

THE WINTERACEAE OF THE OLD WORLD
V. EXOSPERMUM LINNÆ'S BUBBIA TO ZYGOGYNUM

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SUMMARY

Recent collections of *Exospermum* completed the break-down of the generic differences between *Bubbia* and *Zygogynum*. The oldest name for the resulting enlarged genus is, unfortunately, *Zygogynum*. The characters, relating to these reductions, are reviewed. One new name and 30 new combinations are made; two new species and one new subspecies are described.

INTRODUCTION

In his treatise of the homoxylous dicotyledons Van Tieghem (1900) erected the new winteraceous genera *Belliolium*, *Bubbia*, and *Exospermum* in addition to the already existing genera *Drimys* J.R. & G. Forster, *Wintera* Forster ex v. Tieghem (= *Pseudowintera* Dandy), and *Zygogynum* Baillon.

Exospermum was defined by characters of the gynoecium. Van Tieghem recognised two species, *E. stipitatum* and *E. lecartii*, but already Guillaumin (1942) united these under the name *E. stipitatum*, a reduction which I fully support.

To Van Tieghem the importance of his genus *Exospermum* was its position between *Drimys*, *Belliolium*, and *Bubbia* on one side, and *Zygogynum* on the other. In *Drimys* c.s. the carpels are free and in *Zygogynum* they are united into an ovary with several locules and without a relic of an original separation in the walls between the locules. In *Exospermum* he found the carpels coherent, very weakly so in *E. lecartii* and firmly in *E. stipitatum*. In *Drimys* c.s. the ovules are inserted in a position where they 'belong', in the internal angle of the locule or on the (sealed) margins of the carpels; in *Zygogynum* they are inserted abaxially or 'on either side of the median vein' of the carpel, a 'reversal of placentation'. In *E. stipitatum* Van Tieghem observed a situation similar to that in *Zygogynum*, but in *E. lecartii* he found the 'missing link': ovules on the sealed (adaxial) carpel margins, on either side of the (abaxial) median vein, and between these positions on the lateral walls.

* I: *Blumea* 18 (1970) 225–354; II: *Blumea* 23 (1977) 219–250; III: *Blumea* 24 (1978) 521–525; IV: *Blumea* 28 (1983) 311–328.

Van Tieghem mentioned only the occurrence of two rows of ovules in each locule; he never indicated a difference between simple and multiple rows, so this difference is not amongst the original characters delimiting *Exospermum*.

Burt (1936) already united *Belliolum* with *Bubbia*. A. C. Smith wrote in his introduction to *Exospermum* (1943): 'In effect, the genus is more suggestive of *Bubbia* than of *Zygogynum* and might conceivably be combined with the former, although for the present I feel justified in retaining it as outlined by van Tieghem.' However, recent collections, made by McPherson in New Caledonia, showed that *Zygogynum* has to be included in a comparison as well.

Drimys occurs in Malesia, Australia, and South America. *Pseudowintera* and *Takhtajania* are endemic to New Zealand and Madagascar respectively. *Bubbia* occurs in Malesia, Australia, and New Caledonia. *Exospermum* and *Zygogynum* are endemic to New Caledonia. New Caledonia thus harbours *Bubbia* (including *Belliolum*), *Exospermum*, and *Zygogynum*.

COMPARISON OF EXOSPERMUM WITH BUBBIA AND ZYGOGYNUM

When we compare *Exospermum* with the other genera of the Winteraceae, *Bubbia* appears to be the closest relative. *Zygogynum* and *Takhtajania* have united carpels (though in different ways), *Pseudowintera* has its inflorescences axillary to normal leaves of monopodial branches, and *Drimys* has a monopodial structure and a calyx enclosing the bud until anthesis. However, *Exospermum* shares a number of characters with *Zygogynum* and therefore the character states in this genus are to be considered as well.

Bubbia is a very variable genus. For this comparison we will turn first to *Bubbia howeana* (for full description see Vink, 1983), which is typical for *Bubbia*, not only nomenclaturally but morphologically also for a considerable part of the species.

Exospermum, *B. howeana*, and *Zygogynum* have in common a terminal inflorescence and an early rupturing calyx persistent in fruit.

The principal differences of *Exospermum*, as generally conceived, with *B. howeana* and *Zygogynum* are in the following important characters:

- a. inflorescence: the cataphylls of the twig bear solitary flowers in *Exospermum* and *Zygogynum*, branched partial inflorescences ('florescences' in my earlier publications) in *B. howeana*.
- b. petals: in *Exospermum* and most species of *Zygogynum* the petals of the outer series are connate (the inner petals are always free), in *B. howeana* all petals are free.
- c. carpels: coherent to free in *Exospermum*, free in *B. howeana*, connate in *Zygogynum*.
- d. ovules: in more than one row on each placenta in *Exospermum*, in one row in *B. howeana* and *Zygogynum*.
- e. pollen: exine structure with tectum perforatum to microreticulate in *Exospermum*, reticulate in *B. howeana*, and with both types in *Zygogynum*.
- f. ploidy level: $n = 43$, known for three species of *Bubbia*; $n = 86$, known for one species of *Zygogynum*; unknown for *Exospermum*.

Review of characters

Inflorescence. — In the Winteraceae the apex of the flowering twig bears densely crowded cataphylls (bracts) continuing the 2/5 spiral of the leaves. The more distal bracts often have partial inflorescences* in their axils and usually there is a terminal partial inflorescence. Usually one or a few of the lower bracts subtend a bud which supplies the sympodial elongation of the twig after flowering. Often a number of the lowest bracts have seemingly empty axils.

On this theme a number of variations is realised.

