XIII.—Studies in Floral Morphology. III. The Flowering of *Napoleona imperialis*, Beauv.

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In a former memoir published in these *Transactions* (30) the floral development of the "Cannon-Ball" tree, *Couroupita guianensis*, Aubl., was described. The most striking floral feature of this remarkable Myrtaceous genus is the andrœcium, the form, proportions, and position of whose parts produce a curious zygomorphy with cellular gigantism. The Lecythidean andrœcium, and the torus which bears it, were considered of systematic importance and of physiological interest, and deserving of special study with reference to the *Myrtaceæ* as a whole.

In the present communication an attempt is made to throw light on the floral morphology of the genus *Napoleona*, which is generally considered of Myrtle affinity, but with anomalous floral features. The generic floral features considered are viewed as due to transformation and replacement, during descent, of cycles of stamens and of a portion of the stamen-bearing torus, in consequence of which accessory petaloid structures have arisen. Thus, as in *Couroupita*, the chief generic floral features are considered to have arisen by modifications of the andrœcial zone, and notice is drawn to the need of further study of the Myrtle-andrœcium. No immediate explanation is advanced of the original causes of the floral features described for *Napoleona*, but the facts of structure are necessary for a later discussion of the *Myrtaceæ* as a whole.

A general description of *Napoleona imperialis*, Beauv., drawn from various sources

(9), (13), (17), (23), (25), and from my own observations of the plant in Jamaica, may be useful. The first account of the genus *Napoleona* is due to PALISOT DE BEAUVOIS (9), from plants found in abundance in the woods of Oware in 1786. The plants were scraggy shrubs, 7 to 8 feet high, with entire alternate oblong leaves, with short thick petioles and needle-points (text-fig. 1). HEUDELLOT further collected *Napoleonas* at Foñta Dhiallow in Senegambia, and DE JUSSIEU described them in 1844 (13). These are now recognised as *Napoleona Heudelotii*, Juss., differing from *Napoleona imperialis*, Beauv., in stature, leaf-form, and flower-colour (29). In 1853 (23) LINDLEY described *Napoleona* as a bush about as large

TEXT-FIG. 1.

as a *Camellia*, with smooth leathery exstipulate leaves. From plants grown at Kew and Sion House, MASTERS described *Napoleona* in 1869 (25) as a small tree with verticillate branches, and with leaves biglandular at their base. My own observations of *Napoleona imperialis*, Beauv., are from one plant in Castleton Gardens, Jamaica. It was 18 feet high, its stem was sturdy, and its branches were cylindrical and slightly angular. Comparisons have also been made with plants in the Royal Botanic Garden, Edinburgh, and the Botanic Gardens, Cambridge. DE BEAUVOIS depicted the flowers of *Napoleona* as axillary groups on the older branches, and as blue with a violet sheen. Beneath each flower are several small rounded bracts ranged in two rows. The calyx is gamosepalous and of 5 coriaceous lanceolate and persistent similar sepals, whose bases become part of the envelope of the fruit. He described the corolla as *double*, and inserted on the calyx. Its outer portion is a plicated, membranous, highly-coloured structure traversed by many sturdy radiating veins. Its inner portion is a single membranous piece cut into several similar highly-coloured straps. No mention is made of a series of petaloid filaments invariably present in my materials, and situated between the so-called outer and inner corollas. Five stamens with petaloid filaments are recorded. They are coherent at their bases, and adherent to the "inner corolla." Each stamen is described as carrying two distinct bilocular anthers. No reference is made to filaments of aborted stamens characteristically present in my materials. The gynœcium is of 5 carpels and inferior, and the united style has a flattened peltate stigma with 5 angles, to each of which a furrow stretches from the centre of the stigma. The fruit is described as soft and spherical, and becoming at maturity unilocular, so that the numerous seeds are embedded in a fleshy substance.

