

SOME REMARKS ON *HEBERDENIA* A. DC.,
PLEIOMERIS A. DC.,
AND *AFRARDISIA* MEZ (MYRS.)

BY

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Alph. de Candolle proposed a Myrsinaceous genus *Heberdenia* (Pl. V) in 1841 ⁽¹⁾. It was a name apparently suggested by Banks and based on a single species « *Ardisia excelsa* AIT. ». In de Candolle's paper this name is referred to as « *Ardisia excelsa* BANKS » (p. 73) and « *Ardisia excelsa* AIT. » (p. 68) and in another, previous, paper as « *Ardisia excelsa* CHR. SMITH » ⁽²⁾. *Heberdenia* (Pl. V) is indigenous in the Canary Islands.

In trying to segregate the new genus de Candolle found aestivation to be of slight or no significance. The shape of the anthers, occasionally important in *Myrsinaceae* ⁽³⁾, gave no clue to *Heberdenia*. The shape of the pollen grains is partly (« en partie ») ⁽⁴⁾, characteristic but similar to that found in *Ardisia*. Other supposed differences were the relative length of the filament and a constantly 5-merous flower; a 5-merous flower, however, is the rule in *Myrsinaceae*.

As regards the latter point it might be added that I found repeatedly a 6-merous flower in *Heberdenia* among 5-merous

⁽¹⁾ DE CANDOLLE, A., *Ann. Sci. Nat.*, 2^e sér., XVI, pp. 68, 70, 73, 74, 79 (1841).

⁽²⁾ DE CANDOLLE, A., *Ann. Sci. Nat.*, 2^e sér., II, p. 297 (1834).

⁽³⁾ DE CANDOLLE, A., *Ann. Sci. Nat.*, 2^e sér., XVI, pp. 70, 71 (1841).

⁽⁴⁾ DE CANDOLLE, A., loc. cit., p. 74.

(e.g. Pitard 658; Vahl, leg. in 1902). The length of the filaments is equalled in some spp. of *Ardisia*.

Although Alph. de Candolle proceeded, at the end of his paper, to give full descriptions of all his new genera, he seems by error to have omitted a further description of *Heberdenia*.

He placed *Heberdenia* in *Ardisieae*, a tribe first of all characterized by a « corolla gamopetala » ⁽⁵⁾, and was followed in this by all authors till 1902.

In that year Mez published his monograph on *Myrsinaceae* ⁽⁶⁾. Mez, wanting to maintain *Heberdenia* — he judged it to be a « genus maxime naturale » — had, of course, no use for Alph. de Candolle's unsatisfactory argument for separating *Heberdenia* from allied genera, and was forced to advance new evidence.

Alph. de Candolle had given special attention to the corolla of *Heberdenia*. He wrote ⁽⁷⁾ « corolla 5-partita, rotata » which I cannot but interpret as a gamopetalous corolla. The figure made to illustrate this description ⁽⁸⁾ shows a corolla with segments shortly united at the base.

Mez declared the corolla to be choripetalous.

In the genera *Myrsine* L., *Heberdenia* A. DC., *Afrardisia* MEZ and *Ardisia* Sw. the filaments of the epipetalous stamens are basally connate. The filaments are flattened or cylindrical if, and as far as, they are free. The connate part is flat and much widened and together the lower filaments form a thin-walled cup-shaped staminal tube. This short tube is connate with the basal part of the corolla (Pl. V, d, e). Mez was aware of this morphology in other Myrsinaceous taxa but seems not to have noticed it in *Heberdenia* ⁽⁹⁾.

Of course, the cup-shaped staminal tube, as described here, can also be interpreted as a cup-shaped receptaculum bearing free stamens on the edge. This interpretation has no bearing on the present line of reasoning and moreover, to all appearance, the inner lining of the lower corolla is staminal and not receptacular.

The basal parts of the petals in the four genera mentioned above are coherent in bud and during anthesis. As the flower ripens, the petals grow gradually further apart. In *Heberdenia* the final result sometimes is that the petals come apart entirely. The short staminal

⁽⁵⁾ DE CANDOLLE, A., Prodr., VIII, pp. 89, 105 (1844).