Exospermum, *Bubbia*, and *Zygogynum* all have at least a terminal partial inflorescence and usually also a partial inflorescence is present in the axils of some bracts. The partial inflorescences can range from rich compound dichasia to solitary flowers. In (compound) dichasia the lateral axes and lateral flowers are subtended by bracteoles. Bracts and bracteoles are usually fugacious and enclose the flowerbud only till about the time that some to all flowerparts have been initiated. After flowering elongation of the twig is, as described above, from buds in the axils of lower bracts. Sometimes these buds do not develop leaves, but only cataphylls and short internodes (short shoots). In this way a secondary inflorescence is formed in the axil of a bract (scar) of an old inflorescence. Non-flowering twigs elongate from terminal vegetative buds enclosed by cataphylls.

In *Pseudowintera* flowering is confined to leafless lateral short shoots in the axils of normal leaves or their scars. All partial inflorescences consist of solitary flowers and at least the terminal one is present. The elongating pedicel elevates the flowerbud above the bracts before all flowerparts are initiated (Sampson, 1963). In *Pseudowintera* the formation of secondary inflorescences is an integral part of the pattern (Vink, 1970, f. 3) and hence flowers are produced in a given leaf axil in consecutive seasons. Vegetative elongation is flushlike, without cataphylls, and terminal on the twig bearing normal leaves, but sometimes a secondary inflorescence (Nast, 1944; Sampson, 1963) or the terminal flowerbud (Vink, 1970) is replaced by a vegetative shoot; in the latter case arises a situation comparable to that in *Drimys*.

In *Drimys* the terminal partial inflorescence is replaced by a vegetative bud, so there are only partial inflorescences in the axils of bracts and they can range from compound dichasia to solitary flowers. In sect. *Tasmannia* (Vink, 1970, f. 15) the axes and bracteoles of the dichasia are completely reduced and the flowers are fascicled. The bracts enclose the flowerbuds until all flowerparts are well-developed (at least in sect. *Tasmannia*; for sect. *Drimys* I found no references or clues in the herbarium material). Elongation of the twig after flowering is monopodially from a vegetative bud in the terminal position in the inflorescence. The resulting new shoot has no cataphylls at its base, but terminal vegetative buds on non-flowering twigs do have such cataphylls. Development of vegetative buds in the axils of bracts was sometimes observed (Vink, 1970, p. 251). Secondary inflorescences in the axils of bracts were

* In earlier publications I have referred to these partial inflorescences as 'florescences', but Dr. Weberling kindly pointed out to me that this terminology is incorrect for closed systems.

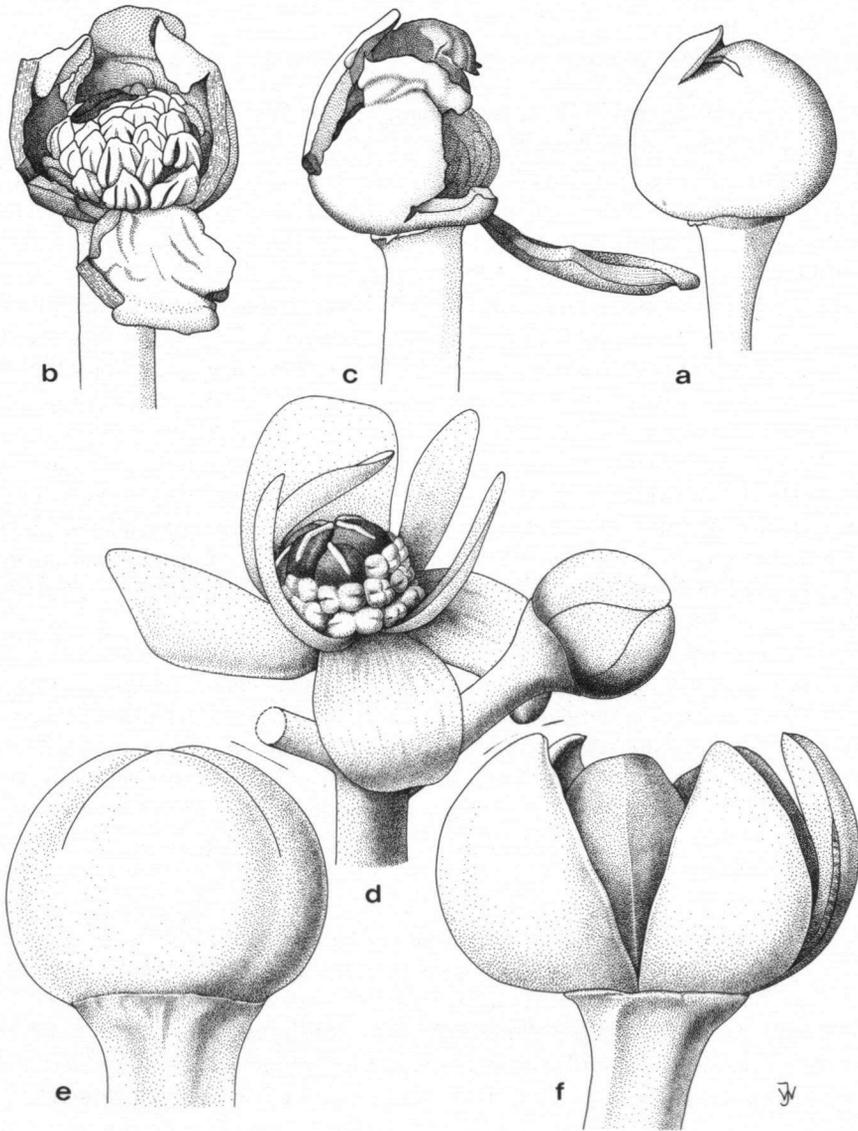


Fig. 1. Petals. — a–c. *Zygotrypa (Bubbia) pauciflorum*. a. Bud, calyx minute, petals largely connate; b. & c. two views of an open flower, the corolla irregularly ruptured ($\times 6$; Carlquist 15584). — d. *Z. (Bubbia) howeanum*. Open flower and bud, petals free ($\times 5$; R. B. Chinnock s.n.). — e. & f. *Z. (Exospermum) stipitatum*. e. Bud, petals halfway connate; f. just opening flower, petals rupturing apart in a regular way ($\times 2\frac{1}{2}$; MacKee 25819).

not found, but sometimes the terminal inflorescence bud produces a short leafless flowering shoot (Vink, 1970, *Drimys insipida*).

