

THE POSITION OF THE GENUS THOMANDERSIA BAILL.

by

C. E. B. BREMEKAMP (Utrecht)
(with Tab. II—IV)

Among the most aberrant types of pollen grains found in plants which have been referred to the family *Acanthaceae*, are those of the genera *Meyenia* N. ab E. and *Thomandersia* Baill. Although the pollen grains were described by LINDAU under different names, those of the first genus as cogwheel-shaped and those of the latter as lenticular, they are really very similar: in both genera they are depressed globose, provided with five or more meridional grooves extending from the equator to about halfway the poles, and without clearly circumscribed germ pores. The difference between the two kinds of grains lies in the presence or absence of ribs: in *Meyenia* the grooves are borne on the top of ribs separated from each other by shallow depressions, whereas in *Thomandersia* the whole surface between the grooves is more or less evenly bent.

Material of *Meyenia* was not yet available to me, but judged from the description the genus differs but slightly from *Thunbergia* L.f. sensu Lindau. In fact, the two genera have often been united. The pollen grains of *Thunbergia* sensu Lindau resemble those of *Meyenia* in the absence of germ pores and in the presence of grooves, but the latter are never meridional: as a rule, they are more or less serpentine (cf. BREMEKAMP in Rec. d. trav. bot. néerl. XXXV, 1938, pp. 142—143, fig. 2 A—G and Tab. XIII B—E).

The genus *Thomandersia* was first described by BENTHAM, in BENTHAM et HOOKER f., *Genera Plantarum* II, p. 1093, 1876, under the name *Scytanthus* T. And. It was based on a West African plant of which a specimen in the Kew Herbarium had been examined by T. ANDERSON, who had labelled it *Scytanthus laurifolius* T. And. As the name *Scytanthus* had been used already by LIEBMANN for a genus belonging to the *Rafflesiaceae*, and in the slightly diverging form *Skytanthus* by BENTHAM and HOOKER f. for one of the genera of the *Apocynaceae*, ANDERSON'S plant had to be renamed. BAILLON apparently was the first to see this, and it was he who, in his "Histoire des Plantes", gave it the name *Thomandersia*.

The new genus had been placed by BENTHAM in the *Barlerieae*, one of the sections of his tribe *Justicieae*, and both BAILLON in his "Histoire des Plantes" and C. B. CLARKE in the "Flora of Tropical Africa" accepted this classification. LINDAU, however, in ENGLER'S *Botanische Jahrbücher* XVIII, p. 55, 1893, and in his monograph of the family in ENGLER u. PRANTL, *Nat. Pflanzenfam.* IV 3b, p. 325, 1895, referred the genus to his new tribe *Asystasieae*. It is difficult to see on what grounds the diverging opinions of BENTHAM and LINDAU may have been based. Speculating on this topic, however, is not worth while, for the descriptions and figures of the five species, which at present are known, show that both views are erroneous, and new facts brought to light by a reinvestigation of the type species, fully confirm this conclusion. The data on which it is based, are summarized in the following paragraph: they are either unfavourable to the views of BENTHAM and LINDAU, or incompatible with them.

The shoots of *Thomandersia* are inarticulate; cystoliths are absent; the bracts more or less irregularly scattered and the bracteoles minute; the corolla is fleshy, and in the bud the two-lobed upper lip overlaps the lateral lobes, which are also overlapped by the large and strongly incurved lower lobe; the four stamens are separately and equidistantly decurrent on the tube; the pollen grains, as has been stated above, are depressed globose and provided with five or six meridional grooves, but lack germ pores; a disc is not developed; retinacula are absent (according to BENTHAM l.c. they are well developed, but this is a mistake: the structures shown in the figure of *Th. Hensii* de Wild. et Th. Dur., in "Illustr. de la Flore du Congo, Pl. LXXVII, 1901", are excrescences of the placenta which, as earlier stages show, are not comparable with retinacula); the fruit is rounded at the base and provided with a leathery or woody pericarp, and apparently either indehiscent or tardily dehiscent; and the seeds are not laterally flattened but ovoid, and either rugose or scaly.

