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Begonia salaziensis (Gaud.) Warb., taxonomy and placentation

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SUMMARY

Begonia salaziensis is the type of section *Mezierea* (Gaud.) Warb. The section contains six species, here arranged in three groups, and is considered the most primitive in the genus. Seeds of *B. salaziensis* were obtained from Mauritius and plants grown from these flowered after 16 months. Among all the *Begonia* spp. studied hitherto, the placentation of *B. salaziensis* appears to be unique. The entire surface of the ovarial cavity is covered by ovuliferous placental tissue. This novelty is placed in an evolutionary transformation series. It is suggested that the placentation in *B. salaziensis* represents the most plesiomorphic state of the character placentation known within *Begonia* to date. The etymology of the name Mezierea is given. The accepted species and their synonyms are listed.

Key-words: Begonia salaziensis, evolutionary transformation series, placentation, section *Mezierea*, taxonomy.

INTRODUCTION

Begonia salaziensis is the type species of section *Mezierea* (Gaud.) Warb. This section probably combines the most plesiomorphic (ancestral) characters of the genus in Africa (Reitsma 1983; Van den Berg 1984). A drawing of this species in the manuscript for the *Flore des Mascareignes* (M.J.S. Sands, Royal Botanic Gardens, Kew, personal communication) drew our attention to the very unusual placentation in this species, which invited the present, more detailed, study. Sands described the placentation of *B. salaziensis* as 'variously parietal or sub-axile'. Such a placentation does not occur in other species of *Begonia* and would not fit the morphological and evolutionary series proposed by Reitsma (1983).

A new type of placentation would add to the exceptional status of the section *Mezierea*, which is also unusual in its distribution on Madagascar as well as on the adjacent islands and the African continent. In this context it was found useful to explore the taxonomic position of *B. salaziensis* among the other species within the section.

MATERIALS AND METHODS

Begonia salaziensis is a rare and endangered species endemic to the Mascarene islands. It occurs on the main islands of Mauritius and Réunion. Living material from wild species growing on these islands is not easy to obtain. Dr Onno Wijnands, director of the

University Botanic Gardens at Wageningen, however, managed to contact Ms Wendy Strahm, at the time a Mauritius resident. On 3 March, 1986, we received mature fruits freshly collected by Ms Strahm at Bassin Blanc on 25 February, 1986. The plants from which the seed was collected grew against moist and shaded boulders in rapidly degrading forest. According to Ms Strahm the species no longer exists at other localities on Mauritius where it has been previously collected, i.e. Kanaka Crater, Savanne, Quartier Militaire and Nouvelle Découverte.

In the greenhouse at Wageningen the seeds proved viable and the plants grown from these flowered for the first time in July 1987. Hand-pollination of female flowers with pollen from male flowers in the same inflorescence resulted in the production of baccate fruits.

Transverse sections (10 μm) of fixed and embedded ovaries were made at the apical, middle and basal part of two ovaries. These were taken from the same inflorescence of a cultivated plant (voucher J.J. de Wilde nr 9310, WAG). The sections were stained with a solution of Toluidine blue in 0·5% HCl.

B. SALAZIENSIS AND ITS TAXONOMIC POSITION WITHIN *BEGONIA* SECTION *MEZIEREA*

Begonia salaziensis (Gaud.) Warb. in Engl., *Nat. Pflanzenf.* 1st edn 3 (6a): 139. 1984; Irmscher in Engl., *Nat. Pflanzenf.* 2nd edn 21: 573. 1925; Doorenbos in *The Begonian* 49: 138. 1981; Smith, Wasshausen, Golding and Karegeannes, *Begoniaceae* Part I and II: 126, 228, Fig. 30, 13. 1986.

Basionym: *Mezierea salaziensis* Gaudichaud, *Voyage de la Bonite* (Botanique) tab. 32. 1851, sine descr. The generic and specific names together as a descriptio generico-specifica validated by the presence of an illustration with analysis (*Int. Code* 1983 Art. 42); Klotzsch in *Abh. Königl. Akad. Wiss, Berlin* 1854, *Begoniaceen-Gattungen und Arten:* 67. 1855 (the specific epithet by mistake spelled '*salaciensis*'); A. De Candolle, *Prodromus* 15: 407. 1864, only for the localities Mauritius and Réunion (= Ile Bourbon); Smith, Wasshausen, Golding and Karegeannes, op. cit.: 266. 1986.