⁽⁶⁾ MEZ in ENGL., Pflanzenr., 9 Heft, IV, fam. 236 (1902).

⁽⁷⁾ DE CANDOLLE, A. in PARKER-WEBB et BERTHELOT, Hist. Nat. Iles Canaries, Phytogr., III, 2, sect. III, p. 169 (Déc. 1845).

⁽⁸⁾ PARKER-WEBB et BERTHELOT, loc cit., tab. 188 (Avril-Mai 1847).

⁽⁹⁾ MEZ, loc. cit., p. 7-8.

PLANCHE V.



Ardisia bahamensis (GAERTN.) A. DC. : a) flowering twig ($\times 1/2$); b) bud ($\times 5$); c) flower ($\times 3$); d) part of corolla ($\times 3$); e) petal and stamen ($\times 3$); f) flower without corolla ($\times 5$); g) placenta ($\times 15$); k) fruiting branch ($\times 1/2$); m) fruit ($\times 2$); n) inside endocarp ($\times 2$); p) longitudinal section, fruit, showing subruminate endosperm surrounding embryo in cylindrical cavity and indented basally by funiculus ($\times 3$); r) transversal section, fruit, showing embryo and subruminate endosperm ($\times 2$).

tube splits into its component parts and each petal, together with the stamen, is shed.

But it also, and more frequently, happens that the corolla is shed as a whole or, possibly, split in one or two places. There is, thus, at least as much to be said in favour of sympetaly as there is evidence against it.

The corolla in *Ardisia* is shortly gamopetalous, sometimes even « brevissime » gamopetalous ⁽¹⁰⁾. I feel that this character, being the only by which *Heberdenia* is supposed to differ from its nearest ally, *Ardisia*, is insufficient as a generic distinction. On the contrary, the sub-choripetalous corolla in *Heberdenia* is a natural limit to a variable degree of sympetaly as found in *Ardisia*. I therefore conclude that *Heberdenia* is a synonym of *Ardisia*.

In 1923 Sprague pointed out ⁽¹¹⁾ that the « earliest valid name of *Heberdenia excelsa* » was *Anguillaria bahamensis* GAERTN. ⁽¹²⁾. Gaertner had stated that his *Anguillaria bahamensis* was identical with *Heberdenia excelsa* BANKS. This identity had been also accepted by Mez ⁽¹³⁾ but Mez had not adopted the specific epithet « *bahamensis* », nor (as was pointed out by Sprague) were the Bahamas included by him in the distributional area of *Heberdenia*. Mez placed two species in *Heberdenia*, one of them from the Canaries and the other from Mexico. Gaertner had placed two species in *Anguillaria*, one from the Bahamas (as was suggested by the epithet given) and the other from Ceylon!

The specimens referred to by Gaertner are in Banks's Herbarium, preserved in the British Museum. I found that they were collected in Madeira (1768) and I believe that Gaertner was in error. Gaertner's material originated from the Canaries and Mez was right not to include the Bahamas in the distributional area of *Heberdenia*. The epithet, « *bahamensis* », then, is unfortunate but has to be adopted as Sprague rightly pointed out. The correct name for the single species described in *Heberdenia* becomes *Ardisia bahamensis* (GAERTN.) A. DC. ⁽¹⁴⁾.

Regarding *Pleiomeris* (Pl. VI), various information was given when it was first proposed as a genus by Alph. de Candolle ⁽¹⁵⁾.

⁽¹⁰⁾ MEZ, loc. cit., p. 59.

⁽¹¹⁾ SPRAGUE, *Journ. Bot.*, LXI, p. 241 (1923).

⁽¹²⁾ GAERTNER, *Fruct. Sem. Pl.*, I, p. 372, tabl. 77, fig. 1 (1788).

⁽¹³⁾ MEZ, loc. cit., p. 159.

⁽¹⁴⁾ DE CANDOLLE, A., *Trans. Linn. Soc. London*, XVII p. 128 (1834).