This plant was dedicated to Napoleon I by M. PORTALIS (Ministre des Cultes), and named *Napoleona imperialis*, Beauv. DE BEAUVOIS's description of the plant is accompanied by a full-size figure of a portion of a flowering branch. Gland-like bodies are shown on the sepals, but no reference to them is made in the text. The plant became the foundation of DE BEAUVOIS's family *Napoleoneæ*, and was viewed by its discoverer as a genus which "determined positively a separation between the *Cucurbitaceæ* and *Passifloreæ*, by being a family well-defined and intermediate."

LINDLEY (20), (21), (23), DE JUSSIEU (13), HOOKER (17), and MASTERS (25), have contributed to the description of the flower. Their observations are here combined with my own. The flowers are single or in groups of 2 to 5 in the axils of distichous leaves. As a rule they do not expand until the leaves have been shed, and frequently remain as inconspicuous buds, which open on the older branches (text-fig. 1 and fig. 3). They are almost sessile, in which feature they agree with other known species of *Napoleona*, except *N. Egertonii*, Bak. f. l., and *N. Talbotii*, Bak. f. l., of Southern Nigeria (29). The flower-bud is angular, inversely pyramidal, and pointed at the top (fig. 1). The fully-expanded flower may be 2 to 3 inches in diameter. Its short pedicel is closely invested by two opposite rows of persistent bracts. The latter are ovate, smooth, and green; frequently their tips are forked, and they carry terminal or marginal gland-like bodies resembling those at the base of the flower-bud of *Camellia* (figs. 1, 2). Neither in the bud nor the expanded flower have I observed any exudation from these gland-like bodies. The calyx comprises 4 or 5 persistent green thick leathery sepals, which constitute a semi-inferior cup (text-fig. 2, figs. 1, 2; *sp.* figs. 3 and 5). In the bud the sepals show a perfectly valvate æstivation, while to right and left of their acuminate tips, and sometimes on their outer surfaces, and at the base of their margins, are gland-like bodies similar to those on the leaves and bracts (fig. 2). In the expanded flower the sepals are curved down and back, and are hidden by the corolla (fig. 3). In the fruit

they persist as do the sepals in the apple. The corolla is gamopetalous and is inserted immediately within the calyx (text-fig. 2, *p.* in figs. 3, 4, 5). Thus in the expanded flower the corolla is on the margin of a shallow receptacular cup of which the calyx forms the reversed rim. In the unopened flower the corolla appears 4- or 5-lobed, with deep furrows between the lobes (fig. 2). The lobes alternate with the sepals (text-fig. 2, fig. 2). Each is plicated and is traversed by 7 or 8 stiff radiating ribs, more prominent on the lower than the upper surface of the corolla. The ribs taper to fine points on the crumpled corolla-margin. Between the ribs the texture of the corolla is membranous. On its upper surface the corolla is smooth and glossy; on all but the base of its outer surface it is velvety. As the flower expands it becomes evident that the furrows between the corolla-lobes are due to radial folding of the corolla. The apparent separation of the corolla-lobes is obliterated as the flower expands, and the corolla is bent down over the calyx so that its crenate margin is in close contact with the stem (text-fig. 1 and fig. 3). There is considerable variation in the colour of the corolla, which is sometimes dark blue, and at times purple or of a deep claret colour. Its toothed margin is of an apricot colour in the opening flower, but is frequently blue as the flower fades. As LINDLEY has noted (21), the corolla is very delicate, fades rapidly, and is subject to marked colour-changes. The corolla thus recognised is equivalent to the outer portion of the *double* corolla described by DE BEAUVOIS, and to the outer ring of the *triple* corolla described by LINDLEY (23).