Type: Gaudichaud s.n. (Ile Bourbon = Réunion, four sheets at P; two duplicates at G).

Stafleu & Cowan (1976) have pointed out that not all plates published in Gaudichaud's *Voyage de la Bonite* (op. cit.) are based on specimens collected during that voyage. This certainly holds for *Mezierea salaziensis* (plate 32, reproduced here in Fig. 1). The very detailed drawing matches the type material and leaves no doubt about the identity of the plant. It represents the only *Begonia* species native to the Mascarene islands which is, moreover, endemic to this region.

It is of interest that on Gaudichaud's third voyage ('*Bonite*'; 1836–1837), Mauritius and Réunion were not visited. He did collect in those islands on his first voyage ('l'Uranie' and 'la Physicienne'; 1817–1820). The plate of *M. salaziensis* corroborates the statement by Stafleu & Cowan (op. cit.) and is a fine example.

Heterotypic synonym: *Begonia aptera* Roxburgh, *Flora Indica* 3: 650. 1832, non Blume 1827. *Type*: Mauritius, Colonel Hardwicke s.n. (not seen).

The name *B. aptera* Roxb. is a later homonym of the validly published name *B. aptera* Blume 1827, and therefore must be rejected. The protologue to *B. aptera* Roxb. mentions Mauritius as the locality where Hardwicke collected the plant. Roxburgh added details on habitat, inflorescences and fruits. From this the identity of the specimen annotated by Hardwicke is clear. Every detail fits *B. salaziensis*. Thomas Hardwicke visited Mauritius

