STUDIES IN THE PROTEACEAE.

II. Floral Anatomy and Morphology of *Macadamia ternifolia* F. Muell.

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Introduction.

It has already been pointed out in a previous paper on *Grevillea robusta* Cunn. (1938 b), in which a review of the important contributions has been given, that the literature pertaining to floral morphology in the members of the Proteaceae is very meagre. The number of investigated genera is very small in proportion to the total number belonging to the family. The present contribution is intended as an addition to our knowledge of the family at least to some extent.

Not only on account of the systematic position of the family which is much disputed, but also, to a larger extent on account of the encouraging results obtained in *Grevillea robusta* Cunn. (Kausik, 1938 b), the present investigation was undertaken with the hope that many interesting facts of floral morphology remain yet to be recorded in the family. This hope has not been frustrated in the present case.

Locally, only three isolated plants of the species under examination here, *Macadamia ternifolia* F. Muell., the Queensland Nut Tree, are available in the Government Horticultural Gardens, Lal-Bagh, Bangalore. The material was collected from these plants and killed in Bouin’s fluid. Sections were cut at different thicknesses to suit the requirements of study. Considerable difficulty was experienced in cutting on account of the presence of abundant tannin in the floral parts and the general hardness of the flowers even in early stages of development. In the case of the developing fruits there was less difficulty in sectioning, as then the material could be easily handled and the outer hard portions of the ovary removed. Heidenhain’s iron-alum Haematoxylin was used throughout, but in the study of floral anatomy, alcoholic saffranin and a counterstain, for contrast, of light green dissolved in clove oil were employed.
The Structure of the Flower.

The flowers are borne in pairs on the main axis of the inflorescence, which is a raceme. Each flower has a long pedicel and consists of four perianth lobes, opposite to which are four stamens. The filaments are adnate to the perianth lobes throughout their basal portions and are free only a little below the anthers. The perianth lobes meet each other along their margins by dove-tailing arrangements (Figs. 14, 15). Slight constrictions are found between the bases of the perianth lobes and the receptacle of the flower (Fig. 14) where the two separate at the time of the opening of the flowers. Within the perianth is a large nectar-secreting disc (Figs. 3, 4 and 14) in the form of a collar at the base of the ovary.

The ovary, which is made up of a single carpel and contains two ovules, is raised on a short gynophore-like stalk (Fig. 14) and ends distally in a long slender style terminated by a large stigma. The wall of the ovary is densely clothed over with short thick-walled hairs, which have basal joint cells (Figs. 20, 21). The hairs break away at the joints as the fruits begin to develop.

In the formation of the ovary, the margins of the carpel are folded inwards on the ventral side, where a longitudinal groove is present. This groove suggests that the fusion of the margins is not quite complete. The groove continues into the style and the stigma. In the latter a small pore-like opening is present along the groove (Fig. 23) and beyond this, the stigma opens out like a funnel, the inside of which is covered over by numerous papillate cells for conducting the pollen tubes (Fig. 22). In a longitudinal section of the ovary, each margin of the inrolled carpel shows a small over-hanging ridge of cells above the attachment of the ovule (Figs. 14, 20).

There are large groups of tannin-filled cells in all the floral parts, including the outer integument and the chalazal region of the ovule.

Vascular Anatomy of the Flower.

The vascular tissue of the flower separates out from the vascular cylinder of the main axis of the inflorescence in the form of a dorsiventral arc consisting of a few bundles (Fig. 1). The arc gradually closes up to become radial (Fig. 1 a) and forms a ring of vascular strands as soon as the pedicel becomes distinct from the main axis (Fig. 2). The vascular ring of the pedicel continues into the receptacle of the flower, where it gives rise to the traces for the several floral organs.

