The Hypobathreae (Rubiaceae - Ixoroideae)
1. Delimitation and division of a new tribe

by

E. Robbrecht (*)

Abstract. — The Hypobathreae is a new tribe of Rubiaceae split from the Gardenieae sensu lato. The latter tribe is shown to remain heterogenous even after transferring many genera to the Coffeeae. The new tribe is divided in two subtribes, Hypobathrinae and Lamprothamninae. The Hypobathrinae are mainly distributed in tropical Asia, where at least eight genera occur: Cowiea, Hypobathrum, Hyptianthera, Morindopsis, Rhadinopus, Scyphostachys, Villaria and Zuccarinia. Madagascar is another centre where the tribe is well represented; there occur Chapeliera, Fernelia, Flagenium and Canephora. The African continent has only one representative, viz. Pouchetia. Amaioua, a South American genus, is tentatively placed here. The most important characters of the Hypobathrinae are found in the fruits: they are drupes with in each of both chambers imbricate seeds pendulous from an apical placenta; correspondingly the embryo has the radicle directed upwards; the fibrous seed-coat consists of linear cells. The Lamprothamninae are confined to tropical Africa (Lamprothamnus, Polysphaeria and Galiniera) and Madagascar (Jovetia, Polysphaeria, ? Lemyrea). They have most characters in common with the Hypobathrinae but have fewer ovules (only 1-3 per chamber) and seeds with a ruminated endosperm. The new tribe is placed in the subfamily Ixoroideae and links the Alberteae with Coffeeae and Gardenieae.

Introduction

In the course of my revision of Tricalysia A. Rich. (Robbrecht 1979) my interest in correctly placing this genus in the system of the Rubiaceae evolved into the study of a large number of Gardenieae and Coffeeae, the former tribe being the classic and the latter the newer place of Tricalysia.

(*) Nationale Plantentuin van België, Domein van Bouchout, B-1860 Meise (Belgium). — Manuscript received January 10, 1980.
Bremekamp (1934: 11) strongly narrowed the Gardenieae by transferring many genera to the Coffeeae (syn. Ixoreae), but only gave examples of genera belonging to these two tribes as conceived by him, so that for the bulk of the taxa of the Gardenieae, in their old and wide sense, the correct place remained to be determined. In this paper I will show that in the Gardenieae s.l. three different groups may be discerned: the Gardenieae s.s., a group of genera to be transferred to the Coffeeae, and a third group for which a new tribe has been established.

This tribe is delimited here. In following papers I will give a survey of the genera, with notes on their nomenclature and distribution and revisions of the African representatives.

Material and methods

This paper is entirely based on studies of herbarium material. An enumeration of the specimens examined will be given in a second paper. The work was carried out in BR; the Asiatic genera studied often being absent or poorly represented in its collections, visits were made to L and material was received on loan from this herbarium (abbreviations following Holmgren & Keuken 1974).

Besides dissected flowers and fruits, I studied seed-coats and pollen both following methods given previously (Robbrecht 1978a: 5).

The Gardenieae, the Coffeeae and their relation

In Hooker’s (1873) and Schumann’s (1891) system of the Rubiaceae the Gardenieae is one of the largest tribes. Its basic characters are the contorted aestivation of the corolla-lobes and the presence of several to numerous ovules in each chamber of the ovary.

Bremekamp (1934), on the occasion of a revision of the genus Pavetta, rejects the main principle of the older classification of the Rubiaceae, viz. the number of ovules (one or more than one) on each placenta. He splits the Gardenieae sensu Hooker and Schumann into two groups. One group of genera (such as Tarenna and Tricalysia), completely similar to the Coffeeae, is transferred to this tribe. The Coffeeae, formerly restricted to genera with only one ovule per placenta, contain in this way also genera with 1-∞ ovules. The
second group is the *Gardenieae* in a more strict sense, characterized by rather large fruits with numerous seeds embedded in a pulpy outgrowth of the placenta.

**Characters of Gardenieae and Coffeeae**

Besides their typical large fruits emphasized by Bremekamp, the *Gardenieae* s.s. are characterized by other features. Petit (1964) stressed the occurrence of several types of sympodial growth. The flowers are often larger than in any other tribe of *Rubiaceae*. F. Hallé (1967: 124) suggested that the testa cells are typical by their thickened and often ornamented radial walls, but gives only one example. An examination of the seed-coat of many African *Gardenieae* (unpublished observations) confirms this, and Tirvengadum (1978) shows that all *Gardenieae* s.s. from Sri Lanka similarly have intricate testa-cells. Study of the seed-coat with the SEM shows that the thickened radial walls become very apparent because of the withering of the outer tangential walls of the testa during the maturation of the seed (e.g. SEM graphs of *Preussiodora*, Robbrecht 1978b). The pollen of the *Gardenieae* is very diverse. It is mostly 3-aperturate and sometimes occurs in tetrahedral tetrads. Colpori and pori (mostly poropori) occur.