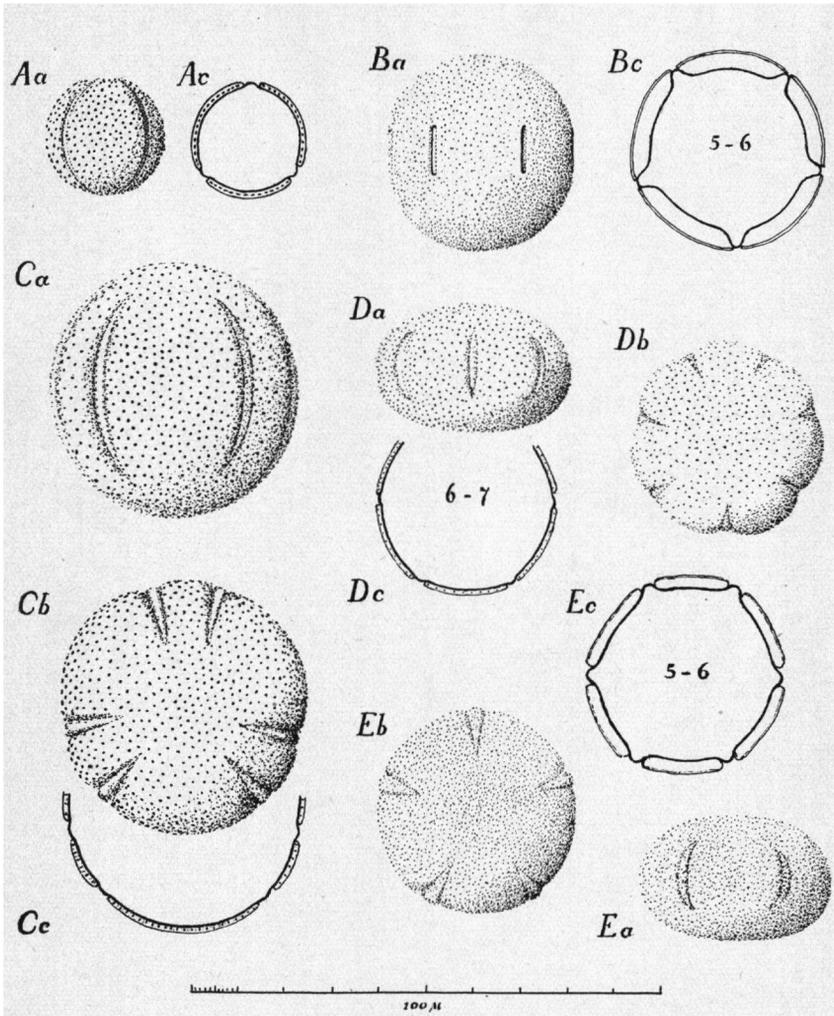
In the *Barlerieae* and in the *Asystasieae* the same parts show quite different characters: here the shoots are always articulate; cystoliths are always present; the bracts are always decussate and the bracteoles, as a rule, well developed; the corolla is more or less filmy, and in the bud the two upper lobes are always overlapped by the lateral ones, in the *Barlerieae* the lower lobe moreover is smaller than the others and overlapped by the lateral ones, whereas in the *Asystasieae*, it is true, the lower lobe overlaps the lateral ones, but it is neither different in size nor incurved; four stamens may be present, but then they are usually united in pairs and jointly decurrent;

the pollen grains are never depressed globose and always provided with germ pores, and meridional grooves may be present (*Asystasieae*) but then their number is either confined to three or there are three groups of three; the disc is always well developed; retinacula are always present; the capsule is in the *Asystasieae* contracted at the base in a long stalk, and in both groups the pericarp is pergameneous, and the fruit is nearly always dehiscent (a few exceptions are said to occur in the genus *Lepidagathis* Willd., but here too the pericarp is of the same consistency as in the dehiscent fruits, and the retinacula are normally developed); the seeds are always discoid, and in the *Barlerieae* they are moreover covered with hairs.