Immediately within the corolla, and adherent with its base, is a ring of distinct petaloid filaments, varying in number from 50 to 70 (text-figs. 1 and 2, and *f* in figs. 3 and 5). They are coherent at their base so that their actual junction with the corolla is a slight membranous torus (figs. 3, 4, 5). These filaments were viewed by LINDLEY as the *second* ring of a *triple* corolla (23), and by MASTERS as the *outer* portion of a *double* corona (25). Each filament is a narrow pointed strap of delicate texture. It is white, tipped with pink, and bent downwards or curled from its middle (text-fig. 1 and fig. 3). A short distance from its base it thickens to a sharp ridge on its upper surface. Beyond the ridge is a depression, followed by a sac-like swelling, the main body of which is a loose parenchymatous tissue. From the swelling outwards the filament tapers rapidly, and the delicate vascular strand which traverses it dies out before the tip is reached. The filaments are less than half the radial dimensions of the corolla. Within the cycle of filaments, and separated from them in the mature flower by a well-marked zone of the receptacle, stands an erect membranous petaloid cup (text-figs. 1 and 2, *c* in figs. 3, 4, 5). It is the inner portion of LINDLEY's triple corolla, and is MASTERS's inner corona. Its margin bears from 30 to 50 teeth, bent downwards and inwards. To each tooth runs an unbranched vein. In radial length this cup is usually somewhat more than half the corolla. In many flowers the teeth are long and prominent, so that the cup appears to be composed of numerous coherent segments, free at their tips. In flowers in which the apparent segments of this and the preceding cycle are comparatively few a more or less definite alternation of the veins of these two cycles is common. On the outer surface of each apparent segment of the cup is a prominence which fits into the groove on the upper surface of the

TEXT-FIG. 2.

petaloid filament immediately outside. On its inner or upper surface the cup is usually of a cream colour. Externally, and particularly at its base, it is pink, while the teeth are pink on both surfaces.

The andrœcium is in such close relationship with the inner surface of this corona, that in the expanded flower the stamen-bases and the corona are on a common torus (*st.* figs. 3, 4, 5). The stamens are coherent for the greater part of their filaments, but between successive groups of 4 there is a more distinct separation than occurs within the groups. Thus the stamen-cycle is divisible into 4 or 5 phalanges which are opposite the petals (text-fig. 2). There are usually 16 to 20 stamens. Collectively their filaments form a cup fused without with the base of the corona, and within with a fleshy undulating ring around the base of the style (figs. 3, 4, 5). The stamen-filaments are strap-shaped; each is traversed by a vein, and resembles in texture the petaloid corona. Their bases are spread almost horizontally within the corona, they are almost erect towards their limit of cohesion, and in their free portions are bent downwards and inwards towards the centre of the flower (figs. 3, 5). The anthers are thus directed into a space beneath the broad stigma, and between the style and the fleshy disc which surrounds its base (*α.* figs. 3, 5). Towards its tip each filament is membranous and sharply curved, first outwards, and then inwards to its point of junction with its anther. By shrinkage of this delicate portion of the filament in the expanded flower, the anther, when dehiscent, is in part drawn from beneath the stigma. Of each phalange of stamens usually only the two outer members bear anthers. The remaining middle two are totally sterile, and their filament-tips, though curved as in the fertile stamens, are short and shrivelled (text-fig. 2, figs. 3, 5). The number of fertile stamens is usually 8 or 10, but may be as low as 5, or as high as 15. The mature anthers are oblong and bilocular, and their dehiscence is extrorse. The space beneath the stigma in which they are lodged is limited, and the tips of the sterile stamens do not enter it (right, fig. 5). The anthers are then in close lateral contact around the style. With the exception of the filament-tips, which are usually red, the stamen-ring is of a rich cream colour.

Immediately within the stamen-cycle, and closely associated with the torus which bears it and the corona, is a thick fleshy yellow disc, more than half as high as the style (*d.* figs. 3, 4, 5, text-fig. 2). Its inner face is obscurely lobed so that from 8 to 15 undulations are produced allowing for the accommodation of the anthers between the disc and the style (figs. 3, 4, 5). The disc is provided with a branched-vein system. Immediately within the disc, and overhung by it, is a broad ditch from which the massive style rises in the centre (*sy.* figs. 3, 4, 5).