The first set of traces to be separated from the receptacular stele is that for the perianth lobes. In this, there arise four paired and as many single strands, the former alternating with the latter (Fig. 3). The strands of the respective pairs fuse with each other and enter the four perianth lobes.
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Figs. 1-19.—Showing vascular supplies to the floral organs; see text for a detailed description. Fig. 1. Separation of the floral vascular tissue from the cylinder of the main axis; Fig. 1a. The same at a higher level. Fig. 2. Vascular ring in the pedicel. Figs. 3-13. The vascular traces at successively higher levels in the flower. In Figs. 5-13 the outer floral parts are excluded. Fig. 14. Longitudinal section of flower showing course of vascular strands. Fig. 15. Transverse section of same to show general arrangement of parts and their traces. Figs. 16-19. Showing separation of foliar trace for comparison.

as four large median strands. Each of the alternating single strands forks into two limbs as it passes out to the periphery of the receptacle and the two limbs enter the margins of two adjacent perianth lobes. Thus each
perianth lobe has essentially three main strands at its base, the median of which is a double strand, while the two marginals are half strands, those of adjacent margins of two perianth lobes being derived from a single strand in the receptacle. These three main strands branch higher up as they traverse the perianth lobes (Fig. 15).

The vascular supplies of the androecium consist of four large strands, one for each stamen and derived from the large median strand of the corresponding perianth lobe on the ventral or adaxial side (Fig. 4). The stamen traces are separated at the very base of the perianth lobes and enter the inner median ridges of the latter, which are formed by the fusion of the filaments and the perianth lobes. The stamen strands are throughout single and become enclosed in a sheath of tannin cells as they enter the anthers (Fig. 27).

The nectar disc does not receive any vascular traces from the receptacle. It is therefore regarded that it has no morphological relationship with the other floral parts. Such a conclusion is also reached by Brough (1933) in *Grevillea robusta* Cunn.

After the departure of the perianth traces, a ring of vascular tissue, consisting of five large and a few smaller strands is left over in the stele (Fig. 3). The smaller strands ascend only a short distance into the stalk of the ovary and become exhausted (Fig. 4). The five larger ones, on the other hand, pursue their courses beyond and enter the single carpel of the ovary where they assume definite positions as a large median dorsal, two median lateral and two ventral or marginal strands (Fig. 5). The ventral strands after giving rise to the ovule traces (Fig. 6), get into the style along with the dorsal and the median lateral strands (Fig. 7). The courses of these strands remain unaltered throughout the entire length of the style, but at the region of the stigma, the ventrals shift themselves towards the median laterals with which they fuse (Figs. 8–10). Finally the fused strands again recede towards the dorsal side of the stigma and unite with the dorsal strand to form a large stigmatic vascular mass (Figs. 11, 12). The latter ultimately disappears at the tip of the stigma, but immediately prior to this shows a slight forking into two short stumps (Fig. 13).

It may be worthwhile at this stage to point out certain significant features in floral structure. The separation of the floral vascular tissue in the form of a dorsiventral arc is so similar to the separation of a leaf trace (Figs. 16 to 19) or a branch trace in the vegetative portions that perhaps rigid distinctions cannot after all be placed between the axial and appendicular organs of the shoot. One may therefore conclude with Arber (1930)
that fundamentally there are only two morphological entities, the shoot and the root.

In the separation of the large median vascular strands of the perianth a similarity seems to exist with the leaves, where too a double median strand (Figs. 16 and 17) is conspicuous. Eames (1931) regards that the vascular supplies of the sepals are similar to those of the foliage leaves of the plant. In agreement with this, the perianth lobes are regarded as sepals. The alternating single strands supplying the margins of adjacent perianth lobes are perhaps really petal traces, the courses of which have become altered on account of a complete disappearance of the whorl of petals. These traces therefore enter the lobes of the only surviving floral envelope.