As the preceding comparison of characters allows no other conclusion than that both the *Barlerieae* and the *Asystasieae* are entirely unfit to receive the genus *Thomandersia* in their midst, we will have to find out whether perhaps somewhere else in the family a place may be found for it. In looking round among the various groups in which the family has been divided, we will soon discover that there are three of them in which the genus would be decidedly better at home than in either of the groups in which it has stayed up to now. These three groups are: the subfamilies *Mendoncioideae* and *Thunbergioideae* and the subtribe *Nelsoniinae* of the *Acantheae* sensu meo, one of the tribes of the subfamily *Acanthoideae* (with regard to the classification of the *Acanthaceae* cf. BREMEKAMP l.c. pp. 130—135).

The three groups just mentioned agree with each other and with the genus *Thomandersia* in the absence of cystoliths and retinacula, in the swollen seeds and partly in the structure of the pollen grains. The latter are in all of them provided with grooves, and they are never equipped with germ pores (according to LINDAU germ pores should be present both in the *Mendoncioideae* and in the *Nelsonioideae*, but these assertions are erroneous). The globose grains of the *Mendoncioideae* (Tab. II B) moreover resemble those of *Thomandersia* (Tab. II E) in the presence of an exine consisting of a thin, but clearly recognizable outer layer and a very thick inner one, and they are also like those of *Thomandersia* provided with five or six meridional grooves; the latter, however, are much shorter than those of *Thomandersia*. In the small grains of the *Nelsoniinae* (Tab. II A) the exine is but thin and does not show the differentiation into two layers; here too the grooves are meridional, but they are always three in number and much longer than in *Thomandersia*: in fact, they meet at the poles. In the grains of the *Thunbergioideae* the grooves show, as a rule, a serpentine course, winding round the grain and returning in themselves; in the genus *Meyenia*,

TAB. II



A. *Staurogyne spec.* (Ambon); B. *Mendoncia Tessmannii* Mildbr.; C. *Argyria potentillifolia* DC.; D. *Incarvillea Olga* Reg.; E. *Thomandersia laurifolia* (T. Anders. ex Bth.) Baill.; a. frontal view; b. polar view; c. optical section through the equator.

The numbers in the centre of the optical section indicate the variability in the number of grooves.

however, they are according to LINDAU's description and figure, of the same kind as in *Thomandersia*.

The *Mendoncioideae* and the *Nelsoniinae* show also other points of resemblance with *Thomandersia*. The indehiscent or tardily dehiscent fruits of the latter find a counterpart in the drupes of the *Mendoncioideae*; and the inarticulate shoots, the scattered and small bracts and minute bracteoles, the peculiar aestivation of the corolla lobes described above, and a rudimentary disc are also met with in the *Nelsoniinae*; the small bracts and minute bracteoles, however, occur in some of the genera only. It is perhaps worth noticing that in comparison with the *Nelsoniinae* the *Acanthinae* sensu meo, the other subtribe of the *Acanthaceae*, show but little resemblance with *Thomandersia*: in this subtribe the likeness remains confined to the presence of meridional grooves and the absence of germ pores in the pollen grains and to the absence of cystoliths.

Against the points of resemblance enumerated above, the differences should be balanced. They are by no means negligible. The *Mendoncioideae* and *Thunbergioideae* are, as a rule, winding plants; their shoots are articulate; the flowers enclosed between large, partly connate bracteoles; the small annular or cupular calyx is subentire or denticulate; and the fruit is, in the *Mendoncioideae*, a one-celled drupe or, in the *Thunbergioideae*, a strongly beaked capsule. The plants belonging to the genus *Thomandersia*, on the other hand, are shrubs with inarticulate shoots, minute bracteoles, a 5-fid calyx and a two-celled obtuse fruit with a leathery or woody pericarp. The *Nelsoniinae* are, as a rule, small herbs; their pollen grains are much smaller than those of *Thomandersia*, and never depressed globose, their exine is not differentiated into two layers, they possess but three grooves, and the latter do not end halfway between the equator and the poles, but extend to the very top; the number of ovules in each of the ovary cells is not, as in *Thomandersia*, confined to two, but is at least six, and often much larger; and the fruits are thin-walled and readily dehiscent.

