XXV.—*On the Nature and Origin of the External Coatings of Seeds.* By JOHN MIERS, F.R.S., F.L.S. &c.

THE above question has not sufficiently attracted the attention of botanists, who have often described the seminal tunics under different appellations, according to their notions of the source of their development; but, in a paper published nearly two years ago*, I pointed out the test by which, as it appeared to me, their true origin can always with confidence be determined. Dr. Asa Gray has lately presented a paper to the Linnæan Society, in which he maintains the view he first enunciated respecting the seed-coats of *Magnolia*; in that paper this eminent botanist details his observations on the development and growth of its ovule, particularly in regard to the period when the osseous deposits are secreted within the primine; from these observations he still contends that the outer fleshy tunic of its seed derives its origin from the primine, and is therefore a portion of its testa. If this doubt were confined solely to the case of *Magnolia*, it would be of small moment, but as it affects a leading feature in the development of most other seeds, it becomes a question of extensive importance; and under this impression, as the facts described by my esteemed friend appeared to me to admit of a different solution, I soon after read a paper before the same Society, in which, carefully avoiding all controversial disputation, I briefly confined myself to a revision of the argument, bringing forward other facts and inferences, with a view of resolving the matter. The Council of that Society published Dr. A. Gray's paper, but, in a manner quite inconsistent with the spirit of scientific progress, refused a place to my observations in its Quarterly Journal, on the score that its 'Proceedings' are not a fit medium for contention on this point of science. I am fully aware how difficult it is to establish any novel views of structural development, and as I am desirous, for the cause of truth, that the matter in question should be decided, I submit it to the consideration of botanists, with the hope that they will throw aside for the moment their previous conclusions, and give their unbiassed attention to the facts and arguments here presented to their notice. With this view I will condense into another form the bearings of the whole question, introducing first a few premises, the import of which seems to have been lost sight of in this inquiry.

1. Vegetable growth in all its stages is regulated by the ordinary laws of mechanical action, and hence all inferences from seeming facts, or those often assumed to be facts, which are in-

* Linn. Trans. xxii. 81.

consistent with the operation of those laws, must be held to be founded in misconception.

2. Every tunic of the vegetable ovule is formed of three elementary parts; its outer and inner surfaces (epiderm and endoderm) consisting of a layer of very consolidated cells compacted with and enclosing a great mass of looser cellular tissue (mesoderm), from which they are not separable, as distinct pellicles, without laceration of their surfaces: these inner cells are filled with various substances that constitute pleurenchyma, &c., destined for the protection of the nucleus.

3. No communication of vessels can pass from the mesoderm of one into the mesoderm of another tunic, except through the common point of their origin.

4. There the mesodermal tissues of all are united, and are connected or are in communication with the secreting surface of the placenta; and I have distinguished by the name of *gangylode* this common point of junction of the coats and nucleus of the ovule.

5. When an ovule is erect, the gangylode is necessarily coincident with the point of attachment of the ovule to the placenta, and here all the nourishing vessels terminate; consequently there will be no future indication of the presence of any raphe in the tissues of the seminal tunics.

6. When the position of an ovule is changed by the act of anatropal inversion, the gangylode, or future chalaza in the seed, becomes far removed from the point of its prior attachment to the placenta; but an intimate communication is still maintained between them by an extension of a portion of the placenta (which I have called the placentary sheath) carrying with it and enclosing the nourishing vessels which constitute the future raphe in the seed. This placentary sheath, though confluent with the outer tunic of the ovule, is still a distinct formation; and no organic connexion, either then or afterwards, exists between their respective mesoderms, except through the medium of the

Fig. 1.

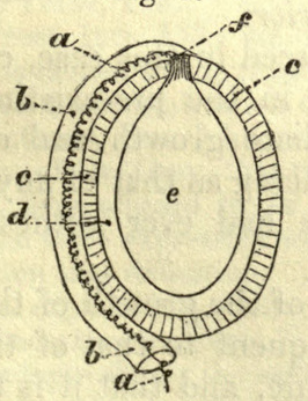
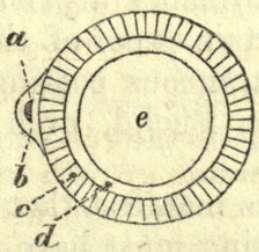


Fig. 2.



