INTEGUMENTARY STUDIES IN THE POLYCARPICAE
I. LACTORIDACEAE

F. BOUMAN

Hugo de Vries-laboratorium, Universiteit van Amsterdam

SUMMARY

Detailed information concerning the initiation and subsequent development of the integuments in representatives of the *Polycarpicae* appears to be at variance with the conventional carpel theory. The integuments of *Lactoris fernandeziana* Phil. are completely of dermal origin. The inner integument is most probably only two-layered during its earlier ontogeny, but becomes 'secondarily' three-layered by periclinal divisions of the cells of the inner layer. The outer integument apparently remains two cells thick.

INTRODUCTION

Many students of floral morphology have focussed their attention on the gynoecium and its constituting parts, adherents to the classical concept of the angiospermous carpel particularly favouring representatives of families of the ranalean assembly for their researches. I believe it is not an exaggeration to say that floral morphology is to a considerable extent 'carpel-centred'.

One of the structures the study of which was rather neglected is the ovule. As a rule some attention is paid to the type of ovule (anatropous, atropous, campylotropous, etc.), to the number of integuments, and to the type of nucellus (crassi- or tenuinucellate), but our knowledge concerning the initiation of the ovule primordium and the subsequent development to a full-grown ovule is very meagre (see also BOUMAN 1971). This is the more remarkable if we consider the desirability of acquiring accurate information about ovule ontogeny and morphology in connection with the morphological interpretation of the carpel, the ovule – at least in the concept of phyllospory of the genitalia of the Flowering Plants – having such a considerable bearing on the interpretative morphology of the gynoecium that a morphological evaluation of the carpel cannot be separated from that of the ovule and its constituting parts.

THE INTEGUMENTS OF LACTORIS

Lactoris fernandeziana Phil., the only living representative of the monotypic family of the *Lactoridaceae*, is an endemic species of the Juan Fernandez islands. Its embryology is very incompletely known, only some fragmentary data obtained from dried and reconstituted herbarium material having been reported by CARLQUIST (1964).

Some years ago Dr. K. Kubitzki (now at Munich) sent us a number of microscope slides of *Lactoris fernandeziana*. Although the sections only show three developmental stages of floral organs, the histological structure of the integuments appeared to be so simple and so regular that a description seems to be justified.

Fig. 1.1 shows a transverse section of a flower above the level of the androecium. Three tepaloid elements surround the gynoecium compounded of three basally connate pistils. Each pistil usually contains 4 to 5 anatropous and bitegmic ovules arranged alongside the margins of the 'carpels'. The micropyle is formed by the inner integument.

Fig. 1.2 shows a median longitudinal section of an ovule during megagametogenesis. The nucellus is relatively small; a small nucellar cap has been formed by periclinal divisions of the nucellar epidermis. The slides suggest a tenuinucellate condition, but in the absence of a sufficient number of ontogenetic stages this cannot be established beyond reasonable doubt. The outer integument is only two cells thick along its whole length and appears to agree histogenetically with the two-layered type of integument rather generally found among the Angio-