The above comparison shows that the differences existing between each of the three groups and *Thomandersia* certainly outweigh the points of resemblance. This means that there is apparently no place for this genus in any of them, and as these groups were chosen for comparison because they show at least some resemblance with our genus, there is obviously no place for it in any of the groups that have been recognized so far. The genus must be regarded, therefore, as representing either a new division or another family. To decide between these alternatives it will be necessary that *Thomandersia* as well as the *Acanthaceae* be compared with the

other members of the group to which they both indubitably belong. This group is the order *Tubiflorae*.

That *Thomandersia* belongs to the *Tubiflorae* is easily seen: the leaves are decussate, the flowers tetracyclic, the corolla pentamerous, gamopetalous and zygomorphic, the stamens inserted on the corolla tube and didynamous, the ovary superior and two-celled, and the placentation marginal.

Among the families belonging to the *Tubiflorae* those in which the corolla is actinomorphic and the androecium complete, do not interest us here, and among the remaining ones the majority too may be discarded; the *Verbenaceae*, *Labiatae* and *Avicenniaceae* because of the collateral ovules, the first two also because of the presence of false dissepiments in the ovary cells, and the third because of the central placentation and large viviparous seeds; the *Globulariaceae* and *Phrymaceae* on account of the one-celled ovary with its single ovule; the *Myoporaceae* because of the large internal glands, drupaceous fruits and albuminous seeds; the *Columelliaceae* because of the meandriform anthers and the inferior ovary; further the *Scrophulariaceae* because of the numerous small ovules and the albuminous seeds; the *Lentibulariaceae*, *Orobanchaceae*, *Gesneriaceae* and *Martyniaceae* because of the one-celled ovary, the first three moreover on account of the numerous small seeds, the *Lentibulariaceae* also because of their insectivorous habit, the *Orobanchaceae* because of their parasitism, and the *Gesneriaceae* because of the cohering anthers, the *Martyniaceae*, apart from the one-celled ovary, because of the reticulate pollen grains without germ pores and the absence of peltate glands (cf. STAPP in ENGLER u. PRANTL., Nat. Pflanzenfam. IV 3b, p. 268, 1895). When all these families have been excluded a group of three is left: the *Bignoniaceae*, *Pedaliaceae* and *Acanthaceae*, and these are the only ones which require serious consideration.

In comparing these three families one can not fail to notice that they resemble each other in almost all essential points. In this respect the following common features deserve special attention: bracteoles are almost always recognizable, though it must be admitted that they may be minute; the ovary is almost always two-celled and the ovules arranged in vertical rows, and the seeds are fairly large and contain a large embryo surrounded by a very thin layer of endosperm. The presence on various parts of the plants of peltate glands, and the occurrence in some of the genera of globose or depressed globose pollen grains provided with meridional grooves not extending to the poles and lacking germ pores, are also noteworthy characters.

That the *Bignoniaceae* possess pollen grains without germ pores, but sometimes provided with meridional grooves not extending to the poles, was discovered by URBAN (Ber. d. d. Bot. Ges. XXXIV, p. 728—758, 1916). URBAN distinguished in this family several kinds of grains, differing mainly in relief, but all resembling each other in the absence of germ pores. The differences in relief will not be discussed in detail: for our purpose it is enough to note that the grains are, as a rule, globose, that they are often provided with meridional grooves, and that in a few genera they remain united in tetrads. Grains resembling in shape and in the arrangement of the grooves the grains of *Thomandersia*, are found in the genus *Incarvillea* Juss. (Tab. II D). In those of the genus *Argylia* D. Don, which according to URBAN l.c. should be very similar to those of *Incarvillea*, I find a globose shape and grooves arranged in pairs (Tab. II C). In both genera they differ from those of *Thomandersia* in the thinner exine, which does not show the differentiation into two layers.