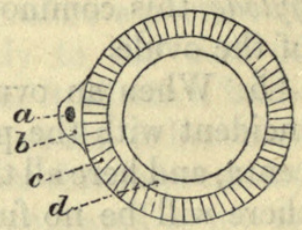
gangylode. Thus, in the annexed longitudinal and transverse

sections of an anatropal ovule, *b* is the placentary sheath, containing the nourishing vessels, *a*, proceeding from the placenta and terminating in the gangylode, *f*; *c* is the primine, *d* the secundine, *e* the nucleus. It is here manifest that the nourishing vessels enclosed in the placentary sheath never find their way into the tissues of the primine.

7. We may therefore infer, as an axiom from the three foregoing premises, that the raphe does not primarily, nor does it subsequently exist within the substance of the primine; and it is equally clear that if any penetration of the vessels of the raphe into its tissues were to exist, the natural course of such entrance would be only through the gangylode or chalazal point of the seed; but no such extension of the raphe beyond that point has ever been observed.

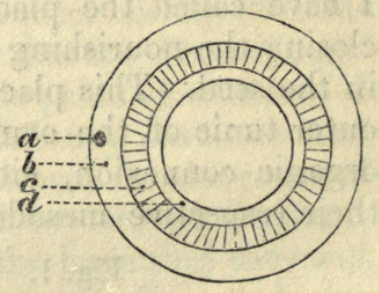
8. It is equally clear, in the course of the growth of the tunics of the ovule into the coats of a seed, that if there be no lateral expansion of the placentary sheath, then the raphe must be found as a distinct cord or compressed fistular line, remaining adnate to one side of the testa, exhibiting itself in transverse section as in the margin, where *a* is the bundle of nourishing vessels, *b* the compressed sheath in which it is enclosed, *c* the testa, *d* the tegmen.

Fig. 3.



9. But if we often find the vessels of the raphe imbedded within the substance of a distinct and entire fleshy coating which completely envelopes the two usual integuments of the seed, then the only conclusion we can draw is, that there has been a growth and extension of the placentary sheath, which has become enlarged into such a thick coating over the entire surface of the testa, as seen in the margin, where *a* shows the vessels of the raphe, *b* the extraneous fleshy coating or arilline, *c* the testa, *d* the tegmen. The testimony *à posteriori* presented by the appearances in the seed in this case, combined with the evidence *à priori* observed in the pre-existing ovule, convey certain proof of the intermediate growth and extension of this extraneous coating, as convincing as that of any demonstration in Euclid, even if no one had ever witnessed this expansion.

Fig. 4.



10. It is manifest that the period of the growth of this extraneous coating must have been subsequent to that of the act of inversion and fertilization of the ovule, and that it is therefore somewhat arilliform in its nature. This kind of coating, being

an expansion of the placentary sheath, I have called an *arilline**, to distinguish it from the true *arillus*, which is always more exterior to it, and not necessarily fleshy, and which is an emanation from, or growth of, the funicle. If the term *arilline*, which is identical with the *arillode* of Planchon and the *faux arille* of St. Hilaire, be objected to, it is easy to give it another name; but that coating, in no case, can be considered to be the *testa*, though sometimes confluent with it.

These considerations are perfectly consistent with the doctrines of Brown and Mirbel, now universally adopted by botanists, in regard to the development of the coats and nucleus of the ovule and the mode of its fertilization and growth.