Lastly, the nature and construction of the ovary in Macadamia F. Muell. are such that they may be considered in the light of the interpretations of Hunt (1937) regarding the origin of the modern Angiospermic carpel. Hunt visualises the forerunner of the carpel as an essentially three-lobed structure, the lobes dichotomising and possessing independent vascular branches. In the carpel of Macadamia F. Muell. indications are seen of such a carpel with three lobes (Fig. 25), the two laterals of which alone show a forking into two branches, while the central is undivided. The forking of the stigmatic vascular mass into two short stumps is perhaps the only evidence of the original branching tendency of the central lobe that is persisting. The condition of the Protead carpel, at least in Macadamia F. Muell., might have resembled at some time the condition of the primitive carpel shown in Fig. 26. Here the outer branches of the lateral lobes (marked a) have become specialised to ovule-bearing and so have closed over gradually, while the inner of the same (marked b) have fused all through their length with the margins of the central lobe to form the style and the stigma. The overhanging ridge of cells above the attachment of the ovules (as seen in a longitudinal section) and the pore on the stigma formed on account of notches in the apposing margins of the carpel are perhaps the only lingering remnants of the regions separating the branches and the lobes of the primitive carpel.

The vascular structure of the ovary supports the above interpretations of the carpel to a large extent. The dorsal strand is not only more strongly developed than either of the other two pairs, but also takes part in a larger measure in the formation of the stigmatic vascular tissue, towards which the other strands converge. The forking of the stigmatic vascular tissue suggests the original branching tendency of the central lobe, which remains externally simple. The ventral strands in the style belong to the inner branches of the lateral lobes which have participated in the formation of the
FIGS. 20–35.—Fig. 20. Longitudinal section of ovary showing the atropous pendulous ovule and the hairs on the ovary wall. Note the overhanging ridge of cells above the ovule attachment marked x. The black areas represent tannin cells. Fig. 21. The hairs on
the ovary wall enlarged to show the joint cells. Fig. 22. Longitudinal section through stigma showing glandular conducting cells. Fig. 23. Stigma enlarged to show pore along the ventral groove. Fig. 24. Fruit showing the two elevations on either side and in front of the style. The ventral groove is also seen. Fig. 25. Ovary shown as if opened out and laid flat. Fig. 26. Diagrammatic construction of carpel. Note the similarity between this and the ovary shown in Fig. 25. Fig. 27. Transverse section of anther. A sheath of tannin cells surrounds the vascular strand. Fig. 28. Part of wall of young anther. Fig. 29-31. Some of the prophasic nuclei of the microspore mother cells showing bud of nucleolus. Fig. 32. Three of the four microspores within the mother cell wall. Fig. 33 & 34. Pollen grains. Fig. 33. × 1350, Fig. 34. × 1800. Fig. 35. Part of wall of mature anther. × 900.

style, while the ovule traces are the vascular strands of the extremely consolidated outer branches, which alone bear the two ovules.

In the developing fruits two small elevations are found (Fig. 24) on either side and in front of the style. These elevations are regarded as representing the inflated distal portions of the outer branches which became inrolled to form the ovary.

The Structure of the Anther and the Formation of the Microspores.

The anther is extremely elongated and its wall shows as usual, the epidermis, endothecium, three middle layers and the tapetum (Fig. 28). The tapetal cells though large, are not very conspicuous even in the earlier stages, as for instance when the prophasic changes are taking place in the microspore mother cells. Each tapetal cell has a large vacuole, a small quantity of cytoplasm and a single nucleus, which does not divide further.

The meiotic divisions in the mother cell nuclei in the formation of the microspores are normal. It may be noted here that the nuclei possess a single large nucleolus, with which is always characteristically associated a bud (Figs. 29 to 31). In most of the nuclei of the mother cells of the young anthers synizesis, whether regarded as an artifact or not, seems to be a very constant feature of considerable duration.

With the formation of the microspores, the original mother cell wall swells up and becomes gelatinous (Fig. 32) before completely disappearing and liberating the spores as pollen grains. The fully developed pollen grains are tetrahedral with a thick exine and a thin delicate intine. The exine is not developed at the four corners of the tetrahedron, where thin areas represent weak spots. A large tube nucleus and a small generative cell lying towards one side are present at the shedding stage (Figs. 33 and 34).

In the mature anther the epidermis is usually torn asunder and the endothecium, with well-developed fibrillar thickenings, is therefore exposed externally to a large extent. The middle layers are very much crushed and
FIGS. 36-42.—Fig. 36. Nucellar primordium showing a group of potential archesporial cells, of which one marked \( x \) develops further. \( \times \) 1350. Fig. 37. Young ovule showing the free integuments. A large parietal tissue is seen above the developing megaspore.
the tapetum is completely broken down (Fig. 35). Dehiscence of the anther 
is similar to that in 

_Grevillea robusta_ Cunn. described by Brough (1933).