The inflorescence of *Takhtajania* is not sufficiently known.

Solitary flowers have rather regularly (*Pseudowintera*), occasionally (*Zygogynum*), or very rarely (*Drimys*) (a) bracteole(s) at the insertion of the pedicel, almost perpendicular to the bract like the bracteoles of dichasia. This is an indication that the solitary flower is a reduced state of a branched partial inflorescence.

In *Exospermum* and *Zygogynum* (Vink, 1977, f. 1 & 2) the partial inflorescences consist of solitary flowers, but in *Bubbia* they are variable. In *B. howeana* they consist of compound dichasia to triads (Vink, 1983, p. 313, f. 1); in e.g. *B. queenslandiana* and *B. semecarpoides* var. *whiteana* they are distinctly reduced and 1-, 2-, and 3-flowered ones occur in the same inflorescence; in other species again they always consist of solitary flowers, e.g. '*B. spec. (MacKee 21204)*' and *B. pauciflora*.

The reduction of the partial inflorescence to a single flower is thus a specific character in *Bubbia*, a generic character in *Zygogynum*. But in the latter genus the reduction continues with a reduction in the number of partial inflorescences: (2–)3–5 in *Z. pomiferum*, 1–3 in e.g. *Z. baillonii*, and only one, the terminal one, in *Z. vinkii*.

Although not of importance for the comparison of the genera, it is worthwhile mentioning here that a few species of *Bubbia*, e.g. *B. comptonii*, even deviate from the for the Winteraceae general picture of centrifugal flowering and have (almost) all flowers of a given inflorescence open at the same time.

Petals. — In *Exospermum* (fig. 1, e & f) and in *Bubbia pachyantha* (New Guinea) the outer petals are connate in the same way as described for *Zygogynum* (Vink, 1977, p. 229–230, f. 3). There the connecting part is thinner than the blades of very young petals; in later stages this thinner part is compressed between the thickening petal blades and a double epidermis penetrates the ring of petals from the adaxial side, providing a predetermined line of rupture. Upon anthesis the petals rupture apart and the resulting 'free' petals have a 'normal' shape; only the margins (except of the apical part) testify of the original union by a thin strip of ruptured tissue along the abaxial side, probably the reason why this phenomenon has been overlooked for so long.

In *B. spec. (MacKee 21204)* and *B. pauciflora* (fig. 1, a–c) the apices of the petals are also free, but in the lower part the ring of petals is almost of equal thickness throughout a cross-section. Here a predetermined line of rupture is absent and upon anthesis the petaloid ring ruptures more or less irregularly in *B. spec. (MacKee 21204)* to very irregularly and often incompletely in *B. pauciflora*.

However, in *B. howeana* (fig. 1 d), in most other species of *Bubbia*, and in *Drimys*, *Pseudowintera*, and *Takhtajania* all petals are free. In *Zygogynum pomiferum* the petals are also free, but some buds have been found with their petals connate for up to one fifth of their length, suggesting that in this species the occurrence of free petals is a secondary state.

The union of the petals can be considered as more complete in *B. spec. (MacKee 21204)* and *B. pauciflora* than in the other taxa. *Bubbia* then shows the full range of completely free to completely connate outer petals.

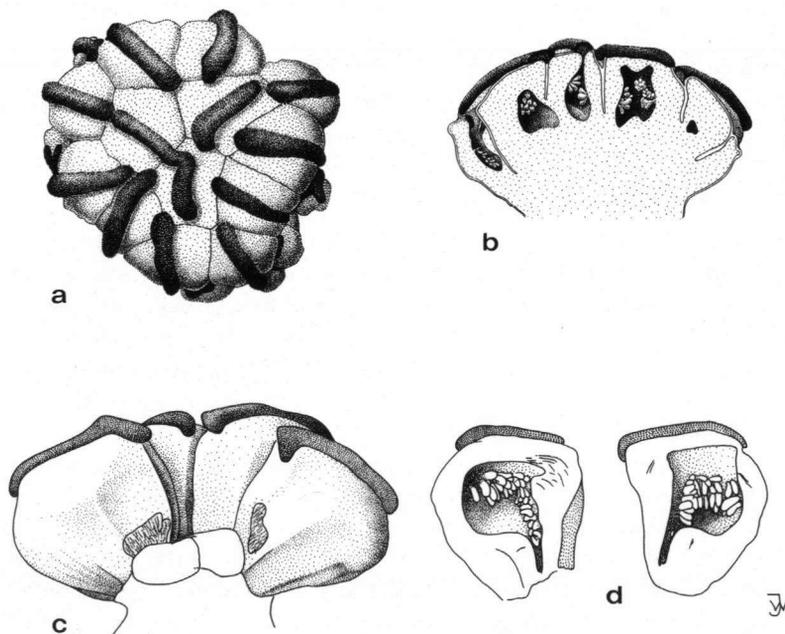


Fig. 2. Pistils of *Zygogynum (Exospermum) stipitatum*. — a. & b. Carpels basally connate, apically strongly coherent ($\times 3$; MacKee 15614). — c. & d. Carpels completely free or very locally (patches of torn epidermis on two carpels) strongly coherent ($\times 6$; McPherson 6129).

The form of the outer petals of *B. spec.* (MacKee 21204) and *B. pauciflora* reminds of that of the calyx, which is also a calyptra with the apical opening closed by the overlapping free apices and also rupturing irregularly, although at a very early stage.

Carpels. — In *B. howeana* and in many other *Bubbia* species, as well as in *Pseudowintera* and *Drimys*, the carpels are free (or solitary). In some *Bubbia* species the carpels are, at least in herbarium material, coherent but essentially also free. This brings us to *Exospermum*.