The style widens upwards into a broad 4- or 5-lobed smooth pale-yellow head. On the upper surface of this head 4 or 5 small stigmatic areas are developed (figs. 3, 4, 5). The vascular supply to the style is elaborate, and stretches into the lobes of the peltate head. In the centre of the head is the pore-like entrance to a restricted stylar cavity (figs. 3, 4). From this pore a shallow orange-coloured furrow runs to each stylar lobe, and ends in a slight oval eminence. The rim of this eminence is a stigmatic surface, and in its centre is a pore leading into a stylar chamber of lysigenous origin (*sl.* figs. 3, 5). The stylar chambers lead into the original stylar cavity towards the base of the style. DE JUSSIEU has affirmed that there are 10 stigmatic openings into the style, but I have never observed more than 5.

The ovary is inferior, deeply sunken in the dilated receptacle, and has 4 or 5 loculi (text-fig. 2; *o.* in figs. 3, 4, 5). Towards maturity the partitions may become obliterated in their upper portions, so that a spuriously unilocular state may arise. In each locus there

are usually 4 ovules in 2 rows, hanging from the top of an axile placenta. Over the ovules a clear space leads from the stylar cavity into each loculus.

The fruit is a spherical berry, as big as a pomegranate, and crowned by the persistent calyx. When mature it contains a mucilaginous edible pulp embedding the seeds. There is a brown woody rind, so full of tannin that when the fruit is placed in water a heavy ink is produced. The seeds are amygdaloid and kidney-shaped, and may be $1\frac{1}{4}$ inch long. The fruit does not appear to dehisce, but the seeds are liberated by rotting of the pericarp.

The distribution of *Napoleona imperialis*, Beauv., is somewhat limited. It has been found in fair abundance round the Bight of Benin, and many specimens have been secured from isolated stations in the Congo. It is one of 14 species whose distribution is limited to Central and Western Africa (29).

To the better understanding of the structural problem which the flowers of *Napoleona* raise, some comment on the views of systematists and others regarding *Napoleona* may be made. Following DE BEAUVOIS's original description, DE FONTAINES (12) in 1820 expressed the opinion that *Napoleona* belonged to the *Symplocineæ*. In 1822 DESVAUX (*Journal de Botanique Appliquée*, iv, p. 130) changed the name of *Napoleona* to *Belvisia*, and ROBERT BROWN (7) held grave doubts of any relationship between *Napoleona* and the *Passifloreæ*. He made superficial comparisons between the corona of *Rafflesia* and of *Napoleona*, and proposed to found a distinct family, *Belvisiæ*, containing *Napoleona* and *Asteranthos*, "to stand near *Symplocaceæ*, and with a tendency towards *Rafflesiaceæ*." In 1833 (18) and 1836 (19) LINDLEY placed the *Belvisiæ* after *Campanulaceæ* and *Sphelocleniaceæ* and before *Columelliaceæ*, but this view he abandoned without further evidence in 1845 (22). In 1839 (11) DE CANDOLLE viewed the *Napoleoneæ* as relatives of the *Vacciniæ*, while ENDLICHER (15) held them to be "doubtful genera of the *Ebenaceæ*." MEISNER (26) in 1843 preferred for them a resting place "between *Passifloriæ* and *Loasaceæ*." In 1844 (20) (21) LINDLEY described materials of *Napoleona*, collected by WHITFIELD in Sierra Leone, and in the same year DE JUSSIEU (13) compared the pollen-grains of *Napoleona* with those of certain *Onagraceæ*. He concluded that the position of *Napoleona* in the natural system was very doubtful, and was not cleared even by strong resemblance to *Asteranthos*. He believed *Napoleona* "to resemble" most clearly the *Sapotaceæ*. In 1848 HOOKER (16) first suggested for *Napoleona* a definite Myrtaceous affinity, a suggestion which so appealed to LINDLEY that in 1853 (23), having abandoned his former opinions, he placed the *Belvisiæ* between the *Rhizophoraceæ* and the *Melastomaceæ*, but with a distinct leaning towards the former. The Myrtaceous affinity of *Napoleona* suggested by HOOKER was accepted by BENTHAM in 1849 (5). He placed *Napoleona* near to the *Barringtoniæ* among anomalous *Myrtaceæ*, and supported his opinion with the statement that "if the corona or ring of filaments (of *Napoleona*), called by some the intermediate and inner corolla, be regarded as sterile stamens, they will be found to be analogous to stamens of *Myrtaceæ* in their insertion on the fleshy disc crowning the ovary, as in their folded arrangement in the bud." Thus was crystallised the idea of the corona of *Napoleona* as a replacement-product of stamens of a Myrtaceous flower. In 1859 (1) AGARDH allied the *Napoleoneæ* with the *Ternstræmiaceæ*, but in 1867 BENTHAM and HOOKER (6), having strengthened their belief in the Myrtle-affinity of *Napoleona*, placed it between *Bertholletia* and *Asteranthos* as their 71st Myrtaceous genus, and allied it closely with such of their Lecythidean genera as *Barringtonia*, *Grias*, *Couroupita*, *Couratari* and *Lecythis*. With this general classification MASTERS agreed in 1869 (25) after a study of the floral structure. The view of BENTHAM and HOOKER was not, however, universally accepted, nor could it be otherwise, for by some the corona was considered a group of modified petals,