_The Ovule and the Development of the Embryo-sac._

The ovary contains two atropous pendulous ovules, each of which arises 
as a nucellar primordium (Fig. 36). In the latter are soon evident a number 
of large cells with conspicuous nuclei. Along with these are also found other 
nucellar cells, but less conspicuous and with smaller nuclei. The larger 
cells form a group of potential archesporial cells, of which only one develops 
further. Though it is usually difficult to pick out this particular cell from 
the others of the same nature, it may be recognised to some extent by its 
median position in the nucellus and the large nucleus, which is usually a 
little in advance of the nuclei in the other cells (x in Fig. 36). Ballantine 
(1909) evidently refers to the same condition when he states that in _Protea 
Lepidocarpon_ R. Br. "A small group of large cells situated below the hypo-
dermal layer includes one which becomes the megaspore mother cell". 
In _Grevillea robusta_ Cunn., on the other hand, a definite archesporial cell 
is always evident even in the early stages (Brough, 1933; Kausik, 1938 b). 
The division of the archesporial cell into the primary parietal cell and the 
megaspore mother cell could not be traced, but it may be inferred that such 
is the case by the presence of a large mass of parietal tissue (Fig. 37), which 
forms in later stages the characteristic glandular apex (Fig. 39) of the 
nucellus.

The integuments arise late; for instance, when the group of potential 
archesporial cells is evident in the nucellus, there is absolutely no indication 
of the origin of the integuments (Fig. 36). After they have been formed, 
they grow rather slowly all round the nucellus, but fail to close over com-
pletely at the apex of the nucellus even when the embryo-sac is fully developed 
and is ready for fertilization. The apex of the nucellus, therefore, lies exposed 
until fertilization, after which the integuments begin to grow again and 
invest the nucellus completely.

Both the integuments are made up of three or four layers of cells. The 
cells of the outer integument contain plenty of tannin (Fig. 20). The 
teguments are completely free from each other, as also the inner from the 
nucellus up to its very base.
The apex of the nucellus is glandular and is exposed before fertilization. This glandular tissue seems to be derived from the parietal cells, and also in part from the epidermis, and takes part in guiding the pollen tubes towards the embryo-sac. It also perhaps serves as a source of nutrition for the micropylar end of the embryo-sac, for, it persists even after fertilization and begins to break down only in the maturing seed containing a large embryo (Fig. 49).

The chalazal region of the ovule contains groups of tannin-filled cells (Fig. 20), which become contiguous as the seed begins to develop and form an extensive pad of cells at the chalaza (Figs. 44 and 47). Immediately above this pad the chalaza also contains a zone of great meristematic activity, where the cells divide rapidly, particularly after fertilization, and form a large nutritive tissue (Fig. 44). A similar condition is also met with in *Grevillea robusta* Cunn. (Brough, 1933; Kausik, 1938 b), but in *Protea Lepido-carpon* R. Br., Ballantine (1909) states that it “remains active until about the time of fertilization”. This tissue is destroyed later by the embryo-sac (Figs. 42, 43 and 47), when the endosperm and the embryo are formed.

The development of the megaspores and the formation of the embryo-sac proceed along normal lines (Figs. 37 to 39). The fully developed embryo-sac contains two synergids with broad posterior ends, the egg, two polar nuclei remaining free but close together till fertilization, and lastly, three distinct antipodal cells (Fig. 39). The micropylar end of the embryo-sac is broad and rounded, while the antipodal end is narrow and pointed. In the formation and growth of the embryo-sac, the surrounding nucellar cells are crushed to a large extent. In these nucellar cells may be recognised in earlier stages, a few elongated ones with very little contents. These are evidently the non-functioning archesporial cells.