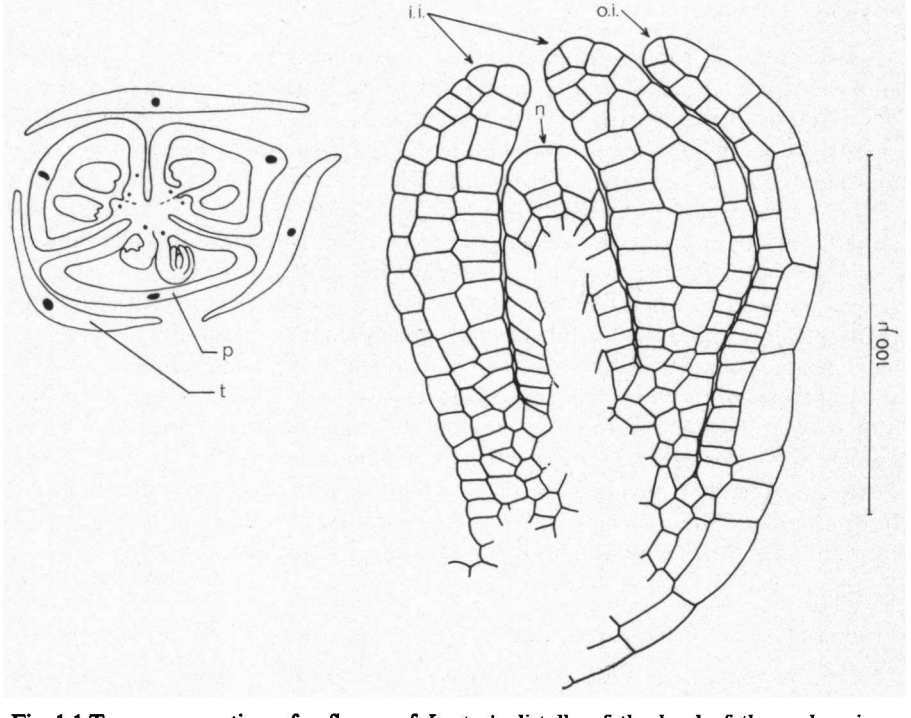

Fig. 1.1 Transverse section of a flower of *Lactoris* distally of the level of the androecium. *t* = tepal; *p* = pistil wall.

Fig. 1.2 Median longitudinal section of a developing ovule. *n* = nucellus; *i.i.* = inner integument; *o.i.* = outer integument.

sperms, which originates from the dermal layer of the ovule primordium and extends both by means of bilaterally dividing dermal initials and by a certain amount of intercalary growth. The inner cell layer of the outer integument differs from the abaxial layer by the relatively large number of intercalary cell divisions. The inner integument also seems to have grown out through the action of a ring of bilaterally dividing dermal initials. The characteristic pattern of two cell layers joined along a zig-zag line can only be discerned in the uppermost portion, however. The integument has become three-layered along most of its length owing to periclinal divisions of the inner cell layer.

Fig. 2 shows a transverse section of an ovule of about the same age as the one shown in *fig. 1.2* and supports the interpretation given. The relatively thin nucellus is surrounded by two integuments, the outer of which is two cells thick along its whole circumference and links up with the funicle, and the inner one consists of three cell layers. The radial orientation of the cells clearly shows the origin of the middle and of the inner layer of the inner integument from periclinal divisions. The integuments are covered by a thin cuticle on both sides.

Fig. 3 shows a transverse section of a developing seed. In comparison with *fig. 2* the increase in girth of the integuments caused by the development of the secondary endosperm (and to a small extent by the growth of the embryo) is brought about by an enlargement of the individual tegumentary cells and not, or hardly, by a prolonged increase in the number of cells. The outer integument remains two-layered, the inner one three-layered. The centre of the developing seed is taken up by the (at least at the level of the section) nuclear endosperm. The nucellar tissue has completely been resorbed. The two integuments have become firmly pressed together, the free space has disappeared, and the bounda-

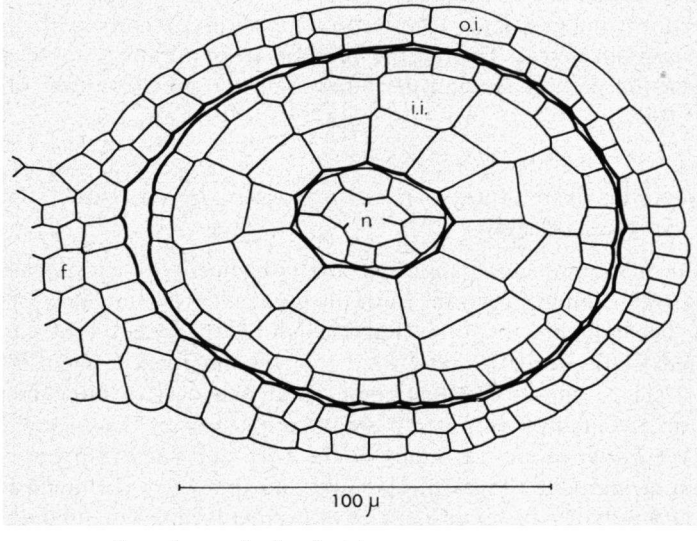

Fig. 2 Transverse section of an ovule. *f* = funicle.