Van Tieghem reported on *E. stipitatum*: 'Being separated on the outside by deep grooves, the carpels are intimately united with their lateral faces into a single body; ... A series of cross-sections of the pistil thus composed shows that the carpels are only connected to each other by their lateral faces of which the epidermes, which are in contact, are distinct over their whole surface; there is no condescence at any point. By its light colour this double epidermis, which divides every separation of two contiguous locules, contrasts vividly with the two neighbouring cortical layers of which the cells filled with yellow essential oil give that colour to the entire carpel.'

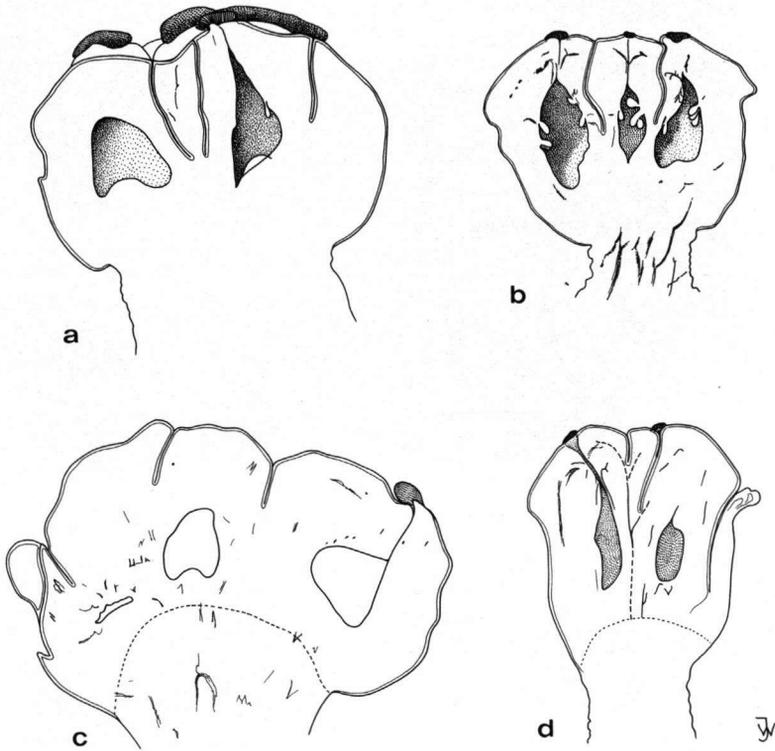


Fig. 3. Longisections of pistils of *Zygogynum (Exospermum) stipitatum*, showing variations in the extent of the continuity of the carpels; curved broken lines in c. & d. indicate differences in tissues (all $\times 6$). — a. Double epidermis extending almost to the base of the locules (just past flowering; *McPherson 6063*). — b. Double epidermis extending to middle of locules (submature bud; *McPherson 2975*). — c. Double epidermis not separating the locules (just past flowering; *MacKee 13832*). — d. One vascular bundle (as broken line where slightly below the surface of the section) supplying different parts of three carpels, branching close to the termination of the double epidermis; abortive carpel at right (just opening bud; *Carlquist 15590*).

On *E. lecartii* he reported: 'A series of cross-sections of the pistil shows also that the carpels are not only not conerescent, but are even very faintly united, hardly adherent. A slight boiling is already sufficient to separate them completely.'

In fact, in quite a number of *Exospermum* specimens the carpels are completely free (fig. 2, c & d). In one specimen (*MacKee 13732*) I observed one flower with 7 firmly coherent carpels and another flower with 4 free carpels. In material, originating from the area covered by Van Tieghem's two species, the ripe fruits always show completely free fruitlets (carpels) without any trace of rupturing of the epidermis.

On the basis of the above the carpels are not principally different from those of *Bubbia*; also their form fits in the wide variation of carpel forms encountered in *Bubbia* (see Bailey & Nast, 1943, pl. III & VI).

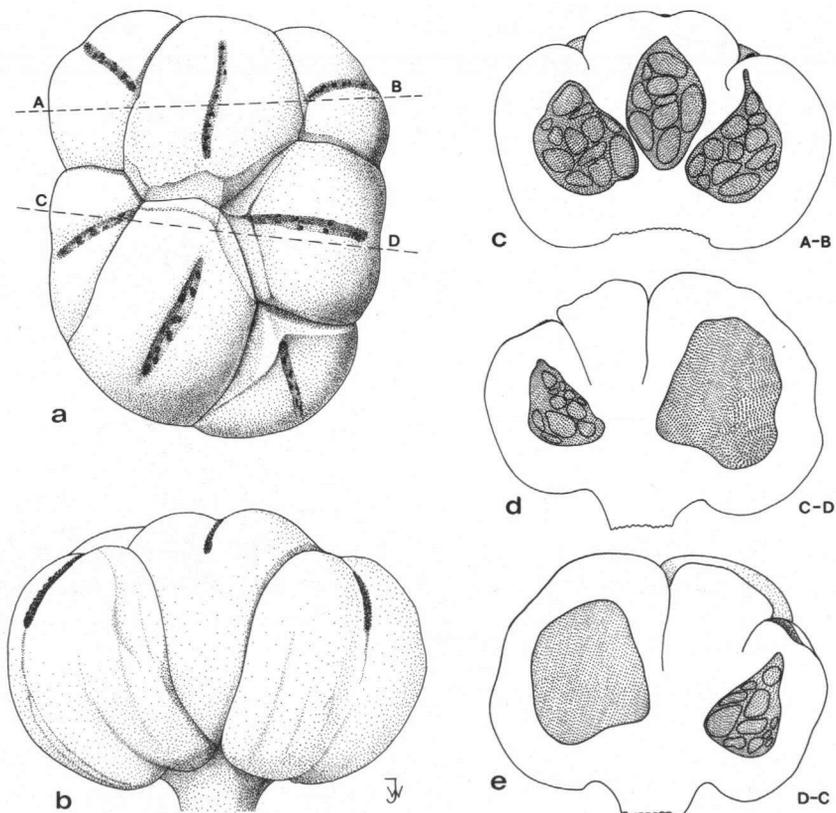


Fig. 4. Fruit with connate carpels of *Zygogynum (Exospermum) stipitatum* ($\times 1\frac{1}{2}$; McPherson 2739). — a. Apical view; b. lateral view, from D; c-d. longitudinal sections showing variation in the continuity of the carpels.