**Fertilization.**

The pollen tubes, on coming in contact with the exposed apex of the nucellus, pierce through the latter and finally enter the embryo-sac. In this, only one synergid seems to be destroyed (Fig. 40). The first male nucleus fuses with the egg nucleus, while the second unites with the two polar nuclei somewhere in the centre of the embryo-sac (Figs. 40, 40a and 40b). The stages showing the actual fusion of the nuclei were not available.

**Post-Fertilization Changes in the Ovule.**

After fertilization several interesting changes take place in the ovule. The integuments, which were originally incomplete at the apex of the nucellus, begin to grow again and form a complete covering (Fig. 47). The inner integument does not show any increase in the number of layers, while the
outer one becomes very thick and consists of many layers of cells storing plenty of tannin (Fig. 47). In *Protea Lepidocarpon* R. Br. (Ballantine, 1909) however, "the inner integument becomes very long and several cells thick, the outer remaining only two cells thick". With the increase in the thickness of the outer integument in *Macadamia* F. Muell., vascular strands arise, which are formed by tracks of elongated cells developing in the outer integument after fertilization. In the fully developed seed, the outer integument forms a hard stony covering.

With the growth of the integuments, the nucellus also becomes more and more massive, especially at the region of the chalaza, where the large mass of nutritive tissue is developed. This is due to the activity of the chalazal meristematic cells. The entire mass of nucellus is completely used up when the endosperm and the embryo begin to develop (Figs. 42, 43 and 47).

**Endosperm.**

The primary endosperm nucleus undergoes repeated free nuclear divisions, by which groups of nuclei become scattered in the embryo-sac (Figs. 41 and 42). With the formation of these nuclei, the embryo-sac grows enormously in size and encroaching on the surrounding nucellus, becomes irregular in outline (Figs. 42, 43 and 45). The surrounding nucellar cells are practically dissolved away and appear in earlier stages as almost unrecognizable remnants floating in the general cytoplasmic mass of the embryo-sac (Fig. 41).

After a number of free nuclei are formed in the embryo-sac, wall formation begins in the formation of the endosperm tissue. In this, only the upper half of the embryo-sac takes part, while the lower remains free nucleate and forms irregular processes for absorbing materials (Figs. 43 and 45). In the upper half two distinct regions may be recognized. Towards the periphery the endosperm cells are small, compact and have rich contents, while those towards the inside are larger with less contents, irregular and loosely arranged (Fig. 45). The peripheral cells are in immediate contact with the surrounding nucellus and so take part in absorbing materials at the sides of the embryo-sac. These cells are comparable to the absorbing cells described in *Grevillea robusta* Cunn. (Kausik, 1938 a; 1938 b).

The lower half of the embryo-sac, where the nuclei remain free without forming cells, grows irregularly towards the nutritive tissue of the chalaza in the form of several processes (Figs. 42, 43 and 45). These processes, containing prominent nuclei which have a very high chromatin content, are of the nature of haustorial structures extending into and breaking down the nutritive tissue here and there (Figs. 43 and 47). Thus the entire mass of the
Figs. 43-48.—Fig. 43. Longitudinal section of developing seed showing the embryo-sac with the upper cellular and lower free-nucleate endosperm. The lower portion is forming processes for absorption. Note the destruction of the nutritive tissue of the chalaza by the invading processes. × 25. Fig. 44. Chalazal region of ovule showing tannin cells and
meristematic tissue. Portions of integuments are also seen, × 400. Fig. 45. Embryo-sac from Fig. 43 enlarged to show details of endosperm. A two-celled embryo is seen, × 80. Fig 45a. A single free endosperm nucleus from Fig. 45 to show the high chromatin content. × 1350. Fig. 46. Two-celled embryo. × 400. Fig. 47. Longitudinal section of seed showing the massive outer integument containing tannin cells (hatched). Fig. 48. Embryo and remnants of endosperm forming the Endosperm Mantle for the radicle. Fig. 48a. Basal lobes of cotyledon in the embryo.

Chalazal nutritive tissue is destroyed completely, as also the nucellus at the sides of the embryo-sac, so that a large cavity is formed within the integument. In this cavity the large embryo lies freely in later stages. The lower portion of the embryo-sac forming the processes is identical with the more definitely organised Vermiform appendage of the endosperm described in Grevillea robusta Cunn. (Kausik, 1938 a; 1938 b).