⁽¹⁵⁾ DE CANDOLLE, A., *Ann. Sci. Nat.*, 2^e sér., XVI, pp. 68, 87, 88 (1841).

He mentioned as characteristics : commonly 6-7 petals, a fixed and peculiar aestivation, and very numerous ovules (« ovules très nombreux »). His remarks concerning pollen characters in *Myrsinaceae* ⁽¹⁶⁾ are much too general to be of any importance in delimiting *Pleiomeris*, and there is no indication that pollen characters are significant in delimiting Myrsinaceous taxa ⁽¹⁷⁾.

Pleiomeris, when proposed, consisted of a single species, *Pleiomeris canariensis* (WILLD.) A. DC., based on *Scleroxylon canariense* WILLD. ⁽¹⁸⁾.

Later authors who referred to the number of ovules repeated Alph. de Candolle's statement « 12-15 » ⁽¹⁹⁾. The drawing by Heyland ⁽²⁰⁾ also shows at least 12 ovules on the placenta and this is again confirmed by A. de Candolle's description ⁽²¹⁾.

After more than half a century of agreement on this point it is somewhat unexpected to find in Mez's revision of 1902 ⁽²²⁾ « placenta prope apicem perpauci- (3-4-) ovulata », while this is supported by fig. 57, F ⁽²³⁾. I have found that Mez examined Alph. de Candolle's authentic specimens and that Mez observed inaccurately (cf. Pl. VI, g, n).

Mez placed *Pleiomeris* in *Myrsineae* on account of its supposed pauci-ovulate placenta but it belongs, if we accept tribes, in the other tribe, *Ardisieae*, the placenta being pluriseriate and multi-ovulate.

As regards the second characteristic mentioned by Alph. de Candolle, the increased and variable number of petals (the generic name *Pleiomeris* alluded to an increased number of perianth-lobes), Mez declared : « flores... typo 5-meri » while allowing in the description for an occasional increase in number.

Alph. de Candolle's authentic specimens show generally 6-merous flowers (Pl. VI, c, d). He stated that the flowers were polygamous ⁽²⁴⁾ whereas Mez said they were hermaphrodite.

I have tried to establish whether — as the herbarium specimens suggest — the flowers are polygamous. The dried specimens carry

⁽¹⁶⁾ DE CANDOLLE, A., loc. cit., pp. 71-74.

⁽¹⁷⁾ ERDTMAN, Pollen Morph. Pl. Tax., pp. 278, 280 (1952).

⁽¹⁸⁾ WILLDENOW, *Magaz. Ges. Nat. f. Fr. Berlin*, III, p. 59 (1809).

⁽¹⁹⁾ DE CANDOLLE, A., *Prodr.*, VIII, p. 105 (1844).

⁽²⁰⁾ PARKER-WEBB et BERTHELOT, loc. cit., tab. 187 (1850).

⁽²¹⁾ DE CANDOLLE, A., in PARKER-WEBB et BERTHELOT, loc. cit., p. 167 (1845).

⁽²²⁾ MEZ, loc. cit., p. 337.

⁽²³⁾ MEZ, loc. cit., p. 338, fig. 57, F.

⁽²⁴⁾ DE CANDOLLE, A., *Prodr.*, VIII, p. 105 (1844).

flowers containing a corolla (and stamens) and an ovary. The ovules are sunken into the surface of the placenta; they are partly covered by tissue (Fig. VI, g). On the same branches occur numerous flowers without corolla (and stamens) but with an ovary. The placenta in these flowers carries exserted ovules which are protruding from the surface of the placenta (Fig. VI, n).

Morphologically it is correct to say — when referring to herbarium specimens — that the flowers are polygamous and that a marked sexual dimorphism occurs.

Although I suggest, after a very careful examination of the herbarium specimens, that Alph. de Candolle may have been justified in describing the flowers as polygamous, the possibility cannot entirely be excluded that the seemingly ♀ flowers are at first hermaphrodite, and that all flowers contain a corolla which is shed. The flowers would then appear to be ♀. If so, there would seem to be proterandry. These points can only be made out in living material *in situ*.