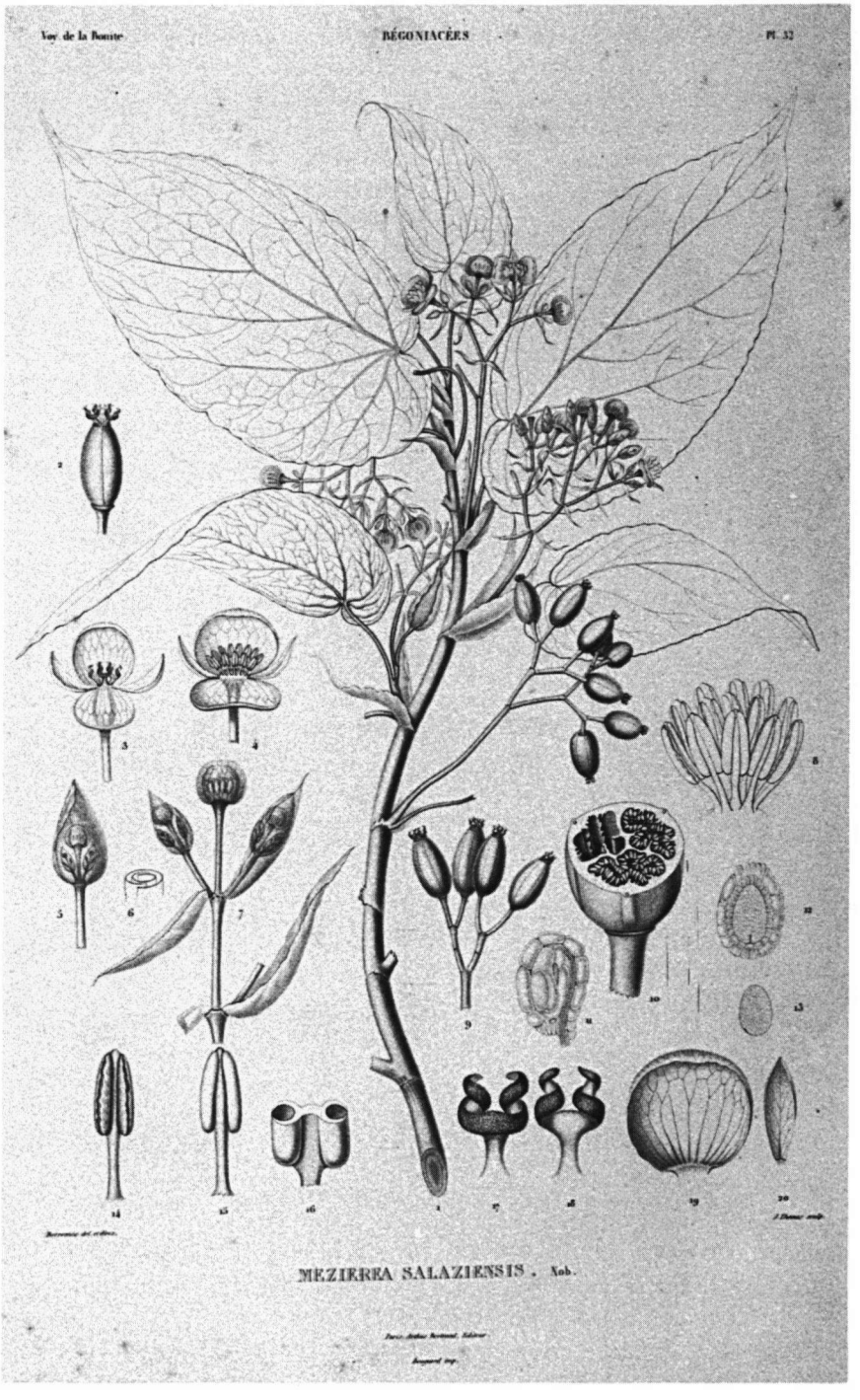

Fig. 1. *Mezierea salaziensis* Gaud. Plate 32 in Gaudichaud's *Voyage de la Bonite*, 1851. For further explanation see text. Photograph: L.J.G. van der Maesen, from a copy of the work present in BR.

in 1811 and specimens of his collection are conserved in BM, G and K (fide *Index Herbariorum* Part 2 (2) collectors E–H, 1957).

Nomen nudum: *Begonia mascariensis* Bojer, *Hortus Mauritianus*: 271. 1837.

Mezierea was proposed as a genus by Gaudichaud in 1851. At that moment the genus contained a single species, namely *M. salaziensis* Gaud. Later, Bentham & Hooker (1867) included *Mezierea* in *Begonia*. Warburg (op. cit., 1894) recognized *Mezierea* as a section within *Begonia* and supplied a detailed circumscription of the section. He admitted five species to it, namely *B. salaziensis* (Gaud.) Warb., the type species of the section, *B. comorensis* Warb., *B. cladocarpa* Bak., *B. meyeri-johannis* Engl. and *B. oxyloba* Welw. ex Hook.f., and correctly removed *Mezierea molleri* C.DC. from the section (= *B. molleri* (C.DC.) Warb., sect. *Tetraphila* A.DC.). He also admitted *B. henriquesii* C.DC. This last name is now considered a synonym of *B. loranthoides* Hook.f. subsp. *loranthoides* (sect. *Tetraphila*) by De Wilde & Arends (1979).

According to Klotzsch (l.c., 1854), the etymology of the name *Mezierea salaziensis* is unknown. From the introduction in Gaudichaud's *Voyage autour du Monde sur la corvette La Bonite* (1851, page 83), it appears that Gaudichaud received, from Réunion, a set of botanical preparations (specifically not herbarium specimens!) which were prepared by M. Lépervanche Mézière, 'botaniste très-distingué de cette localité'. There is no doubt that *Mezierea* is a latinization of the surname. According to Backer (1936), *salaziensis* means: 'originating from Salazie on Réunion or found there for the first time' (our translation).

At present, the section *Mezierea* (Gaud.) Warb. includes the following species (see also Doorenbos 1981, op. cit., and Smith *et al.* 1986, op. cit.):

B. oxyloba Welw. ex. J.D. Hook., 1871
  synonyms: *B. cladocarpa* Baker, 1882,
  B. heddei Warb., 1900,
  B. lehmbachii Warb., 1900,
  B. conraui Gilg, 1904,
  B. kummeriae Gilg, 1904,
  B. petrophila Gilg, 1904,
  B. togoensis Gilg, 1904,
  B. seretii De Wild., 1907,
  B. sassandrensis A.Chev., 1912.

