Polysaccharide food-bodies as pollinator rewards in *Exospermum stipitatum* and other *Winteraceae*

L. B. THIEN, O. PELLMYR, L. Y. YATSU, G. BERGSTROM & G. MCPHERSON

**Summary**: Petals of several species of *Zygogynum*, *Bubbia* and *Exospermum* (*Winteraceae*) have cells containing polysaccharide granules that have a dual function in floral biology. Hydrolysis of granules (starch) in floral tissue apparently results in rapid uptake of water with subsequent opening and/or closing of flowers. In addition, granules may function as pollinator rewards for beetles. In one species, *Exospermum stipitatum*, the rose-purple inner surface of the outermost petals characteristically display chewing damage from beetles. Cross sections of this tissue show a "bi-layered" petal, with the innermost cells densely packed with polysaccharide granules. This is the first report of "food-bodies" occurring in the *Winteraceae*.

**Résumé**: Les pétales de plusieurs espèces de *Zygogynum*, *Exospermum* et *Bubbia* ont des cellules spécialisées qui contiennent des granules de polysaccharides. Ces granules jouent deux rôles dans la biologie florale de ces espèces. Tout d'abord, il semble que leur hydrolyse contrôle la quantité d'eau dans le tissu des pétales, ce qui provoque l'ouverture et la fermeture des fleurs. De plus, quelques-uns de ces granules sont mangés par les coléoptères qui pollinisent les fleurs. Chez *Exospermum stipitatum*, les surfaces internes rose pourpre des pétales externes sont typiquement mâchées par les coléoptères. Le tissu des pétales de cette espèce est disposé en deux assises, l'intérieure étant remplie de façon compacte de granules de polysaccharides. Cette étude est une des premières portant sur les "food-bodies" chez les *Winteraceae*.

Leonard B. Thien, Department of Biology, Tulane University, New Orleans, Louisiana 70118, USA.
Olle Pellmyr, Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York 11794, USA.
Larry Y. Yatsu, Southern Regional Research Center, United States Department of Agriculture, New Orleans, Louisiana 70179, USA.
Gunnar Bergstrom, Department of Chemical Ecology, Goteborg University, S-400 33 Goteborg, Sweden.
Gordon McPherson, Missouri Botanical Garden, St. Louis, Missouri 63166, USA.

The *Winteraceae* is an old family of angiosperms with a fossil record extending to the early Cretaceous (Upper Aptian-Lower Albian; Walker et al., 1983). The 28-30 species of *Winteraceae* (all endemic) on New Caledonia, which is the center of distribution of extant members of the family, are traditionally classified into four genera — *Belliolum*, *Bubbia*, *Exospermum* and *Zygogynum* (Smith, 1943; but see Vink, 1985 for a different opinion).

In *Zygogynum* (Carlquist, 1981), *Belliolum* (Carlquist, 1983) and *Exospermum* (Carlquist, 1982), the rapid opening of flowers is accompanied by a swelling of petals and stamens. Carlquist (1982) suggested that the opening of the flowers is a result of uptake of water resulting from the hydrolysis of starch, yielding soluble sugars that change the osmotic
potential. This study describes the presence of polysaccharide granules in the cells of the petals of open flowers for several members of the Winteraceae, with special emphasis on their role as food-bodies for pollination in Exospermum stipitatum (Baillon) Tieghem ex Pilger. They are also discussed in relation to Carlquist’s (1982) hypothesis of floral opening in the Winteraceae.

MATERIALS AND METHODS

The tree Exospermum stipitatum occurs throughout the tropical forest of central and northern New Caledonia (Morat et al., 1984). Observations were made on, and floral material was collected from, a large population of E. stipitatum on Mt. Panié (alt. 325-400 m) in November and December, 1983 and 1986. In this population, most E. stipitatum exceeded 20 m in height, but only the lowermost flowers could be collected using a telescoping pole clipper (ca. 8 m in length). A total of 15 flowers from 8 trees were collected; some additional petals were collected from fallen flowers below trees in 1986. A voucher from the population is deposited in the Missouri Botanical Garden (McPherson 5929). Insects collected from the flowers were pinned or preserved in 70% alcohol.