or a "compound para-corolla," while others, who could not view it as a group of modified stamens, declared it a "nectariferous emanation from a disc," or a "coronal appendage analogous to that of the *Passifloreæ*." In 1875 EICHLER (14) accepted the classification of BENTHAM and HOOKER, but MIERS (27) remained a dissenter, claiming for *Napoleona* the isolation of a "monotypic representative of a distinct family, the *Belvisiaceæ*." To NIEDENZU (28) in 1893, *Asteranthos* and *Napoleona* formed the *Napoleonoideæ*, the third of 4 groups of *Lecythidaceæ*, but the persistent uncertainty of the homologies of the floral parts was again apparent, for *Napoleona* was considered apetalous.

From the foregoing survey it will appear how necessary is a clearer understanding of the floral structure, and especially of the developmental floral morphology of this strange

TEXT-FIG. 3.

TEXT-FIG. 4.

genus. CRÜGER alone (8) has examined the flower of *Napoleona* during development. He indicated generally the order of floral part-initiation, and showed that while the stamens are late in development they antedate in initiation both the corona and the petaloid filaments. In supplementing in these pages CRÜGER's observations, the salient features of floral development alone are recorded. These are to serve later as a basis for comparative study.

Each flower is initiated in association with two rows of bracts (text-fig. 3), and the sepals (*sp.*) are early defined. They are prominent bodies before the petals appear (*p.*), and the broad style (*sy.*) and ovarial cavity (*o.*) are indicated. The space between the style and the petals is almost completely occupied by a torus (*t.*), which is uniformly developed around the style. From it, later, the fleshy disc, the stamens, the corona, and the petaloid filaments arise. On it stamen-primordia may be already indicated (*st.*) as dome-shaped protuberances involving a large portion of the upper surface of the torus, and pointed inwards towards the style. On enlarging (text-fig. 4) the stamen-primordia (*st.*) become pendent from the upper and inner