The *Coffeeae* have smaller drupes; these are mostly berry-like and have a thin endocarp, but may develop characteristic pyrenes (e.g. *Rutidea*). Monopodial growth (mostly following Roux' model) is common. The seed-coat usually consists of simple parenchyma-like cells (although often with difficult to interpret inclusions in the lumen). The flowers are medium-sized and the seeds are further characterized by the radicle of the embryo directed downwards. The tribe is stenopalynous: most genera have prolate 3-colporate pollen grains with a reticulate exine.

**Delimitation of the Hypobathreae**

Ridsdale et al. (1972: 345) mention that a group of genera of *Gardenieae* s.l. are characterized by large leathery fruits with rows of imbricate seeds: *Hypobathrum*, *Petunga*, *Zucaarinia*, *Diplospora* and *Tricalysia*, with the exception of the last one all tropical Asiatic
genera. Ridsdale (personal comm. 1978) suggested me some other genera to belong to the same group: Villaria, Hyptianthera, Cowiea and Morindopsis.

An examination of all these genera reveals that the morphology of their fruits is indeed very similar: they are bilocular drupes (with a thin endocarp), usually not large and leathery (like stated by Ridsdale et al., op. cit.) but medium-sized (about one cm in diameter) and berry-like. Several to many imbricate seeds are pendulous in each chamber from an apical placenta. Agreeing with this position of the seed, the embryo, a half time taller than the seed, has the radicle directed upwards, a distinctive character from the Coffeeae, where the embryo-radicle is inferior. The seed-coat is very characteristic; it appears fibrous under low magnification; the testa consists of strongly elongated cells, with the lumen usually so narrow that a pattern of cells is no more recognizable. The radial walls are often thickened, but this feature is never as striking as in the Gardenieae since the outer tangential walls remain intact.

In the characters of their flowers most genera of this group agree with the Coffeeae by their mostly hypocrateriform corollas with contorted lobes and with the anthers inserted in the corolla-throat. The placentation, however, already reveals the characteristic arrangement of the seeds in the fruits.

This group of genera is stenopalynous. With very few exceptions the pollen grains are prolate and 3-colporate; the exine is reticulate.

A further search showed that only one other Asiatic genus belongs to the same group, viz. Scyphostachys, a genus recently excluded (Tirvengadum 1978) from the Gardenieae s.s. without assigning it to another tribe. Four Madagascan genera revealed to have the same characteristic fruits and seeds: Chapeliera (syn. Tamatavia), Fernelia, Flagenium and Canephora. On the African continent I found only one genus: Pouchetia. Amaioua, a neotropical genus, differs from the other genera of this group in the organization of its flowers (included anthers and style) and in its porate pollen, but it has exactly the same fruit, seed and seed-coat. I have included it tentatively here.

(1) Two genera in the enumeration of Ridsdale et al. do not belong here. Tricalysia is a genuine member of the Coffeeae. Diplospora is probably an heterogenous aggregate with species belonging to Coffeeae and others to the group discussed here; the type, D. dubia, is closely related to the African genus Tricalysia and belongs to the Coffeeae also.
All these genera form a highly natural group, perhaps one of the most natural ones of the Rubiaceae and in this respect almost comparable with the Vanguerieae. So I do not doubt that they merit distinction at tribal rank.

It is perhaps astonishing that up til now the affinity of these genera was never stressed. The fact that their important characters are to be found in the fruits, that these organs only recently received greater interest in taxonomic studies of Rubiaceae, and also that fruits are so often lacking in collections may be an explanation for this. There are, however, some suggestions by other authors, not only the recent ones (Ridsdale et al. 1972: 345) already mentioned. Capuron (1969: 50) even proposed to merge several of the genera enumerated here into one large genus Fernelia; concerning the latter he states: «il conviendra à mon avis, en raison de l'identité des caractères floraux et seminaux, de réunir à ce genre les Canephora Comm. ex Juss., Chapeliera Rich., Flagenium Baill., Tamatavia Hook.f., Gallenia Dub. et Dop., Lemyrea Chev. et Beille, Galiniera coffeoides A.M. Hom., divers Ixora, sans compter sans doute quelques genres africains et asiatiques.» But there are also some older indications about this group. Korthals (1851: 170) already compares the Asiatic Petunga with the African Pouchetia and the Madagascan Chapeliera; his paper, containing plenty of invaluable observations, is in Dutch (except the Latin descriptions), however, and remained poorly known (2). Miquel (1857) erected the subtribe Hypobathraceae in the Gardenieae but includes only Hypobathrum in it. He mentions the bilocular ovaries with pendulous ovules and the imbricate («oblique superpositis») seeds as important.