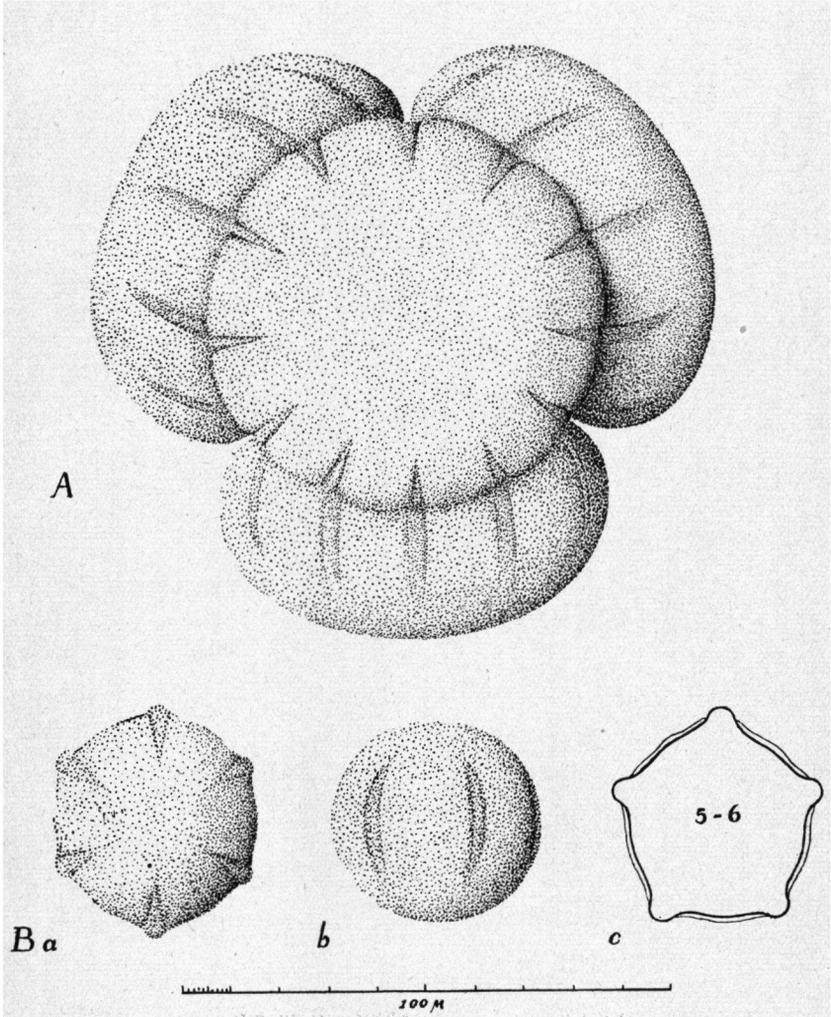
In the *Pedaliaceae* the pollen grains are, as STAPF l.c. has shown, always depressed globose and provided with five or more meridional grooves not extending to the poles and lacking germ pores. The only exception to this rule is found in the genus *Trapella* Oliv., but the inclusion of this genus in the family by OLIVER apparently rests on no better ground than HOOKER's dogma that it is unwise to raise aberrant genera to family rank: in my opinion the affinities of this genus are as yet insufficiently established. In the genus *Sesamothamnus* Welw. I found the grains united in tetrads, but otherwise of the same type as those of the other genera (Tab. III A). The grains of *Thomandersia* are indistinguishable from those of the *Pedaliaceae* (cf. Tab. II E and Tab. III and IV).

The occurrence in the *Acanthaceae* of pollen grains provided with meridional grooves but without germ pores has been discussed already: none of these grains are exactly like those of *Thomandersia*, though those of *Meyenia* come, according to LINDAU's description and figure, very near to them.