margin of the torus into the ditch around the base of the style (*sy.*). The outer portion of the torus, remaining between the stamen-primordia and the petals, is raised into a definite narrow collar (*t₁*) from which the corona and the petaloid filaments are to arise. Immediately beneath the stamens a new series of mounds has meantime appeared on the sloping inner face of the torus (*d.*). These mark the initiation of the disc which is to surround the style. A general enlargement of the flower, as a whole, has meantime taken place, the vascular system of the receptacle has been defined, the placentas (*pl.*) have appeared, and in the angles of the stylar head the lysigenous tracts from the stigmas to the stylar cavity are differentiated (*lg.*). The stamens are soon differentiated into short filaments and curved pendent anthers (*sf.* and *a.* text-fig. 5). The floral receptacle has now widened considerably, and as the disc around the style enlarges (*d.* text-fig. 5) the filament-bases are displaced outwardly and lowered, and the anthers hang over the disc into the moat which it delimits. From the narrow collar between the stamens and the corolla the primordia of the corona and the petaloid filaments have now arisen in close succession (*c.* and *f.* text-fig. 5). Thus all the parts recognised in the mature flower are defined. In the general enlargement of the flower which precedes maturity

TEXT-FIG. 5.

the ovary becomes deeply sunken, and the summit of the receptacle widens until the inverted pyramidal form of the flower as a whole is produced. At the same time the disc around the style has so enlarged that the stamens appear to spring from its outer face, and by intercalary growth adhesion of the andræcium and the corona occurs. Thus, in the expanded flower, the disc, the stamens, and the corona are associated on a common receptacular outgrowth (figs. 3, 4, 5). By similar processes the petaloid filaments and the corolla come to be closely associated in the mature flower, and to adhere at their bases (figs. 3, 4, 5). Nevertheless the facts of development have shown that the adhesion of the petaloid filaments and the corolla, and the separation of the former from the corona, are features of late development. From its initiation the corolla has been an independent floral cycle, while the petaloid filaments, the corona, the stamens, and the disc are later developments, and owe their origin to a common toral growth with which the corolla is not confounded. On grounds of development neither the petaloid filaments nor the corona should then be considered appendages of the corolla, and thus, despite their petaloid nature, the filaments and the corona may be closely associated with the stamens and the disc in descent.

In attempting the interpretation of the floral parts, evidence may be gleaned from their structure during development and at maturity. Reference has been made to the gland-like bodies at the base of the lamina, on the margins of the flower-bracts, and at the tips and bases of the sepals. The structure of these bodies is illustrated in fig. 6, which represents a longitudinal section through a gland on the tip of a sepal. Each gland is supplied by a

sturdy vascular strand ending in contact with a pad of compact thick-walled cells. The pad is clothed by a layer of narrow columnar epidermal cells, with dense cytoplasm, thick smooth stratified outer walls, and delicate radial walls. In the unopened flower this stratified epidermis is uniformly raised, but later a central protuberance is formed by unequal shrinkage of the glandular mass as a whole (figs. 1, 2). The function of the glands has not been determined, but they are present on no other floral parts than the bracts and the sepals.

The stigmas and the lysigenous stylar cavities to which they form the openings also deserve notice. In the immature style a stigma is defined by an area of enlarged columnar epidermal cells (fig. 9). Beneath it is a mass of dense small cells among which are isolated tracheides. This mass extends downwards through the style until the wall of the stylar cavity is reached some little distance above the ovary (figs. 3, 4, 5). It is by rupture and elevation of the columnar epidermal cells that the stigma-lips are produced (fig. 10), and by disintegration of the stylar tracts that a passage is provided for the pollen-tubes. The glands and the lysigenous stylar cavities are characteristic of *Napoleona*, and are absent from the Myrtaceous genera with which it is now habitually grouped. Their systematic value may then be better appraised.

From its initiation the disc around the style is a mass of parenchyma, which gradually differentiates at its centre into irregular anastomosing masses of small, dense, thin-walled cells, with islands and strands of larger vacuolated cells in the meshes (fig. 7). In the thin-walled parenchyma surrounding this mass are the branching ends of the vascular system (figs. 3, 4, 5, 7). The epidermis of the disc is of small, thin-walled cells. I have failed to observe any excretion from this curious ring, and on grounds of structure alone no opinion can be based of its original nature.