The curious fact remains, however, that a phenomenon considered to be a main difference between the subfamilies *Myrsinoideae* and *Maesoideae*, viz sunken or protruding ovules ⁽²⁵⁾, is found to occur in a single plant, perhaps even in the course of life of a single *Pleiomeris*-flower.

Finally it may be said that the manner of aestivation is not significant in *Pleiomeris*.

Mez declared that *Pleiomeris* was most nearly related to the genera *Parathesis* Hook. f. and *Geissanthus* Hook. f. ⁽²⁶⁾. I hold a different view.

Pleiomeris is very close to *Rapanea*. The 6-merous or 5-merous, probably often unisexual flowers and sympetalous corolla fit well within the generic limits of *Rapanea*. Young shoots in *Pleiomeris* carry spurious prophylls covering the terminal bud and the young inflorescences (Pl. VI, s, t, u). This character, though not mentioned, I believe, in literature, is found also in numerous ssp. of *Rapanea* (and *Ardisia*). The manner of growth of *Pleiomeris*, seasonal flushes of young leaves, while the young shoot flowers in the same season, occurs also in many spp. of *Rapanea*. The shoots flower more abundantly in the second season and flowering in subsequent seasons adds to the short, lateral, stubby, verrucose, flower-

⁽²⁵⁾ MEZ, loc. cit., p. 9.

⁽²⁶⁾ MEZ, loc. cit., p. 337.



Pleiomeris canariensis (WILLD.) A. DC. : a) flowering branch ($\times 1/2$); b) older fertile branch ($\times 1/2$); c) δ flower, calyx ($\times 7$); d) δ flower, corolla and stamens ($\times 5$); e) δ flower, petal, profile ($\times 5$); f) δ flower, petal, front ($\times 5$); g) δ flower, placenta ($\times 20$); k) φ flower ($\times 5$); m) φ flower, ovary ($\times 10$); n) φ flower, placenta ($\times 20$); p) φ flower, young fruit ($\times 3$; Dinn 198); r) φ flower, young fruit, vertical section, showing embryo (section) in hole surrounded by endosperm ($\times 2$); s, t, u) prophylls.

bearing branchlets (Pl. VI, a, b). The habit of *Pleiomeris* exactly matches that of *Rapanea*.

Rapanea is said to lack a style. It appears that an articulation separates the sessile stigma from the ovary and in some species a very short style is found below the articulation. After the stigma drops from the ripening fruit, this very short style persists as a minute tip (e. g. *R. comorensis* MEZ ⁽²⁷⁾ and ⁽²⁸⁾; also *R. thomensis* EXELL ⁽²⁹⁾). It is most interesting to find, in some flowers of *Pleiomeris*, quite incidentally it seems, a slightly swollen dark mark in the style, suggesting an articulation. It is to be stressed however, that this vestigial, or, it may be suggested « incipient », articulation is by no means always to be observed. In a single specimen some flowers may show it, others not or it may be entirely absent. I found it, however, in some mature flowers and young fruits of *P. W. Webb. Esq., Bourgeau 1424, Lowe 75 and Dinn 198* (Pl. VI, p).

Pleiomeris is, however, to be maintained as a genus. It may be distinguished by the sexual dimorphism of the flower and, more clearly, by the presence of a style and staminal filaments. The best character for segregation is the presence of a pluriseriate, multi-ovulate placenta in contrast to the uniseriate, pauci-ovulate placenta of *Rapanea*. A study of the leaf-anatomy in *Myrsinaceae* by Grosze ⁽³⁰⁾ supports the view that *Pleiomeris* is a distinct genus.

A third genus to be considered is *Afrardisia* MEZ ⁽³¹⁾. *Afrardisia*, as segregated by Mez, consisted of 10 spp.; they are confined to continental tropical West Africa and a single one occurs in S. Tome ^(32 and 33). The genus is distinguished from *Ardisia* by having only a few ovules on the placenta, and these are arranged in a single whorl. Eastern Asiatic *Ardisias* sometimes have few ovules but these are scattered over the placenta, not regularly arranged in a single row as in *Afrardisia*. Mez suggested that these eastern Asiatic few-ovuled *Ardisia* were derived from the general multi-ovuled stock of *Ardisia*.