The *Bignoniaceae* are a rather vaguely delimited family, and it is therefore no wonder that, apart from the considerable number of ovules, no general difference between this family and the genus *Thomandersia* can be found. The family, however, has been divided in a number of tribes that are much better defined, and are therefore more suitable for a comparison with our elusive genus. The most aberrant of these tribes is probably that of the *Crescentieae* with its baccate or at least indehiscent fruits and numerous wingless seeds arranged in several rows. The resemblance between these plants

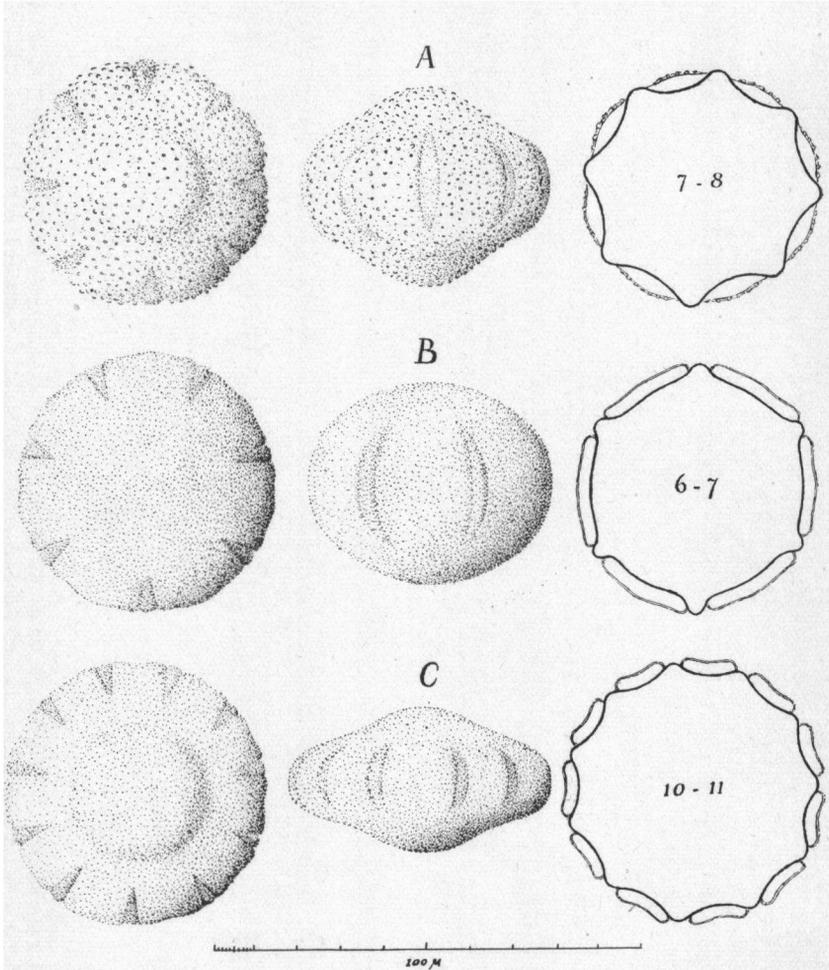
and the *Pedaliaceae* and *Acanthaceae*, and also with *Thomandersia*, is apparently very slight. In the other tribes the fruits are always dehiscent and the seeds, as a rule, flattened and winged; very rarely the seeds are swollen and angular, but then the wing is still recognizable in the form of a rim; in some genera, however, they are fusiform and at both ends provided with a tuft of long hairs. In the *Pedaliaceae* and *Acanthaceae*, certainly, the fruits are most often dehiscent but, except in the genus *Sesamothamnus* Welw. and perhaps in the nearly related *Sigmatosiphon* Engl. ex Stapf, the seeds are never winged, and fusiform seeds with tufts of hairs at the ends are entirely unknown in both families. The seeds of *Thomandersia* too are quite different from those of the *Bignoniaceae*. The fruits of the *Bignoniaceae* and *Tecomeae* are, like those of the *Acanthaceae*, *Thomandersia* and most of the *Pedaliaceae*, two-celled, but they are septifragal, a character by which these tribes differ from all other *Tubiflorae*. The capsule of the *Eccremocarpeae* is one-celled and that of the *Tourrettieae* four-celled and, as in the majority of the *Bignoniaceae*, their leaves are compound and go out in tendrills: in habit, therefore, they differ widely from *Thomandersia*, the *Acanthaceae* and the *Pedaliaceae*. Four-celled ovaries and fruits occur also in some of the *Pedaliaceae*, but when the fruits of the latter are capsular, the dehiscence is loculicidal, the false septa splitting longitudinally, whereas in *Tourrettia*, where the capsule opens at the top only, the dehiscence is both loculicidal and septicidal and at the same time septifragal, the valves separating both from the true and from the false dissepiments. We may conclude therefore that in none of the tribes of the *Bignoniaceae* room can be found for the genus *Thomandersia*, and that their affinity with the latter is certainly but remote.

