable save in Akebia among the Lardizabalaceæ.

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EXPLANATION OF PLATE.

Fig. 1. Transverse section, stem of *Berberis vulgaris* (diagrammatic).

Fig. 2. Transverse section, young stem of *B. vulgaris*, showing deep-seated ring of large cork cells. × 450.

Fig. 3. Transverse section, stem of *B. elegans*, showing calcium oxalate crystals in medullary ray cells. × 450.

Fig. 4. Longitudinal section, stem of *B. vulgaris*. Sieve tubes showing sieve plates and callus plugs. × 450.

Fig. 5. Longitudinal section, stem of *B. vulgaris*. Xylem and medullary ray. × 450.

Fig. 6. Epidermal cells and hairs of *B. Darwinii*. × 40.

Fig. 7. Transverse section, stem of *B. aristata*, showing folding of the walls of sub-epidermal parenchyma. × 450.

Fig 8. Transverse section, stem of *B. angulosa* (diagrammatic).

Fig. 9. Transverse section, spine of *B. ætnensis* (diagrammatic).

Fig. 10. Longitudinal section, stem of *B. empetrifolia*. External cortex, showing bridging of intercellular spaces. × 450.

Fig. 11. Transverse section, stem of *B. Boschanii* (diagrammatic).

Fig. 12. Longitudinal section, stem of *B. Wallichiana*, showing short blunt medullary rays. × 450.

Fig. 13. Transverse section, rhizome of *Achlys triphylla* (diagrammatic).

Fig. 14. Transverse section, stem of *Podophyllum Emodi* (diagrammatic).

Fig. 15. Transverse section, stem of *Berberidopsis corallina*. × 450.

Figs. 16 and 17. Transverse section and longitudinal section, stem of *B. corallina*. Stone cells of pericycle. × 450.

Fig 18. Longitudinal section, stem of *B. corallina*. Xylem elements with loose reticulate markings. × 450.

Fig. 19. Transverse section, rhizome of *Vancouveria hexandra* (diagrammatic).

Fig. 20. Transverse section, stem of *Hydrastis canadensis* (diagrammatic).

Fig. 21. Transverse section, stem of *Jeffersonia dubia* (diagrammatic).

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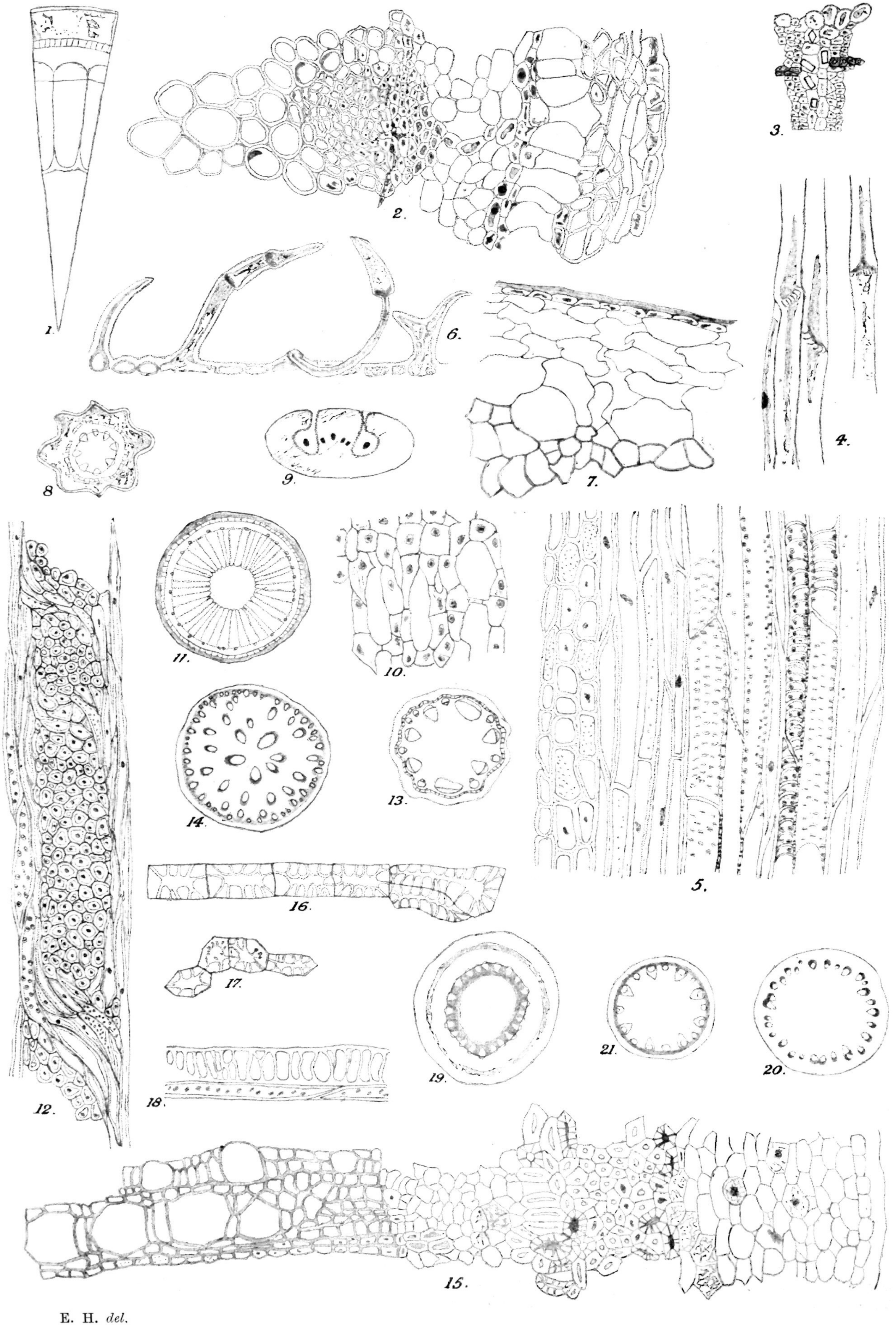

E. H. *del.*