For none of the other genera mentioned here has a tribal or subtribal name ever been established. Since Hypobathrum is also a very typical member of the group I will adopt Miquel’s name, in the rank of tribe however.

Position and division of the Hypobathraceae

The Hypobathraceae may be placed in the subfamily Ixoroideae near the Gardenieae and the Coffeeae.

(2) Korthals’ paper was e.g. not taken into account in Darwin’s (1976) survey of the nomenclature of the Rubiaceae. Jackieae Korthals (as «groep») and Randiaceae Korthals (as «afdeeling») are to be added to this conspectus.
The Alberteae is another tribe with superior embryo-radicles placed near the Gardenieae. It is undecided, however, if it will be possible to maintain this tribe. Bremekamp (1966) regards the type genus as incertae sedis. None of the genera of this tribe show the other typical features of the Hypobathreae, except Polysphaeria: the fruits of the latter (with in each chamber one pendulous seed with a deeply ruminated endosperm and with a seed-coat similar to Hypobathrum) may be regarded as derived from the fruit structure of the Hypobathreae.

The fruits of Galiniera, a monotypic African genus, are fully comparable with those of Polysphaeria: there are, however, usually two (sometimes one) seeds pendulous from an apical placenta in each fruit-chamber. The seeds have a deeply ruminated endosperm and an embryo with the radicle directed upwards. The testa differs from that of Polysphaeria since it consists of almost isodiametrical parenchyma-like cells.

Polysphaeria was placed in the Alberteae by Hooker and Schumann and transferred to the subtribe Cremasporinae of the Coffeeae by Verdcourt (1958: 247), who restricted this subtribe to Cremaspora and Polysphaeria. Cremaspora has the highly unusual combination of a descendent ovule and an embryo with inferior radicle; it has a very typical seed-coat with strongly thickened radial walls and easily withering outer tangential walls. This genus represents perhaps a tribe on its own.

Galiniera was placed in the Gardenieae by Schumann and transferred to the Coffeeae by Verdcourt (1958: 271), with some doubt however.

In my opinion Galiniera and Polysphaeria are nearly related to one another: their inflorescences, flowers, placentations, seeds, embryos, seed-coats and pollen grains fully correspond. Both genera in most characters also match with the natural group discussed above: the only differences are found in the number of ovules, the rumination of the endosperm, and the less elongated testa-cells of Galiniera. They may easily be accommodated within the Hypobathreae as a separate subtribe.

Lamprothamnus Hiern, a genus from Eastern Africa, was referred by its author to the Alberteae; Verdcourt (1958: 248) transferred it to the Coffeeae, based upon the structure of flowers and pollen grains. The fruits of L. zanguebaricus Hiern (the type species) have one or two pendulous and deeply ruminate seeds in each of
both chambers; the embryo-radicle is directed upwards and the testa-cells are very long, with a narrow lumen and strongly thickened radial walls. The genus so characteristically belongs to the Hypobathreae that it seems the best one to serve as the type of the subtribe mentioned above.

Jovetia, a genus recently described from Madagascar and placed in the Coffeeae by Guédès, also belongs here. It has one to three pendulous seeds in each fruit-chamber, which have their endosperm distinctly although not deeply ruminated. I suspect Lemyrea to be a member of the Lamprothamminae too, but I could not yet examine material of this other Madagascan genus.

Taxonomy

Tribus Hypobathreae (Miquel) Robbrecht stat. nov.


Plantae saepius fruticosae. Flores corollae lobis contortis; antherae saepius in fauce affixaæ, exsertae; ovarium biloculare; ovula in quoque loculo 1-∞, saepe biserialia, pendula. Fructus drupacei, endocarpio tenui; semina e placenta apicali pendula; embryonis radicula superiora.

Genus typicum : Hypobathrum Blume.

— subtribus Hypobathrinae

Ovula in quoque loculo plures ad numerosa. Semina imbricata, interdum oblique superposita; testa fibrosa.


Good figures showing the typical characters of the Hypobathrinae are given by Drake del Castillo (1897 : pl. 443, Chapeliera & pl. 446, Flagenium), Pitard (1923 : fig. 21, Hypobathrum hoaense) and Koolders & Valet (1915 : fig. 530, Petunga microcarpa, & 564, 565, Zuccarinia macrophylla).
subtribus Lamprothamninae Robbrecht subtrib. nov.

Ovula in quoque loculo 1-3. Semina endospermio profunde (raro paucum) ruminato; testa fibrosa, interdum colliculata.

Genus typicum: Lamprothamnus Hiern.


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REFERENCES