Floral material of Zygogynum bicolor Tieghem was collected at 950 m on Plateau de Dogny (McPherson 5873) and for Z. baillonii Tieghem at 800 m on Mt. Dzumac (McPherson 5833). Flowers of Z. pomiferum subsp. pomiferum (Baillon) Vink were obtained on Mt. Do at 850 m (Thien 300), and flowers of Z. vieillardii Baillon were collected at 800 m on Prokoméo (McPherson 6020). Flowers of Bubbia pauciflora (E. G. Baker) Dandy were collected from plants on Mt. Panié at 550 m (McPherson 5928). Entire flowers or floral parts were fixed in FAA and/or a fixative of 2% glutaraldehyde/0.5 m cacodylate, pH 7.0. In the laboratory, subsamples (ca. 2 mm²) were excised from the specimens and serially dehydrated in a graded series of aqueous ethanols, placed into acetone, and embedded in Spurr’s epoxy resin. Alternating thick thin-sections were cut with a diamond knife on a Sorvall Porter-Blum Mt-2 ultramicrotome and dried onto glass slides. The sections were stained with a 1% aqueous solution of basic fuchsin and/or periodic acid-Schiff’s (PAS), following Jensen (1962).

RESULTS AND DISCUSSION

The flowering season of E. stipitatum spans 3-4 months during which individual trees produce a few flowers per day. The floral structure (Sampson & Tucker, 1978) consists of a shallow cup-shaped calyx which encloses the bud during a very early stage in floral development. There are 12-15 petals (usually yellow) in 3-4 tetramerous whorls, with the reflexed outermost rose-purple on the inner surface essentially functioning as sepals (Fig. 1). The numerous stamens have an unordered phyllotomy (Endress, 1987a, 1987b); the 4-8 carpels are free, or nearly so, and tightly appressed in the protogynous flowers (Sampson & Tucker, 1978).

The flowering process is similar to that of Zygogynum (Thien, 1980). The flowers are functional for two days, with the female phase (stigmas receptive) exhibited on the first day, and the male phase (anther dehiscence) on the following day. The four outermost petals open
permanently on the first day, while the inner petals remain closed, forming a chamber (Fig. 1). The remaining petals open on the second day. Throughout anthesis, a floral odor is produced (Thien et al., 1985), which evidently acts as a primary attractant for the insects (Pellmyr, Thien & Bergstrom, 1989). Ten of the 15 flowers of *E. stipitatum* collected from the 8 plants contained a total of 26 beetles (*Palontus exospermii*, Curculionidae) inside the closed chamber formed by the inner petals. All the flowers containing beetles displayed chewing damage on parts of the inner surface of the outermost petals (Fig. 1); in two flowers, large portions of the petals were eaten. None of the flowers displayed any damage to the carpels. Sections of floral buds prepared just prior to opening by Carlquist (pers. comm.) show petals and stamens rich in starch grains. He assumed that the starch is hydrolyzed yielding sugars in solution, thus affecting the osmotic potential resulting in an inflow of water. It is interesting to note that Carlquist (pers. comm.) failed to find starch in the carpels. As noted, no flowers of

Fig. 1. — First day (female phase) flower of *Exospermum stipitatum*. The arrow indicates a portion of the inner surface (the food-body) of an outer petal eaten by beetles (× 2).
Exospernum displayed any damage to the carpels, possibly because the tissue lacked starch (see Young, 1986 for a discussion of various factors affecting tissue damage by beetles).

Cross sections of the outermost petals of E. stipitatum revealed a "bi-layered" tissue, with the layers differing in density of granules in the cells (Fig. 2, 3 and 4; see also Carlquist, 1982). The cells nearest the adaxial surface were densely packed with granules (Fig. 2); these granules stained with basic fuchsin and PAS, which indicated that they contain polysaccharides. These polysaccharide-rich cells were eaten by the beetles (Fig. 2, 3 and 4). Cells in the lower portion of the petals (Fig. 4) also contain the polysaccharide granules but at a lower density; these cells were also eaten.

Cross sections of the outermost petals of Zygogynum bicolor, Z. baillonii, Z. pomiferum subsp. pomiferum and Bubbia pauciflora revealed the presence of uniformly distributed polysaccharide granules at a lower density similar to the abaxial portion of the petals in E. stipitatum. In contrast, the outermost petals of Z. vieillardii lacked the polysaccharide granules altogether. Thus, the outer petals of E. stipitatum display a specialized anatomical condition not found in other species investigated in the Winteraceae. It seems plausible that the polysaccharide granules in open flowers represent a specialized condition derived from the proposed original function of starch in floral movements. These remaining starch granules serve an important role in the plant-pollinator interaction.