Takhtajania has a bicarpellate unilocular ovary (Leroy, 1978; Vink, 1978).

Zygogynum has $2-\infty$ carpels completely united into an ovary with as many locules. There is no trace of an original separation in the walls separating the locules (Vink, 1977). This is clearly different from the situation in *Exospermum* as described above.

However, in *Exospermum* collections recently made by McPherson in the Panié Massif (New Caledonia) the ripe fruits have *connate* fruitlets (fig. 4). It turned out that this fusion is also visible in flowers. There the double epidermis does not extend down to the base of the carpels, that is to a level below the locules. In all, 11 collections of fertile material from the Panié Massif are available to me and all show, to various degree, a fusion of the carpels. The apices and the parts of the lateral walls adjacent to the stamens are always free, but the contiguous carpel walls are connate

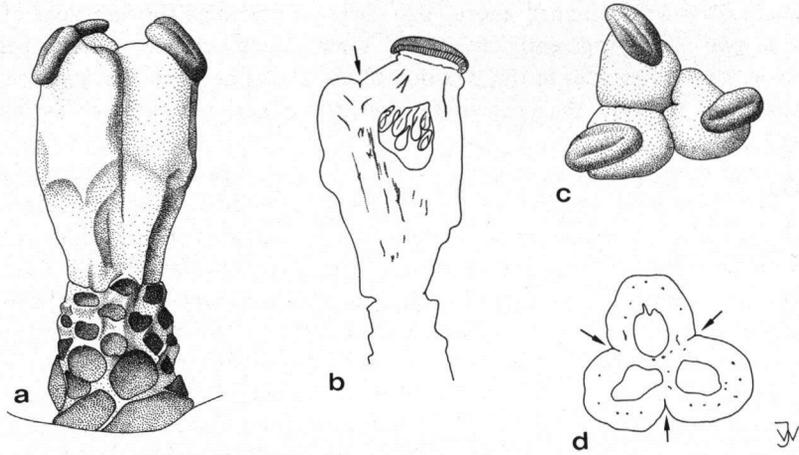


Fig. 5. Pistil of *Zygogynum* (*s.s.*) *baillonii*, showing double epidermis (arrows) slightly (b) or more distinctly (d) penetrating the pistil ($\times 6$; MacKee 32379). — a. Lateral view; b. longisection; c. apical view; d. cross-section.

over 0.2 to 0.8 of their length (figs. 2, 3). In several cases axial bundles extend into the wall between two locules, dividing only slightly below the terminus of the double epidermis to provide branches to different parts of the neighbouring carpels (fig. 3d); this situation is comparable to that in *Zygogynum*.

In this way the Mt Panié *Exospermum* is the 'missing link' between the remainder of *Exospermum* (and some *Bubbia* species) with free – whether or not coherent – carpels and *Zygogynum* with completely fused carpels.

At this stage an important question is whether a morphological difference between the *Exospermum* pistil with connate carpels and the *Zygogynum* pistil can be defined.

In *Exospermum* (in all material known up till now) there is at least a narrow zone with a double epidermis along the apical and abaxial margins of contiguous carpel walls. In fruit these epidermes neatly separate. Both in flower and in fruit the individual carpels are still distinctly outlined on the outside of the pistil c.q. fruit. (The fruit shown in Carlquist, 1982, f. 12, was added as illustrative material, but originated from Katrikoin in the centre of New Caledonia; Carlquist, pers. comm.).

In e.g. *Z. bicolor* (Vink, 1977, f. 7c) the individual carpels are on the outside of the pistil only indicated by their stigmas. In *Z. pomiferum* (l.c., f. 6 & 7b) the individual carpels are more distinctly delineated and their apices are more or less free. In *Z. baillonii* (l.c., f. 8a–c) even a double epidermis between the apices was found. In this species a double epidermis was recently also found in the lateral walls of the pistil (fig. 5) and this situation completely links up with that in *Exospermum*, so there is no morphological distinction possible between the fusion of carpels in *Exospermum* and that in *Zygogynum*.

Ovules. — As mentioned above, Van Tieghem described the insertions of the ovules in two rows. Apparently he was, by some unlucky chance, made to believe that there were differences in the insertion of the ovules between *E. stipitatum* and *E. lecartii*, but the type specimen of *E. stipitatum* also shows exactly what he described for *E. lecartii*.

A further development was the description of the insertion of the ovules in *Exospermum* as 'scattered over the walls of the locule, a modified type of placentation that is suggestive of certain Nymphaeaceae and Lardizabalaceae' by Bailey & Nast (1943, p. 477). Curiously enough they passed over this important deviation in their discussion. A median longitudinal section of a carpel indeed shows the bodies of the ovules covering a fairly large area of the lateral walls, but Leinfellner (1966) pointed out that there are in reality two placentas, each with two to three rows of ovules. Sampson & Tucker (1978) have made further observations and they demonstrated that the ovules are initiated in a single row on each placenta, but that during their development adjacent ovules become aligned in different directions. I found a similar situation in *B. spec.* (MacKee 21204) and in *B. megacarpa*; in the latter also a retarded carpel with ovule primordia neatly in one line was found. All have much higher numbers of ovules than other Winteraceae: *Exospermum* c. 50–100, *B. spec.* (MacKee 21204) c. 40–50, *B. megacarpa* c. 50–70, and the close packing of the ovules causes them to fall out of line. Sampson & Tucker conclude for *Exospermum*: 'We prefer to consider the ovule bases as being arranged in a single irregular row, rather than two or three rows, but one can adopt either description with almost equal justification' (see also their beautiful photographs).