The stamen-filaments have no special structural features. Both upper and lower epidermal layers are of large stratified cells with thick outer and inner walls, while the core of a filament is of highly ventilated parenchyma embedding a delicate vascular strand. The membranous curved tip of the filament is a late development, and in the sterile stamens an anther is not even initiated, and sterilisation is complete.

In general structure the corona resembles the stamen-filaments from its beginning, and its only special structural feature is the series of protuberances already noted on its outer lower surface. Each protuberance is merely a mound of loose thin-walled parenchyma over which the regular epidermis is raised. Thus, from its structure alone, nothing is learned of the homology of the corona.

Nor can the original nature of the petaloid filaments be inferred from their structure during development, though they resemble in structure both the stamen-filaments and the corona. The protuberances which they bear are not, as has been suggested by some, aborted anthers. They are late developments resembling in structure the protuberances on the corona. Whatever be the functions of these protuberances is not indicated by their structure alone.

At its base the corolla agrees structurally with the filaments and the corona, but in its free outer portions its lower epidermis is irregular, and renders the corolla velvety by the numerous short outgrowths which it bears (fig. 8).

Thus, on grounds of structure alone, no opinion can be based of the original nature of the disc, the corona, and the petaloid filaments, and their arrangement at initiation and grouping at maturity must be brought once more into court. It is open to those who accept the corolla as a true corolla to consider the petaloid filaments accessory structures, with no reference in origin to the degeneration and replacement of a stamen-cycle. Guided by their position and grouping at maturity, rather than by their position and grouping at initiation,

some may incline to accept this view. But if the initial position of the petaloid filaments, their late development, and early complete independence from the corolla be the guide in seeking their origin, then their original close association with the corona, the stamens, and the disc on a common receptacular torus may also be accepted as evidence that the petaloid filaments, the corona, the stamens, and the disc have been of like nature and common origin in descent. If the latter view be adopted, the corolla may still be considered a true corolla, and the interpretation of the petaloid filaments, the corona, and the disc must be sought in the comparative study of the relatives of *Napoleona*. At present the only developmental facts available for an organism with which *Napoleona* is now grouped are from *Couroupita* (30). The latter has a definite independent corolla within which a well-marked torus is formed as in *Napoleona*. On the greater part of this torus numerous cycles of stamens arise, but on an outer portion of the torus which is delayed in development a petaloid structure arises, and later bears abnormal stamens. In *Lecythis*, *Lecythopsis*, and *Bertolletia*, which are near relatives of *Couroupita*, this petaloid structure is entirely sterile, and may be viewed as the outcome of complete sterilisation of an outer portion of the stameniferous torus. If valid comparisons with these organisms may be made, the petaloid filaments and corona of *Napoleona* may reasonably be interpreted as replacement-products of outer cycles of stamens of a Myrtle-type of flower, and the opinion of BENTHAM, already cited, will stand. The disc around the style may further be considered the inner remnant of the torus, or a new development from it, which, remaining sterile, has become glandular. To these views I am at present inclined. But whatever be the true interpretation of the floral parts of *Napoleona*, the present observations will serve to focus attention on the Myrtle-andrœcium, and the structures associated with it, as deserving systematic developmental study. The structural facts considered in these pages will be employed later in the general discussion of the floral morphology of the *Myrtales*.

SUMMARY.

The present paper is a continuation of the studies on floral morphology published in these *Transactions*. It provides an account of the flowering of *Napoleona imperialis*, Beauv., and deals particularly with the petaloid filaments, the corona, and the disc, which are characteristic features of the flower.

It is shown that the structure of the floral parts neither during development nor at maturity will decide the origin and nature of the floral parts mentioned above.

But the order of floral part-initiation and their early grouping may be used in default of more cogent evidence.

If such developmental facts are relied upon, and comparisons with Myrtaceous genera, with which *Napoleona* is habitually grouped, be valid, the following conclusions may be reached:—

(1) The petaloid filaments and corona of *Napoleona* are replacement-products of outer cycles of stamens of a Myrtle-type of flower. This opinion has already been held by BENTHAM, and to it the author subscribes.