In floral biology, the term food-bodies usually denotes tissue that is eaten by pollinating insects, particularly beetles, although vertebrate pollination systems may also show this floral characteristic (Faegri & van der Pijl, 1979). Van der Pijl (1960) suggested that such energy-rich tissue near the sporangia may have been a means of pollinator attraction in the flowers of early angiosperms (see also Eames, 1961). In flowers, food-bodies may occur as modified tips of stamens, staminodia, or petals (Calycanthus, Grant, 1950), carpellary appendages (Victoria amazonica (Poepp.) Sowerby, Prance & Arias, 1975), or basal regions of petals (Asimina obovata (Willd.) Nash, Norman & Clayton, 1986; Cymbopetalum (the entire inner surface of the petal) Schatz, 1987; other genera of Annonaceae, Gottsberger, 1977, 1989). Inflorescences of plants may also possess food-bodies important in floral biology; an example is the smooth and waxy inside surface of bracts in Cyclanthus bipartitus Poiteau (Beach, 1982). In some instances the term food-bodies has been incorrectly applied to other types of structures because of error in interpretation of their biological function; for example, "food-bodies" has been applied to glandular hairs on staminodia of Eupomatia that secrete sticky substances attractive to beetles (Eames, 1961). These hairs are almost collapsed at the time of entry of insects (the beetles do eat the protein-rich staminodia; Hamilton, 1898; Endress, 1984; Woodland, 1982).

The food-bodies of flowers pollinated by beetles may be rich in lipids or protein and starch (Beach, 1982; Rickson, 1979; Young, 1986) or in carbohydrates. In Asimina obovata (Annonaceae), the basal portions of the inner petals have food-bodies that are corrugated, wine red, and produce a small volume of sweet exudate (Norman & Clayton, 1986). This tissue, which is eaten by beetles, shows little starch when stained with iodine but contains over 50% carbohydrate. Schatz (1987) also reports the presence of food-bodies at the base of inner petals in many species of Annonaceae pollinated by beetles in Central America.

The small (2-3 mm) beetles extracted from the floral chambers of E. stipitatum were identified as members of Palontus exospermii (Coleoptera; Curculionidae, Endaeini; Kuschel, 1989). This new genus consists of 11 species, all but one from the main island of New
Fig. 2-4. — Cross sections of outer petal of *Exospermum stipitatum*: 2, bi-layered outer petal with arrow marking boundary of the food-body (layer of cells with the higher density of granules). The V-shaped area (top) was caused by beetles partially eating the food-body (× 90); 3, cells of food-body with (arrow) high density of polysaccharide granules (ca. × 400); 4, cells of abaxial portion of outer petal with (arrow) polysaccharide granules (low density), (× 400).
Caledonia and one species from the Loyalty Islands. Host records include Nothofagus and Epacridaceae. The larvae are not known, but closely related genera have larvae that eat flowers, leaf-buds, or new leaves. We have sought larvae in all floral parts of Exospermum but have not been successful. It should be noted that the Endaeine genus Elleschiodes not only pollinates its host, Eupomatia, but also produces larvae that develop in the androecial remains (Armstrong, pers. comm.).

Acknowledgments: We thank the Director of the Service des Forêts et du Patrimoine Naturel in New Caledonia for permission to work on the island. Tanguy Jaffré and Jean-Marie Veillon graciously provided advice and research facilities within ORSTOM. The Erna and Victor Hasselblad Foundation provided a grant making the research possible.

BIBLIOGRAPHY


View This Item Online: https://www.biodiversitylibrary.org/item/48796
Permalink: https://www.biodiversitylibrary.org/partpdf/276409

Holding Institution
Missouri Botanical Garden, Peter H. Raven Library

Sponsored by
Missouri Botanical Garden

Copyright & Reuse
Copyright Status: In copyright. Digitized with the permission of the rights holder.
Rights Holder: Muséum national d'Histoire naturelle
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://biodiversitylibrary.org/permissions

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.

This file was generated 16 April 2022 at 06:26 UTC