⁽²⁷⁾ PERRIER DE LA BATHIE, Fl. Madag., fam. 161, p. 141-142, fig. XXV, 7 (1953).

⁽²⁸⁾ MEZ, loc. cit., p. 9.

⁽²⁹⁾ EXELL, Cat. Vasc. Pl. S. Tomé, p. 233, fig. 14 b (1944).

⁽³⁰⁾ GROSZE in ENGL., Bot. Jahrb., XLI, Beibl. 96, pp. 2, 38 (1908).

⁽³¹⁾ MEZ, loc. cit., p. 183-184.

⁽³²⁾ MOSS in HUTCH. and DALZIEL, Fl. West. Trop. Afr., II, p. 15 (1931).

⁽³³⁾ EXELL, loc. cit., p. 233.

I suggest the following hypothesis for the phylogeny of the Myrsinaceous genera discussed here.

Ardisia bahamensis is primitive. The number of perianth lobes is not very stable, pentamery is normal, 6-merous flowers occur rarely. The number of ovules is more than 30 (Pl. V, g), which is about the highest number found in the genus. Its nearly choripetalous corolla represents the starting point of an increasing degree of sympetaly. The contrast between the presence of numerous ovules, spirally arranged, and a single whorl of few ovules marks the difference between *Ardisia* and *Afrardisia*. This character seems to have reached the end of a line of evolution in *Afrardisia*.

Grosze studied the leaf-anatomy in the *Myrsinaceae*. He found the presence or absence of epidermis cells of which the inner wall changed into mucus, systematically significant ⁽³⁴⁾. « *Heberdenia* » shows this character, *Ardisia* rarely; but it is interesting to find that a group of related *Ardisia* spp., all occurring in Central America — Cuba to the Amazon basin — show this character also.

It is remarkable that in « *Heberdenia* » the corolla-lobes are indistinctly and irregularly imbricate to valvate (Pl. V, b). In the majority of *Ardisia* spp. and in *Afrardisia* they are dextrorsely imbricate. A number of allied Central American spp. of *Ardisia*, however, show the same aestivation that I found to exist in « *Heberdenia* » ⁽³⁵⁾.

Pleiomeris canariensis is primitive, though perhaps more advanced than is *Ardisia bahamensis*. Primitive characters are the very unstable and widely changing number of perianth lobes, the subulate style and minute, entire stigma, and the comparatively large number of ovules ($15- \pm 25$). Advanced ones are the sympetalous corolla and possibly polygamous dimorphic flowers. *Pleiomeris* is, I suggest, of the parent stock of *Rapanea* taxa. Its multi-ovulate placenta became in *Rapanea* pauci-ovulate (ovules in a single whorl). The difference between *Pleiomeris* and *Rapanea* is of a similar nature to that between *Ardisia* and *Afrardisia*. It remains to be considered whether the unstable and changing position of the ovules is to be viewed as an indication that *Pleiomeris* is a taxon preceding the phylogenetic development of the two subfamilies in *Myrsinaceae* or whether this phenomenon is, within the family, of no systematic importance.

⁽³⁴⁾ GROSZE, loc. cit., p. 13.

⁽³⁵⁾ MEZ, loc. cit., p. 59, 60.

It seems possible, in future, that support may be found for the concept that a trend of Myrsinaceous evolution, beginning in taxa like *Ardisia bahamensis* and *Pleiomeris canariensis*, in the region of the Canaries, spread westward to America, and continued from there to tropical Asia, to reach finally its ultimate goal, the African continent.

Summary

Heberdenia A. DC. is reduced to *Ardisia* Sw. The correct name for *Heberdenia excelsa* (AIT.) A. DC. is *Ardisia bahamensis* (GAERTN.) A. DC.

The description of *Pleiomeris* A. DC. is emended. The genus is most nearly allied to *Rapanea*. In Myrsinaceous phylogeny a trend of evolution may have moved from the region of the Canary Islands towards America, from there to trop. Asia, to end in Africa.

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