Pollen. — In the Winteraceae the pollen grains are shed in permanent tetrahedral tetrads; only in some species of *Zygogynum* monads occur.

In *Exospermum* the structure of the exine is defined as tectum perforatum to microreticulate (Pragowski, 1979). In *Bubbia* the exine is, in all species investigated so far, reticulate. This would be a good differentiating character. However, in *Zygogynum* both types of structure are found: *Z. acsmithii* (tetrads) and the species with monads have a tectum perforatum or microreticulum, whereas the other species have a reticulate exine. Therefore, in *Zygogynum* this is a character on the specific level and that could equally well be true for the single species of *Exospermum*. In fact, *B. spec.* (MacKee 21204) can be seen as an *Exospermum* with reticulate pollen exine.

As *Pseudowintera*, *Drimys*, and *Takhtajania* all have reticulate pollen exine as well, I consider the tectum perforatum to be a new (specific and local) development.

Ploidy level. — The role of tetraploidy cannot be assessed as the number of counts (Ehrendorfer c.s., 1968) is too low for this purpose. Counts are published for three species of *Bubbia*, one from each New Guinea, Australia, and New Caledonia, all in the same species group as *B. howeana* in table 1; here the same chromosome number as in *Pseudowintera* and in *Drimys* sect. *Drimys* was found: $n = 43$. *Zygogynum baillonii* appeared to be tetraploid: $n = 86$; this may be related to the large size of the stomata, reported by Bongers (1973) to be characteristic for the whole genus. Up till now no counts for *Exospermum* have come to my knowledge.

Anyhow, polyploidy is not a decisive argument in drawing generic limits; e.g. Ehrendorfer c.s. (1968) report infrageneric polyploidy in the Magnoliales and Laurales for the genera *Magnolia* and *Liriodendron* (Magnoliaceae), *Annona* (Annonaceae), *Hedycarya* and *Siparuna* (Monimiaceae), *Hernandia* (Hernandiaceae), and *Chloranthus* (Chloranthaceae).

Table 1.

	<i>Z. acsmithii</i>	<i>Z. spec. div., e.g. Z. bicolor</i>	<i>Exospermum North (Mr Panité)</i>	<i>Exospermum South</i>	<i>B. spec. MacKee 21204</i>	<i>B. pauciflora</i>	<i>B. spec. McPherson 6197</i>	<i>B. spec. div., e.g. B. howeana</i>	<i>B. spec. NGF 44125</i>	<i>B. megacarpa</i>	<i>B. sylvestris</i>	<i>B. pachyantha</i>	<i>B. clemensiae</i>
	New Caledonia								New Guinea				
1. part. inflor. 1-flowered	1	1	1	1	1	1	1	o	1	o	o	o	o
2. petals connate	1	1	1	1	1	1	o	o	o	o	o	1	1
3. carpels connate	1	1	1	o**	o	o	s	o	o	s	o	o*	o
4. ovules > 1 row on placenta	o	o	1	1	1	o	o	o	o	1	1	o	o
5. pollen microreticulate etc.	1	o	1	1	o	o	o	o	?	o	o	o	o

s: carpel solitary; * carpels coherent; ** carpels coherent or not.

The comparison

In table 1 the distribution of the characters under discussion is given for a number of species or species-groups, representing the states of these characters in the genera *Zygogynum*, *Exospermum*, and *Bubbia* as currently conceived.

Zygogynum pomiferum is left out, as the free petals are thought to represent a secondary state, derived from connate petals, and thus not to be comparable to primarily free petals. *Exospermum* is split into two parts to show the differences in fusion of the carpels. The New Guinea species of *Bubbia* have only preliminarily been surveyed and the representation of their character states may not be exhaustive.

The characters are listed for their apomorphic states, indicated in the table by '1'; the plesiomorphic states are indicated by '0'. The flowers of *NGF 44125* are too young to check the pollen exine.

The table clearly reveals that this complex cannot be resolved into groups (genera). A compatibility diagram according to Meacham (1981) shows that there are only four pairs of compatible characters: 1–3, 1–5, 2–3, and 2–5. With these four pairs four different bipartitions can be made and cladograms based on these all have parallel developments in their higher branches.

Connate carpels and microreticulate pollen exine are (up till now) only found in New Caledonia; these character states are absent from New Guinea (and Australia as well). In New Guinea the remaining characters 1–2–4 form a set of compatible characters; as there are no combinations of apomorphic character states, the branches of the resulting cladogram cannot be ordered.

The New Caledonia taxa taken separately have three sets of three compatible characters: 1–2–3, 1–2–4, and 1–2–5; with these three different tripartitions can be made and cladograms based on these all have parallel developments in their higher branches.

The remaining question is whether an artificial separation into *Zygogynum* plus *Exospermum* 'North' and *Bubbia* plus *Exospermum* 'South' is possible. This means that we have to consider *Exospermum* on the specific level.

Exospermum on the specific level

If *Bubbia*, *Exospermum*, and *Zygogynum* are combined into one genus, this genus contains the most primitive type as represented by *B. howeana*, as well as one of the most advanced types of the Winteraceae, *Zygogynum*; this is a highly undesirable situation.

As far as I can see this situation could only be avoided if a division of *Exospermum* could be made into two species, one *E.* 'South' (with free carpels) that could be united with *Bubbia*, and the other one *E.* 'North' (with partly fused carpels) that could be united with *Zygogynum*.

Both species recognised by Van Tieghem, *E. stipitatum* and *E. lecartii*, belong to *E.* 'South', which is known from Inédète to Col d'Amieu. Especially the collections from the southern end of its range differ from *E.* 'North' (Panié Massif) in smaller numbers of stamens and carpels and in smaller flowers and leaves. However, as is shown in table 2, there is a considerable overlap and when both parts are taken together the differences seem to be part of a clinal variation with decrease in size and numbers from North to South. Leaf anatomy reveals as only differences a thicker lamina and a thicker adaxial epidermis in the specimens from the Panié Massif and these are apparently correlated with larger leaf size.