The question in regard to the seed-coats of *Magnolia* having been fully discussed in my former paper †, I need only here refer to the main points at issue in that case. Dr. Asa Gray, having at first overlooked the existence of the inner integument, was led to conclude that the two outer tunics of its seed are the growth of the two coats of the ovule‡; but he afterwards admitted that its bony shell must be held to be its testa §; at the same time, not prepared to renounce his favourite prepossession that the scarlet coating is a growth of the primine, he maintained that the two constituted one integral tunic, "a baccate testa:" this term, of no definite meaning, was invented by Linnæus, prior to the existence of any distinct nomenclature being given to the several tunics, and before their nature and origin were inquired into. Gaertner, in the use of this term as applied to *Magnolia*, explains that its testa is covered by a fleshy envelope analogous in its nature to that of an arillus, and in describing the seed of that genus, he defines its envelopes as consisting of three distinct tunics ||. Drs. Hooker and Thomson had in the meanwhile adopted the opinion of Dr. Gray regarding the outer seed-coats of *Magnolia*, and in this respect they differ from all preceding botanists¶.

* Linn. Trans. xxii. 89.
† Linn. Trans. xxii.
‡ Gen. Unit. States, i. 60.
§ Hook. Kew Journ. vii. 244.
|| De Fruct. Intr. 133; vol. i. 343; Linn. Trans. xxii. 86.

¶ This is denied by the reporter, in a marginal note made on my paper; but, with all the consideration due to that authority, I submit, as far as my memory extends, that I know of no one who has previously entertained the opinion of Dr. Gray, that this scarlet coating is the testa. Gaertner's definition, here alluded to, is dated 1788; and those who subsequently adopted the same expression would have explained their meaning, if they differed from that definition. Jussieu, however (1789), distinctly confirms Gaertner's explanation (Gen. Pl. 281), when he ascribes to *Magnolia* "semina baccata seu arillata." DeCandolle, in his 'Systema' and 'Prodromus,' adopts simply the same phrase "semina baccata," without further explanation. Spach (Phaner. vii. 469) says positively "arille charnu." Endlicher (Gen. Pl. 4737) also defines it "integumentum exterius carnosum

Against this combined authority I demurred, by showing * that the cord of the raphe being found within the scarlet coating, it was absolutely impossible, if that tunic owed its origin to a mere growth of the primine, that the raphe could have quitted its normal position outside the primine †, and have subsequently insinuated itself into its tissues.

Dr. A. Gray, in his last paper ‡, again repeats that the scarlet coating and bony nut are both derived from a growth of the primine, as he witnessed upon the inner surface of the latter the gradual deposition of osseous cells, subsequently forming the hard shell. There can be no doubt of the fact of this deposition, but I dissent from the inference just mentioned. If what my excellent opponent designates a "baccate testa" be one tunic resulting from the mere growth of the primine, we ought to find it consisting of three parts, as stated in my second preceding definition; but, on examination, we find double the number, or two distinct tunics, the outer having its endoderm and epiderm, which in the ripe seed I found a black and softer surface, easily scraped off, and showing the nut beneath of its usual pale yellowish colour. I will not enter into the question whether the previous growth of the primine is due to "merismatic division," as supported by Dr. Gray, or whether it is due to other sources, after the theories of different physiologists. But when it has attained to nearly its full growth, the mode of the solidification of this tunic is probably effected by means of the intercellular passages, so clearly indicated by Link, as existing between the cells of fleshy tissue; osseous matter, secreted probably from the nourishing vessels, would here readily flow into those spaces and become absorbed into or deposited round the cells of that tissue. By these means the whole internal mesodermal mass would become solidified into a compact hard shell, and the previously harder epidermal surface of the primine would now be comparatively the softer, and be readily scraped off the nut, as I found it in *Talauma*. This view corresponds with the structure observed in the ripe fruit; while, on the other hand, under the supposition of Dr. Gray, that the two outer seed-coats had previously existed under the form of one single homogeneous tunic,

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coloratum, testa subossea." Lindley (Veg. Kingd. 417), speaking of *Magnoliaceæ*, and referring to the tribe *Magnolieæ* as distinct from *Illicieæ*, remarks, "seeds often covered by an aril." The only botanist who speaks ambiguously on the subject is St. Hilaire, who says generally, that where the seed-coats are of different natures and confluent together, he will, for the sake of convenience, consider them as one.