B. meyeri-johannis Engl., 1892.

B. salaziensis (Gaud.) Warb., 1894
  synonym: *B. aptera* Roxb. 1832, non Blume 1827.

B. comorensis Warb., 1895
  synonyms: *Mezierea salaziensis* Gaud. var. *comorensis* A.DC., 1864,
  B. seychellensis Hemsl., 1916,
  B. salaziensis Warb. var. *comorensis* (Warb.) Smith and Wasshausen, 1984.

B. pycnocaulis Irmsch., 1961.

B. humbertii Keraudren, 1983.

The species now recognized may be arranged in three groups. These are to be distinguished as follows (see also Table 1):

(1) Inflorescences bisexual; tepals four in both male and female flowers (except *B. humbertii* which shows two tepals in the male flowers); placentation parietal with fertile placental tissue covering the wall of the ovarial cavity as well as irregular intrusions of ovuliferous placental tissue into the cavity. The ovarial cavity partly partitioned by fusion

Table 1. Table 1 is explained in the text. The arrow indicates a supposed general direction of evolutionary transformation and migration, and not a linear series

Species	Distribution	Tepals in male flowers	Tepals in female flowers
B. oxyloba	Continent & Madagascar	2(4)	2
B. pycnocaulis	Continent (Tanzania)	2	2
B. comorensis	Comores and Seychelles	2	2
B. meyeri-johannis	Continent (East Africa)	4	2(4)
B. humbertii	Madagascar	2	4(2?)
B. salaziensis	Mauritius & Réunion	4	4

We are in doubt about the number of perianth segments in the female flowers of *B. humbertii* Keraudren. The species was published for the first time in *Flore de Madagascar et des Comores*, Famille 144—*Bégoniacées*, 1983. In the protologue it is clearly stated that the male flowers contain two tepals, whereas the female flowers possess four tepals. This is also illustrated (plate 32). The same volume, however, has a coloured plate (plate 1). Although the French phrases 'en haut' and 'en bas' are interchanged in the explanation that accompanies the plate, it is clear that the uppermost two photographs represent fruits and flowers of *B. humbertii*, respectively. On the photograph both male and female flowers are clearly visible, and it is obvious from the picture that the flowers of both sexes contain two tepals. For this reason, in Table 1 the number of tepals in female flowers of *B. humbertii* is as indicated and provided with a questionmark.

of the placental tissue in the centre (see paragraph 4). To this group belong *B. humbertii* and the closely related, but distinct, *B. salaziensis*. They seem vicarious species. *B. humbertii* is endemic to Madagascar, *B. salaziensis* confined to Mauritius and Réunion.

(2) Inflorescences unisexual and the plants (probably) dioecious; tepals four in male flowers and two (rarely four) in female flowers; fertile placental tissue confined to the irregularly shaped intrusions of placental tissue into the ovarial cavity. Ovules absent from the ovary wall (see Reitsma, l.c., fig. 4B). Only *B. meyeri-johannis* is known. It is a woody straggler confined to the mountains in East Africa where it occurs at altitudes between *c.* 1300 m and 2600 m. Within *Begoniaceae*, dioecism represents a rare and probably advanced character state.

(3) Inflorescences bisexual; tepals two in both male and female flowers (rarely four in male flowers); pseudo-septa at least partly consisting of sterile tissue, the fertile placental tissue confined to the expanded part of the septum (see Reitsma, l.c., fig. 4A and C). Three species are known: *B. oxyloba*, *B. comorensis*, and *B. pycnocaulis*. *B. oxyloba* is widely distributed on the continent and in our view occurs on Madagascar as well (reported by the synonymous name *B. cladocarpa*). *B. comorensis* is confined to the Comores and the Seychelles islands. *B. pycnocaulis* is only known from two collections in the Uluguru Mts in Tanzania. In our opinion this species takes a position intermediate between *B. oxyloba* and *B. comorensis*. A forthcoming monographer of the section will have to decide the correct rank and status of *B. pycnocaulis* within the otherwise distinct species group.

The data, partly summarized in Table 1, suggest that representatives of the section *Mezierea* migrating westward have reached the continent on at least two independent occasions.