Although the altitudinal ranges are not the same, the differences are not induced by differences in altitude, as is documented by collections from comparable altitudes on Mt Panié and near Katrikoin.

Table 2.

<i>Exospermum</i>	'South'	'North'
number of petals	10–15	10–13
number of stamens	65–188	97–205
number of carpels	(3 or) 4–10	7–19
pedicel length in mm	5–52	12–47
pedicel diameter in mm	(1–)2–5	3–8
petal length in mm	14–20	19–28
longest leaf in cm (incl. petiole)	10–22	17½–26
altitudinal range in m	350–800	20–650

This leaves us only with the difference between 'carpels completely free' and 'carpels for 0.2–0.8 connate'. Even if the distinction between zero and 0.2 would be acceptable – and I think it is not – *E. 'North'* and *E. 'South'* are so much alike that it is unacceptable to place them in different genera.

I think that the fusion of the carpels is a part of the clinal variation observed in the other characters and that all *Exospermum* collections are samples of one, variable, species.

CONCLUSION

Bubbia (including *Belliolum*), *Exospermum*, and *Zygogynum* have to be united. The oldest name for this enlarged genus is, unfortunately, *Zygogynum*.

The Winteraceae now consist of the following genera:

- *Zygogynum*: sympodial elongation after flowering; inflorescence terminal; calyx rupturing at an early stage, persistent; petals free or the outer series united; carpels free to united into a plurilocular pistil.
- *Takhtajania*: probably sympodial elongation after flowering; inflorescence terminal; calyx rupturing at an early stage, probably persistent; petals free; carpels united into a unilocular pistil.
- *Pseudowintera*: monopodial elongation of twig; inflorescences axillary to leaves; calyx rupturing at an early stage, persistent; petals free; carpels free.
- *Drimys*: monopodial elongation after flowering; inflorescence pseudo-terminal; calyx rupturing upon anthesis and usually dropping, sometimes persistent; petals free; carpels free.

NEW TAXA

Three undescribed taxa had to be used in this paper to make the picture more complete. As they are of the *Bubbia*-type, they were indicated as *B. spec.* to avoid confusion, but below they are described in *Zyggynum*.

Zyggynum cristatum Vink, *nov. spec.*

Frutex vel arbuscula. Petioli 0.6–1.5 cm longi. Laminae foliorum obovato-oblongae, 6–14.5 × (1.5–)2–4 cm, coriaceae, apice rotundato vel retuso, basi attenuata, subtus non nisi stomatibus strato albo obtectis. Inflorescentiae partiales uniflorae. Pedicelli 30–58 mm longi. Calyx subcrassus, irregulariter lobatus. Petala exteriora 3–5, in alabastro connata, sub anthesi irregulariter separata, 10–18 × 5–9 mm; petala interiora 8–16, discreta. Stamina 68–95 connectiviis non productis. Pollen in tetradis exutum, exinio reticulato. Carpella 4–9, discreta; stigmata longissima, apices carpellorum leviter excurrentia; ovula 43–50, in utraque placenta uni- vel pauciseriata. Fructus ignotis. — *Typus*: *MacKee 21204* (P), Mt Me Ori, New Caledonia.

The specific epithet refers to the very long stigmatic crest.

Zyggynum cruminatum Vink, *nov. spec.*

Arbor. Petioli 1.5–2 cm longi. Laminae foliorum obovato-oblongae vel oblongae, 12–21 × 3.5–7 cm, (sub)coriaceae, apice obtuso vel rotundato, basi acuta; stratum album abaxiale non observatum. Inflorescentiae partiales uniflorae. Flores alabastris tantum cogniti. Pedicelli usque 40 mm longi. Calyx subcrassus, leviter lobatus. Petala c. 16–19, discreta. Stamina c. 200–275 connectiviis non productis. Pollen ignotum. Carpella c. 35–50, discreta; stigmata apicibus carpellorum aequilonga. Fructus ignotis. — *Typus*: *Kairo NGF 44125* (L), Baime Creek, Wau Subdist., Morobe Dist., Papua New Guinea.

The specific epithet ('filled like a purse') refers to the large number of stamens and carpels in the flowerbud.

Zyggynum tieghemii Vink (see page 53)subsp. *synchronanthum* Vink, *subsp. nov.*

Inflorescentiae partiales uniflorae, simul florentes. — *Typus*: *McPherson 6197* (L), Tiébaghi Massif, N. of Koumac, New Caledonia.

NEW COMBINATIONS

New combinations in *Zyggynum* are made for only those names that are expected to survive the current revision.