As the embryo begins to develop, the endosperm is in its turn destroyed (Figs. 47 and 48) so that the mature seed is non-endospermic. A few cells however persist at the region of the micropyle and extending down a little (Figs. 48 a and 49) and also at the lower portions of the embryo-sac (Figs. 48 and 50). The persisting endosperm cells at the micropyle are devoid of contents and form an almost structureless cap or sheath (except at the very tip where the cell outlines may be recognized) for the radicle of the embryo, the Endosperm Mantle (Figs. 48 and 49).

Embryo.

The fertilised egg remains without dividing for a long time. For instance, when the endosperm is already a mass of cells, with the distinction into the upper and lower regions (Fig. 45), there is only a two-celled embryo (Fig. 46). Further stages in the development of the embryo could not be studied, as most of the ovules seem to degenerate after fertilization. Perhaps embryogeny is very similar to that in Grevillea robusta Cunn. (Brough, 1933; Kausik, 1938 a and 1938 b). The fully developed embryo (Fig. 48) consists of two massive cotyledons, each with two basal lobes (Fig. 48 a), a short hypocotyl and a radicle provided with a pointed root-cap. The tip of the radicle fits into the long and narrow micropyle formed by the growth of the inner integument after fertilization (Fig. 49).

The Seed.

Of the two ovules of an ovary, 'only one develops successfully into the seed, while the other is suppressed. The mature seed has a very thick outer coat (Fig. 47), which becomes extremely hard and stony. This is formed by the outer integument. Within this hard coat are the thin and crushed inner integument, a few surviving layers of the peripheral portions of the nucellus and the remnants of the endosperm. All these are pressed firmly
Figs. 49–53.—Fig. 49. Portion from Fig. 48 enlarged to show the inner integument, dis-organising apex of the nucellus and the Endosperm Mantle forming the sheath for radicle. \( \times 280 \). Fig. 50. Remnants of endosperm at the lower end of the embryo-sac, enlarged from Fig. 48. \( \times 80 \). Fig. 51. Degenerating embryo-sac. \( \times 630 \). Fig. 52. Ovule degenerating after fertilization showing the collapsed embryo-sac. \( \times 80 \). Fig. 53. An abnormal ovule showing two nucelli and common inner and outer integuments.

together and fusing with the outer hard coat of the seed, form a smooth and shining internal lining for the outer integument. Inside the seed there is a large cavity containing the massive embryo.

Degenerations and Abnormality.

During the course of this investigation, several cases of degenerations and one instance of abnormality were noticed. The ovules seem to degenerate
almost at any stage of development, both before and after fertilization. Several cases of degenerating ovules containing young and growing embryo-sacs, and also those with fully developed embryo-sacs ready for fertilization (Fig. 51), were met with.

Instances of degenerations of ovules after fertilization were more numerous. Many of the ovules containing embryo-sacs after fertilization, in some of which even a few free endosperm nuclei were seen, were found to have degenerated (Fig. 52). The embryo sacs in these ovules are very narrow and crushed. The funiculi of the degenerating ovules are usually slightly longer than those of normal ones.

The single instance of abnormality consisted in the presence of two nucelli in an ovule, with common inner and outer integuments (Fig. 53). This abnormality has perhaps arisen by a splitting of the original nucellus. In each nucellus there is an embryo-sac showing remnants of pollen tube, the fertilized egg and a few free endosperm nuclei. The vascular tissue of the chalazal region of the ovule is forked into two limbs, each of which passes towards the base of an embryo-sac. Since this abnormal condition was met with only accidentally and in a solitary case, it is impossible to determine the fate of such ovules.

Conclusions.