The three entities distinguished here are not entirely in accordance with the conclusions of Van den Berg (1984). This author assigned one pollen type to the species (names)

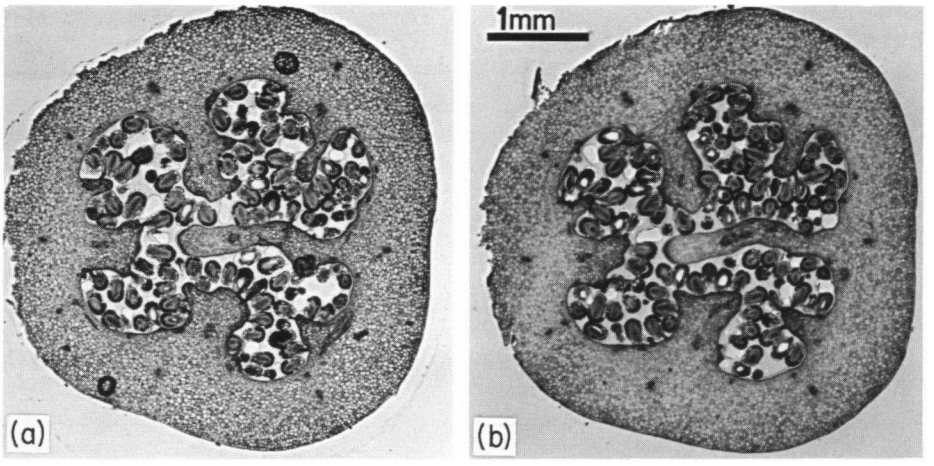

Fig. 2. *Begonia salaziensis* (Gaud.) Warb. Transverse sections of an ovary; (a) section about half way; (b) idem near the bottom.

B. comorensis, B. seychellensis, B. meyeri-johannis, and *B. cladocarpa*, and another, slightly more derived, to *B. oxyloba* and *B. pycnocaulis*. He also examined pollen grains of *B. humbertii* (Van den Berg, l.c., appendix 1, p. 81) but this material was not attributed explicitly to one of the pollen types mentioned above. Although Reitsma (1983) did not study placentation in detail in *Begonia* species outside continental Africa, he had already analysed and pictured three species that belong to the section *Mezierea*, namely *B. oxyloba, B. comorensis* (syn. *B. seychellensis*) and *B. meyeri-johannis*. It was therefore tempting to compare Reitsma's findings with the situation found in *B. salaziensis*.

DESCRIPTION AND INTERPRETATION OF THE PLACENTATION OF *B. SALAZIENSIS*

Figure 2a and b shows sections made in the middle and basal parts of one ovary; they are more or less similar. There are four larger and four smaller intrusions from the ovary wall into the ovarial cavity. Figure 3a and b shows sections of a second ovary, made from the apical and basal part respectively. Here there are three larger intrusions from the ovary wall; they are free in the apical part (Fig. 3a) but fused in the basal part of the ovary. On that level the ovary is distinctly 3-locular. The larger intrusions of the first ovary (Fig. 2a and b), however, are free from one another in the middle as well as in the basal part of the ovary. Thus it appears that the intrusions may remain free or fuse in the basal part during the development of an ovary.

When Reitsma, l.c. 1983, devised a classification of continental African Begonia's, based on their placentation, he found that in the sections *Mezierea, Squamibegonia*, and *Tetraphila* the placentation often changes going from the bottom of the ovary towards its top. As expected, this often also holds for *B. salaziensis*. That we have to do with ovuliferous placental tissue (and not with carpellar dissepiments) is clearly demonstrated by Fig. 3c.