- Zygogynum amplexicaule* (Parmentier) Vink, *comb. nov.* – *Drimys amplexicaulis* Vieillard ex Parmentier, Bull. Sc. France & Belg. 27 (1895) 231 in obs., (1896) 308, t. 10 f. 34. – *Bubbia amplexicaulis* (Parmentier) Dandy, J. Bot. 72 (1934) 40.
- Zygogynum amplexicaule* (Parmentier) Vink var. *isoneurum* (v. Tieghem) Vink, *comb. nov. et stat. nov.* – *Bubbia isoneura* v. Tieghem, J. de Bot. 14 (1900) 294.
- Zygogynum archboldianum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia archboldiana* A.C. Smith, J. Arn. Arbor. 23 (1942) 433.
- Zygogynum argenteum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia argentea* A.C. Smith, J. Arn. Arbor. 23 (1942) 436.
- Zygogynum tieghemii* Vink, *nom. et comb. nov.* – *Drimys balansae* Baill., Adansonia 10 (1873) 335. – *Bubbia balansae* (Baill.) v. Tieghem, J. de Bot. 14 (1900) 293. – *non Zygogynum balansae* v. Tieghem, J. de Bot. 14 (1900) 341.
- Zygogynum bullatum* (Diels) Vink, *comb. nov.* – *Drimys bullata* Diels, Bot. Jahrb. 54 (1916) 243. – *Bubbia bullata* (Diels) A.C. Smith, J. Arn. Arbor. 23 (1942) 426.
- Zygogynum calophyllum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia calophylla* A.C. Smith, J. Arn. Arbor. 23 (1942) 436.
- Zygogynum calothyrsum* (Diels) Vink, *comb. nov.* – *Drimys calothyrsa* Diels, Bot. Jahrb. 54 (1916) 244. – *Bubbia calothyrsa* (Diels) A.C. Smith, J. Arn. Arbor. 23 (1942) 427.
- Zygogynum clemensiae* (A.C. Smith) Vink, *comb. nov.* – *Bubbia clemensiae* A.C. Smith, J. Arn. Arbor. 23 (1942) 431.
- Zygogynum comptonii* (E.G. Baker) Vink, *comb. nov.* – *Drimys comptonii* E.G. Baker, J. Linn. Soc. Bot. 45 (1921) 267. – *Bubbia comptonii* (E.G. Baker) Dandy J. Bot. 72 (1934) 41.
- Zygogynum crassifolium* (Baill.) Vink, *comb. nov.* – *Drimys crassifolia* Baill., Adansonia 8 (1868) 199. – *Bubbia crassifolia* (Baill.) Burttt, Hook. Ic. Pl. 34 (1936) sub t. 3315, p. 2.
- Zygogynum glaucum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia glauca* A.C. Smith J. Arn. Arbor. 23 (1942) 433.
- Zygogynum howeanum* (F. Muell.) Vink, *comb. nov.* – *Drimys howeana* F. Muell., Fragm. 7 (1869) 17. – *Bubbia howeana* (F. Muell.) v. Tieghem, J. de Bot. 14 (1900) 293.
- Zygogynum longifolium* (A.C. Smith) Vink, *comb. nov.* – *Bubbia longifolia* A.C. Smith, J. Arn. Arbor. 23 (1942) 429.
- Zygogynum megacarpum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia megacarpa* A.C. Smith, J. Arn. Arbor. 23 (1942) 434.
- Zygogynum montanum* (Laut.) Vink, *comb. nov.* – *Tetralthalamus montanus* Laut. in K. Schum. & Laut., Nachtr. (1905) 319. – *Bubbia montana* (Laut.) A.C. Smith, J. Arn. Arbor. 23 (1942) 426.
- Zygogynum oligocarpum* (Schlecht.) Vink, *comb. nov.* – *Drimys oligocarpa* Schlecht., Bot. Jahrb. 50 (1913) 71, f. 1. – *Bubbia oligocarpa* (Schlecht.) Burttt, Hook. Ic. Pl. 34 (1936) sub t. 3315, p. 3.

- Zygogynum pachyanthum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia pachyantha* A.C. Smith, J. Arn. Arbor. 23 (1942) 428.
- Zygogynum pancheri* (Baill.) Vink, *comb. nov.* – *Drimys pancheri* Baill., Adansonia 10 (1873) 336. – *Bubbia pancheri* (Baill.) Burtt, Hook. Ic. Pl. 34 (1936) sub t. 3315, p. 1.
- Zygogynum pauciflorum* (E.G. Baker) Vink, *comb. nov.* – *Drimys pauciflora* E.G. Baker, J. Linn. Soc. Bot. 45 (1921) 268. – *Bubbia pauciflora* (E.G. Baker) Dandy, J. Bot. 72 (1934) 41.
- Zygogynum polyneurum* (Diels) Vink, *comb. nov.* – *Drimys polyneura* Diels, Bot. Jahrb. 54 (1916) 244. – *Bubbia polyneura* (Diels) Burtt, Hook. Ic. Pl. 34 (1936) sub t. 3315, p. 3.
- Zygogynum queenslandianum* (Vink) Vink, *comb. nov.* – *Bubbia queenslandiana* Vink, Blumea 28 (1983) 318.
- Zygogynum queenslandianum* (Vink) Vink subsp. *australe* (Vink) Vink, *comb. nov.* – *Bubbia queenslandiana* Vink subsp. *australis* Vink, Blumea 28 (1983) 322.
- Zygogynum schlechteri* (Guillaumin) Vink, *comb. nov.* – *Bubbia schlechteri* Guillaumin, Bull. Soc. Bot. Fr. 89 (1942) 3.
- Zygogynum semecarpoides* (F. Muell.) Vink, *comb. nov.* – *Drimys semecarpoides* F. Muell., Vict. Nat. 8 (1891) 15. – *Bubbia semecarpoides* (F. Muell.) Burtt, Hook. Ic. Pl. 34 (1936) sub t. 3315, p. 3.
- Zygogynum semecarpoides* (F. Muell.) Vink var. *whiteanum* (A.C. Smith) Vink, *comb. nov.* – *Bubbia whiteana* A.C. Smith, J. Arn. Arbor. 24 (1943) 145. – *Bubbia semecarpoides* (F. Muell.) Burtt var. *whiteana* (A.C. Smith) Vink, Blumea 28 (1983) 325.
- Zygogynum sororium* (Diels) Vink, *comb. nov.* – *Drimys sororia* Diels, Bot. Jahrb. 54 (1916) 245. – *Bubbia sororia* (Diels) A.C. Smith, J. Arn. Arbor. 23 (1942) 427.
- Zygogynum sylvestre* (A.C. Smith) Vink, *comb. nov.* – *Bubbia sylvestris* A.C. Smith, J. Arn. Arbor. 23 (1942) 430.
- Zygogynum umbellatum* (Ridley) Vink, *comb. nov.* – *Drimys umbellata* Ridley, Trans. Linn. Soc. Bot. 9 (1916) 11. – *Bubbia umbellata* (Ridley) Dandy, J. Bot. 72 (1934) 41.

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