The anatomy of the flower shows that the perianth lobes are of the nature of sepals, while the whorl of petals has disappeared altogether. It is therefore regarded that the Proteaceae are derived from dichalmydeous ancestors. A similar view is also held by Joshi (1936) with regard to the flowers of Stellera chamaejasme Linn., a member of the Thymelaeaceae, with which order the Proteaceae are claimed to be related by several authors. There is however one difference; while the disc scale in the flower of Stellera Linn., is a much reduced part of the corolla, the scale in Macadamia F. Muell. has no such claim.

The presence of a single whorl of perianth is perhaps correlated to a large extent with the prevailing dry climate in which the members of the Proteaceae are generally found. The outer whorl of the flower, namely that of the sepals, has assumed such special and protective features by a dovetailing of the margins of the lobes that it forms not only an effective covering for the essential organs of the flower, but is also capable of becoming easily displaced by the pollinating agents at the time of pollination. The specialization of the outer whorl has resulted in a total elimination of the whorl of petals as the latter became less and less effective as a floral envelope. In the absence of cross-pollination, the single perianth whorl persists as a
“cap” and close or self-pollination is induced at least as a last measure. The topics relating to pollination and the phenomenon of “capping” in Grevillea robusta Cunn. have been discussed by Brough (1933) and his conclusions may also be applicable here.

In the structure of the ovary, a primitive condition of the carpel as visualised by Hunt (1937) in the form of an essentially three-lobed structure is perhaps indicated to some extent. Both in structure, as well as in anatomy, the Protead carpel, as revealed in Macadamia F. Muell., seems to have retained some of the features of such a primitive carpel.

Several features, which may be regarded as primitive, are also met with in the structure and development of the ovule. In comparing the ovule of Myrica Gale with the fossil seed Trigonocarpus Kershaw (1909) states: “The ovules of some of the Pteridosperms and many of the fossil Gymnosperms have been described as having a free nucellus.

“This character of a free nucellus in these older fossil seeds may indicate that the integument had not as yet become an integral part of the seed. A free nucellus, therefore, may be regarded as a primitive character which has been lost in the greater number of Angiosperms, where the integument and nucellus are fused together almost to the apex of the ovule.”

It is interesting to note the presence of a free nucellus in Macadamia F. Muell., belonging as it does to a family considered primitive. But Benson and Welsford (1909), commenting on the work of Kershaw, remark that the presence of a free nucellus is “almost universal among Angiosperms”.

The other features of the ovule regarded as primitive are: the apex of the nucellus which is exposed on account of an incomplete growth of the integuments before fertilization; the presence of abundant tannin cells in the floral parts, which seems to be characteristic of plants belonging to the primitive orders; the increase in the nucellar tissue due to the activity of meristematic cells; and the presence of vascular strands in the outer integument of the developing seed. This last is perhaps associated with the enormous increase in the thickness of the integument after fertilization and therefore, in response to a greater need for the supply of materials.

The causes underlying degenerations of the ovules at practically all stages are rather hard to determine. The more numerous instances of degenerations after fertilization suggest that the failure of cross-pollination, due both to the absence of the proper pollinating agents and to the scarcity of plants locally, is an important factor. Self-pollination does not seem to induce the formation of seeds to a great extent. On the other hand, the failure in seed production may be inherent in the members of the Proteaceæ,
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for, Ballantine (1909) remarks: "In many of the South African representatives of the Proteaceae only a small percentage of the flowers set seed."

Summary.

The vascular anatomy of the flower shows that the perianth in Macadamia ternifolia F. Muell. is the whorl of sepals, while the corolla has completely disappeared. Thus a dichalmydeous ancestry is suggested for the Proteaceae. The adnation of the stamens to the perianth is of recent origin.

The nature of the carpel is discussed in the light of the interpretation of Hunt (1937) regarding the origin of the modern Angiospermic carpel.

The structure of the anther is described. The pollen grains contain a tube nucleus and a small generative cell at the shedding stage.

The nature and development of the ovule are pointed out. The embryo-sac develops along normal lines.

Fertilization and changes in the ovule after fertilization are described. The nature of endosperm, some stages in the development of the embryo and the parts of the mature seed are dealt with.

Several instances of degenerations of ovules and one instance of an abnormal ovule with two nucelli and common inner and outer integuments are recorded.

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LITERATURE.


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