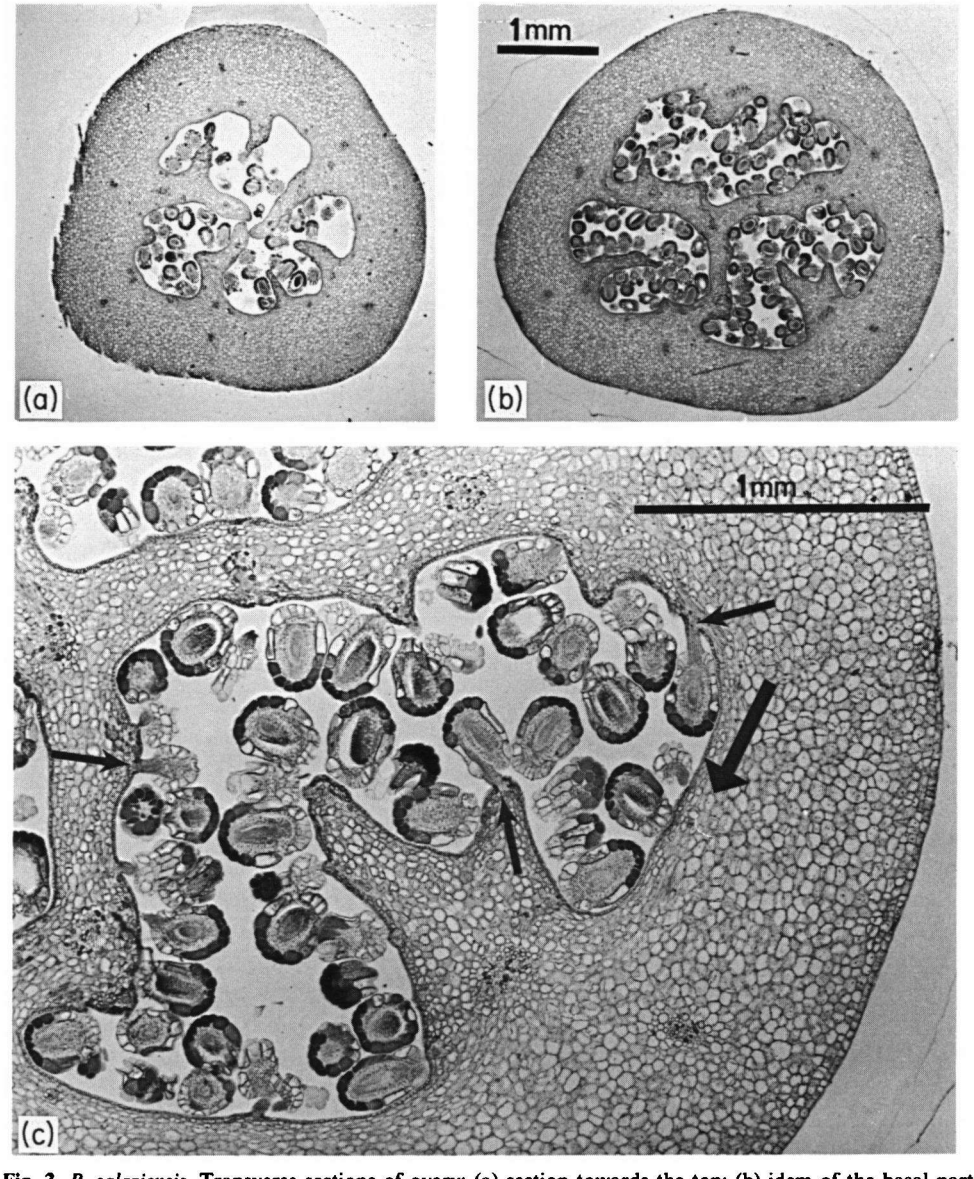

Fig. 3. *B. salaziensis.* Transverse sections of ovary; (a) section towards the top; (b) idem of the basal part, compare this section with the one shown in Fig. 2b, where the placental intrusions in this part of the ovary are not fused; (c) magnification of the lower right portion of the section shown in Fig. 3b. The three smaller arrows indicate ovules attached to various places of the ovarial cavity; the larger, thick arrow indicates the transition zone between smaller and larger parenchymatous cells of the ovary wall.