The general characters of the *Pedaliaceae* too are vague, and even after the exclusion of the aberrant genus *Trapella* Oliv. they remain difficult to grasp. In fact, surveying the diagnosis of the family given by STAPF (l.c. p. 253), one wonders why this family has not been united with the *Acanthaceae*. It is true that all the genera of the *Pedaliaceae* appear, for one reason or another, sufficiently distinct from the *Acanthaceae*, but the fact that these reasons are seldom in more than two or three genera the same, makes one somewhat suspicious with regard to the delimitation of this family. None of the distinctive characters given in STAPF'S diagnosis appear to be general: the number of carpels, which in the *Acanthaceae* is never more than two, is in the *Pedaliaceae* in "some" of the genera three or four; false dissepiments, which in the *Acanthaceae* are entirely unknown, are in the *Pedaliaceae* often met with: in "some"



A. *Sesamothamnus Lugardii* N.E.Br.; B. *Rogersia bigibbosa* Dinter; a. polar view; b. frontal view; c. optical section through the equator.

TAB. IV



A. *Petraea zanguebarica* J. Gay; B. *Pterodiscus luridus* Hook.; C. *Josephinia imperatricis* Vent; right: polar view; centre: frontal view; left: optical section through the equator.

genera, however, they are completely wanting; the ovules are in the *Pedaliaceae* often horizontal or even pendulous, whereas in the *Acanthaceae* they are almost always erect: in the *Thunbergioideae*, and in the *Nelsoniinae*, however, they are more or less horizontal and "some" of the *Pedaliaceae* are provided with erect ones; the fruits are in the *Acanthaceae* almost always smooth, whereas in the *Pedaliaceae* they are, as a rule, covered with smooth or hamulate spines or provided with horns or wings, but here too there are exceptions: in the genera *Sesamum* L. and *Sesamothamnus* Welw. the fruits are quite smooth, and in *Linariopsis* Welw. they are merely tuberculate. The presence of peltate glands in the *Pedaliaceae*, a character on which some emphasis has been laid by STAPP, is not confined to this family, for they are found also in the *Acanthaceae* and in the *Bignoniaceae*, and even in some of the *Scrophulariaceae*; and the presence at the base of the pedicels of a peculiar kind of nectaries (according to EICHLER metamorphosed flowers) is limited to "some" of the genera.

In describing the structure of the flower STAPP mentions the occurrence of a large gland at the top of the connective. A similar gland-tipped connective occurs in some of the *Bignoniaceae*, but is entirely unknown in the *Acanthaceae*. If this gland was a general feature of the *Pedaliaceae*, it would be of great importance for the determination of the position of *Thomandersia*, for in the latter the connective is not gland-tipped. A reinvestigation, however, has shown that in some of the *Pedaliaceae* these glands are hardly recognizable, e.g. in the genus *Petraea* J. Gay, whereas in *Josephinia* Vent. they are replaced by fine mucro, and in *Linariopsis* Welw. they are, as STAPP'S own figure (l.c. p. 255, fig. 97 J) shows, completely lacking: in fact, the anthers of the latter are not at all unlike those of *Thomandersia*.