* Linn. Trans. xxii. 86. † See the preceding second definition.

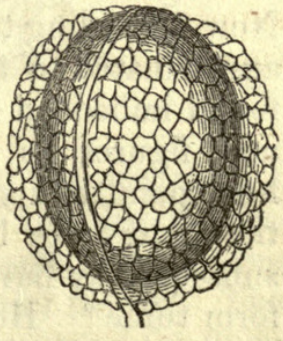
‡ Journ. Linn. Proc. ii. 106.

it would be impossible to assign any reasonable cause why the inner moiety of that tissue became solidified, while its exterior half escaped the same operation.

Dr. A. Gray suspects that I have "formed a wrong idea of the raphe*," and that I have "mistaken for the raphe in *Magnolia* the cord of vessels it contains;" and yet in a preceding page† he designates that cord (the only one existing in that seed) as the "conspicuous cord of the vessels of the raphe," and so figures it as I have done: this is an incongruity only attributable to a *lapsus calami*. The structure of the seed of *Pæonia* (as demonstrated in my paper) quite conforms with the views I have here entertained.

Dr. A. Gray, having watched the increment of the ovule, without being able to detect the growth of any extraneous coating over it, complains that this circumstance has not received its due weight‡; but I suggest, in fairness, how far a negative observation can be expected to preponderate against the positive testimony of the several high authorities who have witnessed and recorded similar developments. Having quoted some of these on a former occasion§, I need not here allude to the facts observed by Dr. Planchon, showing the successive growth of an analogous coating over the seed of *Euonymus*; also the gradual production of a similar tunic in the seeds of *Opuntia*; and, again, the progressive appearance of the same kind of fleshy envelope in *Clusia*. I also cited the minute details of Gasparini, who witnessed the same fact in *Opuntia* in the several stages of its growth. No one will feel disposed to question the still higher authority of the celebrated Mirbel, who minutely describes and figures this "production nouvelle," consisting of "deux couches de tissu cellulaire, qui n'appartient pas primitivement à l'ovule, mais qui s'applique à sa surface et finit par lui servir d'enveloppe comme ses tegumens propres." In this discussion we should not confine ourselves to the single case of *Magnolia*, but ought to be guided by analogy in other instances. With this view, I pointed to examples, such as *Zanonia* and *Feuillæa*, as types of numerous cases where the extraneous coating over the testa is membranaceous and expanded, and which cannot come under the category of a "baccate testa." I also alluded to the tunic in *Tacsonia*||, where the osseous testa of the seed is enclosed within a free, reticulated, membranous sac, upon which the cord of the

Fig. 5.



* Journ. Linn. Proc. ii. 110.
‡ *Ibid.* ii. 107.
|| Linn. Trans. xxii. 93.
† *Ibid.* p. 108.
§ Linn. Trans. xxii. 97.

raphe is visible, extending from the hilar point of the placentary attachment along one side of this sac to the opposite extremity: the only point of organic connexion between the testa and this sac is at the latter termination, where the vessels of the raphe penetrate the shell, to reach the chalaza of the inner integument. Will the advocates of Dr. Gray's hypothesis contend that this free outer membrane and the osseous shell are of identical origin, both resulting from the growth of one ovular tunic? Will it be denied that this free membrane is a production of the original placentary sheath, drawn away from the placenta with its nourishing vessels, and subsequently extended over the whole surface of the ovule?