(2) The fleshy disc around the style is the inner remnant of the stamen-bearing torus which, through sterilisation, has become glandular.

Thus the andrœcium of *Napoleona*, and the structures associated with it, will merit special consideration in a later systematic discussion of the *Myrtaceæ* as a whole.

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DESCRIPTION OF FIGURES IN TEXT.

(All the figures are of *Napoleona imperialis*, Beauv.)

Fig. 1. Two flower-bearing branches of the plant in Castleton Gardens, Jamaica. (About half natural size.)

Fig. 2. Floral diagram. Passing inwards from the subtending leaf (black) the succession of floral parts represented is: sepals, petals, petaloid filaments, corona, stamens, disc, and gynoecium.

Fig. 3. Plan of radial longitudinal section of a young flower at the stage when the sepals (*sp.*), petals (*p.*), style (*sy.*), ovary (*o.*), receptacular torus (*t.*), and stamen-primordia (*st.*) are defined. ($\times 14$.)

Fig. 4. Plan of radial longitudinal section of a young flower at the stage when the placentas (*pl.*), disc (*d.*), stylar chambers (*lg.*), and the collar which bears the corona and the petaloid filaments (*t₁.*) are defined. ($\times 14$.)

Fig. 5. Plan of radial longitudinal section of a portion of a young flower at the stage when the stamens are differentiated into filaments (*sf.*) and anthers (*a.*). The disc is enlarged (*d.*), and the corona (*c.*) and petaloid filaments (*f.*) are initiated. ($\times 14$.)

DESCRIPTION OF FIGURES IN PLATES.

(All the figures are of *Napoleona imperialis*, Beauv.)

PLATE I.

Fig. 1. A flower-bud showing the axile position of the flower, the two rows of gland-bearing bracts, and the valvate sepals with glands towards their tips. ($\times 2$.)

Fig. 2. An opening flower-bud showing the sepal-glands at the tips and base of the sepals, and in the centre the unopened crumpled corolla. ($\times 2$.)

Fig. 3. Median longitudinal section of an expanded flower. The floral parts are lettered, *sp.* (sepals); *p.* (petals); *f.* (petaloid filaments); *c.* (corona); *st.* (stamens); *d.* (disc); *a.* (anthers); *sy.* (style); *o.* (ovary); *st.* (stigma). ($\times 4$.)

Fig. 4. Median longitudinal section of a flower from which the sepals, petals, petaloid filaments, corona, and stamens have been removed, all except their bases which are lettered as in fig. 3. ($\times 4$.)

Fig. 5. Median longitudinal section of an opening flower from which the calyx has been cut on the left, except its base (*sp.*). The stamen on the right (*st.*) is sterile. The parts are lettered as in figs. 3 and 4. ($\times 4$.)

PLATE II.

Fig. 6. Longitudinal section of gland on tip of a sepal of a bud. A strand of tracheides runs up to the base of a pad of dense cells, and the epidermis on the outer (right) side of the gland is of columnar cells. ($\times 50$.)

Fig. 7. Radial longitudinal section of the disc around the base of the style of an expanded flower. The central mass of tissue is apparently glandular, and the end of a fine vascular strand is shown on the left. ($\times 50$.)

Fig. 8. Transverse section of the free terminal portion of the corolla. Its upper (inner) epidermis is smooth and stratified; its outer (lower) epidermis is irregular and slightly hairy. ($\times 50$.)

Fig. 9. Longitudinal section of an immature stigma, and the terminal portion of a stylar tract. The stigma is composed of prominent epidermal cells; the stylar tract is of small cells including a few tracheides. ($\times 50$.)

Fig. 10. Longitudinal section of a mature stigma which gives access to a lysigenous stylar chamber. ($\times 50$.)

DR. J. M. THOMPSON ON THE FLOWERING OF *NAPOLEONA IMPERIALIS*. BEAUV.

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