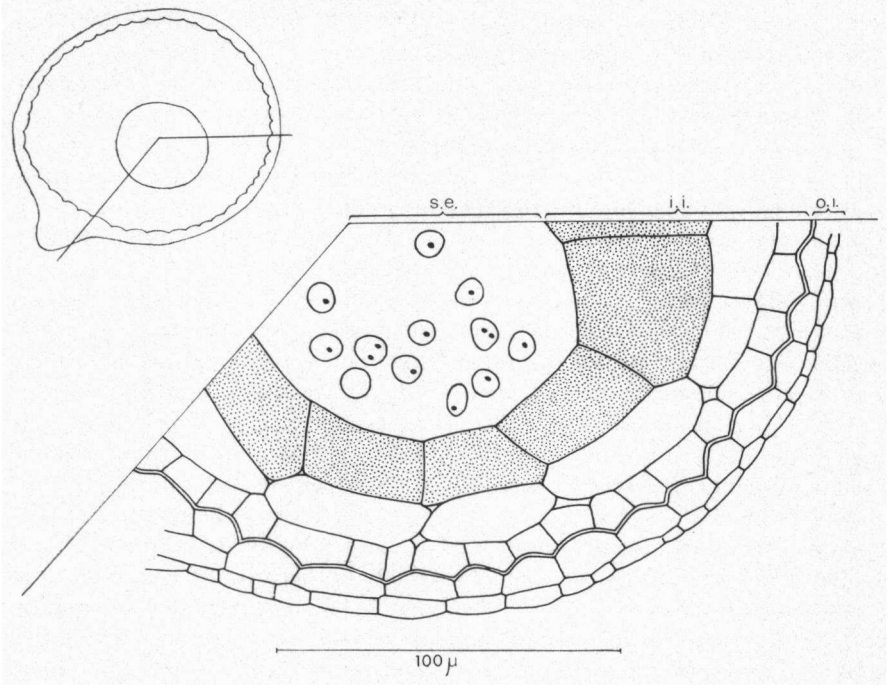

Fig. 3. Transverse section of a developing seed. *s.e.* = secondary endosperm.

ry is marked by a conspicuous, common cuticular layer. The innermost cell layer of the inner integument is very deeply stained, presumably by the presence of tanniferous substances. During the subsequent maturation of the seed the cellular structure of the seed coat becomes almost completely obliterated (see CARLQUIST 1964).

TEGUMENTARY STRUCTURE AND ITS BEARING ON THE CONVENTIONAL CONCEPT OF THE CARPEL

As reported in the previous paragraph, the integuments of the *Lactoridaceae* have a relatively simple structure. Both integuments are completely of dermal derivation. The outer one is two-layered throughout, the inner one at least partly three-layered, owing to periclinal divisions of the inner cell layer of its earlier two-layered stage. This 'secondary' increase in thickness of integuments is a phenomenon repeatedly encountered among Angiosperms (BOUMAN 1971).

Among the *Polycarpicae* the family of the *Lactoridaceae* is not the only one with dermal integument initiation. The inner integument of the ranalean forms is usually and possibly even consistently of dermal origin, but subdermal cells may contribute substantially to the formation of the outer integument. The

outer integument in, e.g., the *Winteraceae* (*Drimys*, *Pseudowintera*) and the *Degeneriaceae* is completely of dermal derivation, in contradistinction to the outer integument of *Magnolia*, in which genus the subdermal cells provide a substantial contribution (details will be given in a forthcoming publication). The above-mentioned difference in integument initiation is the more striking because it seems to be at variance with the traditional interpretation of the carpel. In the families *Degeneriaceae* and *Winteraceae*, often considered to be very primitive – if not the most primitive – taxa of the Dicotyledons, the pistils are characterized by the absence of a style, the stigmatic crests being decurrent along the margins (sutures) of the carpels, and by the incomplete closure of the carpels at full anthesis so that the ovules are partly exposed. The integuments are 2- or only locally 3- to 4-layered in contrast to the multilayered condition found in the *Magnoliaceae* (where carpels are closed at anthesis). Reasoning along the train of thought expressed in the postulate of the foliar carpel one would expect to find in the most ancient angiospermous taxa with incompletely closed pistils, as an expression of the original, protective function of the integuments against dystrophic animal attack, desiccation, etc., a type of ovule with thick, well-developed integuments, so that the occurrence in woody *Ranales* of ovules with thin integuments of dermal origin is distinctly incongruous.

It is hoped that the incidental records in this and in forthcoming publications will more than in the past focus the attention of other phytomorphologists on the morphology and ontogeny of the ovule and its constituents. Linked with the knowledge of other characters, further studies of histogenetic patterns in integument development may contribute significantly to a better understanding of the relationships within the Spermatophytes.

ACKNOWLEDGEMENT

I wish to thank Professor A. D. J. Meeuse for vetting and translating my original manuscript.

REFERENCES

BOUMAN, F. (1971): The application of tegumentary studies to taxonomic and phylogenetic problems *Ber. Dtsch. Bot. Ges.*(in the press).

CARLQUIST, S. (1964); Morphology and relationships of Lactoridaceae. *Aliso* 5: 421–435.