Perhaps the most telling evidence in support of the view I have here endeavoured to maintain on the one hand, and against the opinion supported by Dr. Gray, on the other, is to be found in the case of *Euonymus*. Complete details of the gradual and progressive growth of the outer fleshy coating of its seed are recorded by Dutrochet*, who shows that it is not formed till after the impregnation of the ovule; that it first appears as a thickening about the hilum; it then becomes cupuliform, gradually extending itself over the ovular integuments, and finally is seen to envelope the whole seed. One of the most important features observed in the growth there described and figured, is that the vessels of the raphe are enclosed in the soft fleshy tissue of this extraneous coating: this coating has generally been regarded by botanists as an arillus, because of the indubitable fact of its subsequent independent growth, and because it is sometimes incomplete or open at one extremity,—a condition I have shown to be an insufficient element in constituting the true character of an arillus†. Dr. Asa Gray has, however, described and figured these same facts ‡, showing first the anatropal ovule of *Euonymus*, in fig. 6, with the lateral raphe in its placentary sheath agglutinated to the primine; figs. 7 & 8 exhibit the progressive increment of this fleshy coating over the primine, and fig. 10 its completion as an entire "pulpy red arillus." Now, according to this, his own evidence, if the raphe be at first agglutinated to the primine in the ovule, and it be afterwards found imbedded in this "pulpy arillus," which he acknowledges and figures as of extraneous growth, proceeding from the hilar point of its placentary attachment, how can the vessels of the raphe have left their first-shown position in the ovule, and subsequently have found their way into the tissue of the arilliform tunic? How can so manifest a development be explained

* Mém. du Mus. viii. 270. tab. 1. fig. 30.
† Linn. Trans. xxii. 83.
‡ Gen. Unit. States, ii. 187. pl. 171.

upon any other principle than that I have above demonstrated? The facts here shown are completely fatal to Dr. Gray's later conclusions. The outer fleshy seminal tunic in *Euonymus* certainly cannot be held to be a true arillus, as generally supposed, but an arilline; in all respects it is analogous to the fleshy coat in *Magnolia*. If, therefore, the outer seed-coat of *Euonymus* be acknowledged to be an arilline, or extraneous tunic distinct from the growth of the real ovular integuments, so, *pari passu*, must the scarlet coating of *Magnolia* be of the same nature: as the previous condition of the ovule, and the subsequent structure of the seed, are precisely similar in both cases, it follows as a necessary rule, that the nature and origin of these seminal tunics must come under the same category.

In order to render the fact of this expansion of the placentary sheath more palpable, I will proceed to demonstrate the manner in which the raphe is developed under other circumstances, which, though of ordinary occurrence, has been only cursorily alluded to on a former occasion*—I mean, a branching raphe. In this instance, the ovule before impregnation exhibits the usual appearance seen in the first of the preceding figures, with a simple lateral band enclosing the nourishing vessels; but during its growth into a seed, either these, or other vessels springing from the same source, spread themselves in dichotomizing branches over the whole surface of the integument, which is generally described as the testa; but if such vessels were really existing within the true testa, they would necessarily have entered its tissues at the point *b* of the chalazal extremity, whence spreading through its mesoderm, they would infallibly show, in the ripe seed, the appearance in the adjoining figure 6,

Fig. 6.

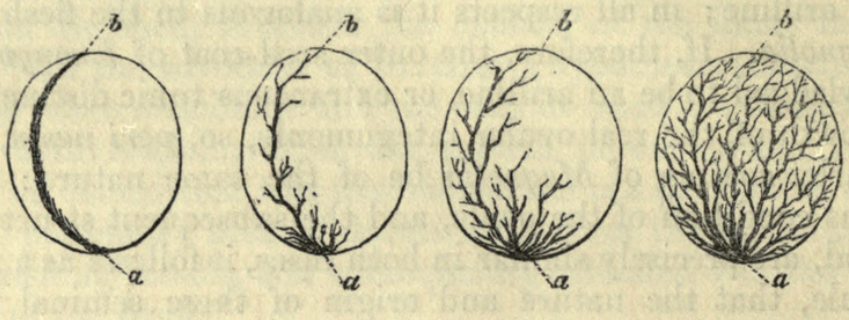
Fig. 7.

where *a* is the hilar point of attachment. On the contrary, I have invariably found, that the starting-point of this distribution of the vessels is at the opposite hilar or micropylar end of the seed, as in figure 7, where *a* and *b* refer to similar points. The development of this form of raphe is easily accounted for upon the explanation I have given, and the following figures will ex-