This photograph shows that ovules are attached to the large fused intrusions, as well as to the smaller free one and also to the inside of the ovary wall (small arrows). This indicates that fertile placental tissue completely covers the interior of the ovarial cavity. The photograph also shows that there is a uniform distinct layer of small epithelium cells, one cell thick, that covers the whole surface of the cavity. In addition, there is a distinct transition

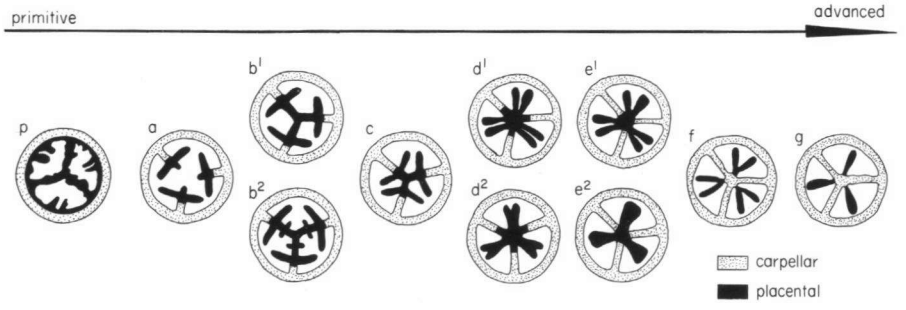

Fig. 4. Evolutionary tendencies in placentation of African Begonias. The cross-sections are schematic and not to scale. a–g occur in the following sections/species respectively: (a) *Mezierea, Tetraphila* partly; (b1) *Tetraphila*, (b2) *B. baccata* and *B. crateris*; (c) *Tetraphila*; (d1) and (d2): some species of *Tetraphila* (*B. cavallyensis* and *B. ebolowensis*); (e1) and (e2) *Squamibegonia*; (f) *Sexalaria, Augustia* partly, *Rostrobegonia* partly; (g) *Augustia* partly, *Rostrobegonia* partly, *Scutobegonia, Loasibegonia*; (p) *B. salaziensis* (a–g from Reitsma, 1983, page 50; p original).

zone between smaller and larger parenchymatous cells in the ovary wall (see larger, thick arrow in Fig. 3c). As the ovules are attached to the small-celled parenchyma, it must be concluded that this tissue is placental.

This type of placentation, so far, is unique in the genus. It was not observed in the *Begonia* species studied by Reitsma, and it has not been reported earlier in the *Begoniaceae*. Thus, this type of placentation does not occur in Reitsma's (hypothetical) evolutionary transformation series of the character 'placentation' (see Fig. 4).

In order to accommodate this new character state in Reitsma's series, we postulate that the placental intrusions (including those that present themselves as septa) completely consist of ovuliferous placental tissue. Intruding carpellary margins, even shallow ones, are absent. The ovuliferous lateral outgrowth of the placentae (resulting in a topographically septal placentation) encountered in Reitsma's series (see Fig. 4a, b1, b2 and c) are, in our case, supposed to be adnate to the carpellary ovary wall where 'arms' of different placentae meet and fuse. This results in the schematic distribution of carpellar (stippled) and placental (black) tissue as indicated in Fig. 4 (compare also Reitsma, l.c., fig. 2).

If the hypothesis presented here is accepted, the new placentation-type fits smoothly into Reitsma's transformation series where it takes an additional position just before his type a. This implies that it might well represent the most primitive state of the character placentation hitherto known within the genus *Begonia*.

REMARKS AND CONCLUSIONS

(1) The observations presented here confirm the correctness of Sand's description of the placentation of *B. salaziensis* as: 'variously parietal or sub-axile'. At least topographically this represents the situation seen in a cross-section of an ovary of this species. This interpretation of the situation leads to acceptance of a special but unambiguously parietal type of placentation in this taxon.

(2) The three types of placentation found in the section *Mezierea*, as presented here, suggest a natural sequence which might be linked with a tendency to perianth reduction as shown in Table 1. These findings support Reitsma's conclusion (l.c., 1983, p.51) that 'the type of placentation provides an indication for the phylogenetic level of a species or species-group'.

(3) Our findings corroborate the suggestions by Van den Berg (1984, p. 78), mainly based on palynological evidence, that the section *Mezierea* should be considered as the most primitive section of the genus *Begonia*, and that it shows: 'a centre of origin in the area formerly made up out of Madagascar, the Comores and the Seychelles, and a westward migration leading to the widespread distribution as shown by *B. oxyloba*'. To this 'centre of origin' we add Mauritius and Réunion.

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