The stigmata of the *Pedaliaceae* are more like those of the *Bignoniaceae* than those of the *Acanthaceae*: as in most of the *Bignoniaceae* they are rather large and equal, whereas in the *Acanthaceae* they are either of medium size only, and then always more or less distinctly unequal, or small. In *Thomandersia* they are both small and slightly unequal. In this character the genus differs therefore somewhat from the type of the *Pedaliaceae*, and approaches that of the *Acanthaceae*.

Apart from the structure of the pollen grains, the only difference between the *Acanthaceae* and the *Pedaliaceae* that in my experience has proved reliable, is one which at first sight looks rather insignificant, and to which so far no attention has been paid. It is the absence in the *Pedaliaceae* of transverse ridges between the petioles

and their presence in the *Acanthaceae*. In *Thomandersia* these ridges are wanting, and in this character as well as in the structure of the pollen grains there is therefore complete agreement with the *Pedaliaceae*.

Characters that also are more favourable for the inclusion of the genus in the *Pedaliaceae* than in the *Acanthaceae* are: the scattered bracts, the separately decurrent filaments, the leathery or woody pericarp, and the ovoid seeds. More favourable for the *Acanthaceae* are the small size of the stigmata and, perhaps, the habit. The *Pedaliaceae* are mostly herbaceous plants, and of the three genera that are fruticose two, *Sesamothamnus* Welw. and *Sigmatosiphon* Engl. ex Stapf, show an entirely different aspect: their shoots are succulent and spinous, and the small leaves are fascicled on brachyblasts arising from the axils of the spines; *Uncarina* Stapf, the third fruticose genus, however, is not unlike *Thomandersia*, for its species are large-leaved. In the *Acanthaceae* this growth form is, no doubt, far more common.

If *Thomandersia* is included in the *Pedaliaceae*, it is easily seen that almost all its distinctive features are matched somewhere: the zygomorphic corolla finds its counterpart in the genus *Petraea* J. Gay; its fleshy texture recurs in the corollas of *Sesamothamnus* and *Sigmatosiphon*; the two-celled ovary with its superposed ovules is repeated in the genera *Pedaliium* [v. Royen] L., *Pedaliophytum* Engl. and *Pterodiscus* Hook., where however the lower ovules only are erect; racemose inflorescences are met with in *Sesamum* and *Cerathotheca* Endl. and also in the three fruticose genera mentioned above; in *Sesamum* and *Ceratotheca* moreover the racemes are long and lax, and in the fruticose genera the bracts are small. All in all, the genus is therefore doubtless more at home in this family than in the *Acanthaceae*. That it occupies in the *Pedaliaceae* a somewhat isolated position does not count for much: as STAPF (l.c. p. 259) rightly remarks, this applies to nearly half the genera brought together in this family, and as it would, according to him, be quite easy to divide the fourteen genera over six or seven tribes, the inclusion of *Thomandersia* would merely raise this number to seven or eight.

The question of the subdivision of the *Pedaliaceae* would become urgent if the family was to be united with the *Acanthaceae*, a measure which in view of the comparatively slight differences certainly would be justified. Still, in that case too, the genera of the *Pedaliaceae* might be kept together, and as a subfamily *Pedalioidae* they could be placed alongside the *Mendoncioideae*, *Thunbergioideae* and *Acanthoideae*. As the distinction between this enlarged familá

and the nearly related *Bignoniaceae* would remain uncertain, it might be better, however, to regard these four groups as separate families, and at the same time to raise some of the tribes of the *Bignoniaceae* to family rank: that e.g. the *Crescentieae* would deserve this promotion can hardly be denied. It might be argued that our morphological knowledge of the *Bignoniaceae* is not yet sufficiently advanced to justify such a step, and that for the moment it is therefore advisable to keep them together. If this is conceded, it would be better to unite the *Pedaliaceae* and *Acanthaceae*, but this should be regarded as a provisional measure only, by which for the time being we must abide because of our insufficient information with regard to the allied *Bignoniaceae*.