* Linn. Trans. xxii. p. 88.

hibit, in a more forcible manner than words can express, the gradual extension of the placentary film, carrying within its

Fig. 8. Fig. 9. Fig. 10. Fig. 11.



expanding tissues the branches of vessels, where they find ample room to spread and subdivide themselves in the manner seen. This explanation is conformable with the fact, and consistent with the usual rules of increment. But under the former assumption, that the vessels so disposed lie within the tissues of the real testa, we must suppose the annihilation of the primitive placentary sheath, and the production of a fresh set of vessels from the placenta, subsequent to the fertilization of the ovule, which must pierce an entrance through the epiderm of the primine, at a point near the micropyle, and which thence distribute themselves through the mesodermal tissue of that integument,—a supposition palpably absurd, and in violation of the ordinary laws of mechanical growth.

At other times, as in the Almond, the original cord of vessels does not throw out dichotomizing branches from its base, as shown above, but, following the expansion of the sheath, it becomes separated and distributed all round the seed into irregular bundles, which extend from the hilum to the chalaza, and which anastomose with one another at ganglionoid points, just as an entangled skein of thread appears when pulled out by a lateral strain. In *Amygdalus*, the arilline, testa, tegmen, and very attenuated albumen, are all confluent with one another, into apparently one tunic.

Those who are not satisfied with my explanation must be prepared to define upon consistent principles, which has never been attempted before, how and by what means the vessels of the raphe become distributed in the manner we find them. This increment of the placentary sheath appears to me incontrovertible. It is, however, a consideration that concerns not only the botanical, but the zoological physiologist; for if it be true that at a period immediately subsequent to the act of its fertilization, the ovule becomes covered with an entire film, which probably exerts some yet unknown and important function towards the future perfection of the embryo, it presents an exact analogy

with the animal ovum, where a similar coating is well known to be produced over it, exactly at a corresponding period.

In a separate paper*, I have pointed out many singular anomalies observable in the structure of seeds, that are not reconcileable with the ordinary hypothesis. I have since collected numerous other curious and novel facts tending to support my views, showing the unusual developments observed in the *Colletieæ* and in the *Rhamnaceæ* in general, the still more novel form of growth of the seeds of the *Anacardiaceæ*, the peculiar structure in those of the *Styraceæ*, *Canellaceæ*, *Winteraceæ*, *Lardizabalaceæ*, and several other families, of which, after patient research and careful investigation, I have prepared monographs, which in succession will appear in this Journal, and which will afterwards be reproduced in my 'Contributions' accompanied by numerous plates and copious analytical details. In most cases, in the above-mentioned families, the outer coating of the seed appears under the form of a crustaceous shell, exterior to, and quite free from a fleshy tunic, which encloses the cord of the raphe within its tissues: although the former coating is usually designated as the testa, it cannot under any hypothesis be considered as a development of the primine: it appears to me a perfect arillus,—satisfactory proof of which is offered in *Lardizabala*, *Lithræa*, and numerous other instances.

XXVI.—*Some Observations on Professor Agassiz's Criticisms on the "Catalogue of Shield Reptiles in the Collection of the British Museum."* By Dr. J. E. Gray, F.R.S., V.P.Z.S., P. Ent. Soc. &c. &c.

I have lately received, through the kindness of the author, a copy of Professor Agassiz's "Contributions to the Natural History of the United States: First Monograph, in Three Parts: I. Essay on Classification. II. North American Testudinata. III. Embryology of the Turtle, with thirty-four Plates," a highly valuable and very important contribution to the natural history of the Testudinata; and which is accompanied with a large number of remarkably well executed plates, showing the development of the embryo and the young animal of several species of the Testudinata inhabiting the United States, and some plates showing the change in the general colours of one of the species. In the Appendix and Errata to this work there occur, among observations respecting the 'Catalogue of Shield Reptiles,' the following remarks: "Among his [Dr. Gray's] North American *Emys* there are several which are only nominal species. I trust

* Linn. Trans. xxii. 97.