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Development and Morphological Interpretation of the Cupule in *Fagaceae*

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Summary

The development of the (partial) inflorescences and cupules has been investigated in *Castanea sativa*, *Fagus sylvatica* and *Quercus robur (Fagaceae)*. The cupule is best interpreted as composed of a more or less highly branched system of modified (compact, sterile) ultimate parts of the inflorescential cyme. The cupular valves do not correspond to just one branch, but to a branching system of several to many axial orders. In *Quercus*, the seemingly simple, cup-like cupule is composed of two (morphologically complex) parts each of which corresponds to one of the four valves present in *Castanea* and *Fagus*. The pherophylls (= subtending phyllomes) of the branching system are represented by the cupular appendages (scales, thorns).

In *Fagus sylvatica* the male inflorescence is a cymose system lacking the primary terminal flower (to be interpreted either as a simple cyme or a reduced thyrse consisting of but two cymes). In the female inflorescence the two flowers are of the same axial order.

Introduction

One of the most characteristic and peculiar features of the *Fagaceae* is the cupule, a massive, robust and often compound envelope of the fruits. Despite the fact that the family contains the most important representatives of large parts of the temperate forests, especially in the Northern Hemisphere, the morphological complexity of the cupule has to date not been elucidated in a satisfactory way. The most detailed previous developmental study (Macdonald 1979b) is based on light microscopical observations alone. The SEM was a helpful tool in the present investigation.

The inflorescences of the *Fagaceae*, usually unisexual catkins or catkin-like structures, are racemes or thyrses in most cases. The male inflorescences of *Fagus* have not yet been convincingly interpreted in a comparative morphological sense.

This publication is an extended part of a doctoral dissertation (Fey 1981).

Material and Methods

The following collections, fixed in FAA, have been used for investigation:

Castanea sativa Mill.	Fey 11, 8. 6. 1976—29. 5. 1980, Botanical Garden Zurich, Fey 12, 10. 7. 1978—18. 10. 1978, Pura, Ticino, Fey 13, 31. 7. 1978—18. 10. 1978, Pura, Ticino;
Fagus sylvatica L.	Endress 792, 6. 9. 1969—31. 5. 1970, Leimbach, Zurich, Fey 3, 29. 4. 1974—15. 9. 1974, 23. 6. 1975—20. 8. 1975, Staufberg, Aargau,

	Fey 4, 8. 5. 1974—15. 9. 1974, 23. 6. 1975—20. 8. 1975, Staufberg, Aargau,
	Fey 7, 28. 3. 1977—14. 4. 1979, Botanical Garden Zurich,
	Fey 8, 9, 10, 13. 6. 1979—10. 8. 1979, Botanical Garden Zurich;
Quercus robur L.	Endress 784, 30. 8. 1969—24. 5. 1970, Leimbach, Zurich,
	Fey 14, 8. 6. 1976—10. 8. 1979, Botanical Garden, Zurich.

The development of the partial inflorescences and cupules was studied in microtome serial sections and SEM-micrographs.

Results

Male Inflorescences

Fagus sylvatica

The flowers are contracted into a pendulous head. Inflorescences studied from 5 trees were composed of from 6 to 23 flowers. Inflorescence primordia were found in July (1979). The first two floral primordia of an inflorescence arise almost simultaneously. An occasional rudimentary apex between them, which does not develop further, reveals the lateral position of the two floral primordia (Fig. 24). The primordia are slightly different in size. On both sides of each flower primordium a further primordium arises. This ramification pattern is repeated several times. The inflorescence is, therefore, to be interpreted as cymose, consisting of two dichasia, the terminal branchings being, at least partly, monochasial (Figs. 1, 2, 25). This pattern is also reflected by the vasculature in the pedicel. Basipetally, towards the ramification level, the stele in each peduncle opens into three distinct collateral bundles (Fig. 3a). These bundles rearrange in a regular pattern into the stele of the pedicel. The regularity is shown in that the two neighbours of each bundle arise from the flower of the next heigher or lower level of ramification (Fig. 3b). The inflorescence can be viewed as a dichasium without a terminal flower of the first order axis, or as a thyrse composed of two dichasia. Bracts are either lacking in the inflorescence or

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Figs. 1—7. *Fagus sylvatica.*

Fig. 1. Male inflorescence with floral primordia. Transverse section series.

Fig. 2. Male inflorescence, older bud stage. Transverse section series. Vascular bundles of odd number orders dotted.

Fig. 3. Vascular pattern in the base of the male inflorescence. Schematic figures. Vascular bundles of axes of odd number orders dotted.

a) Higher level.

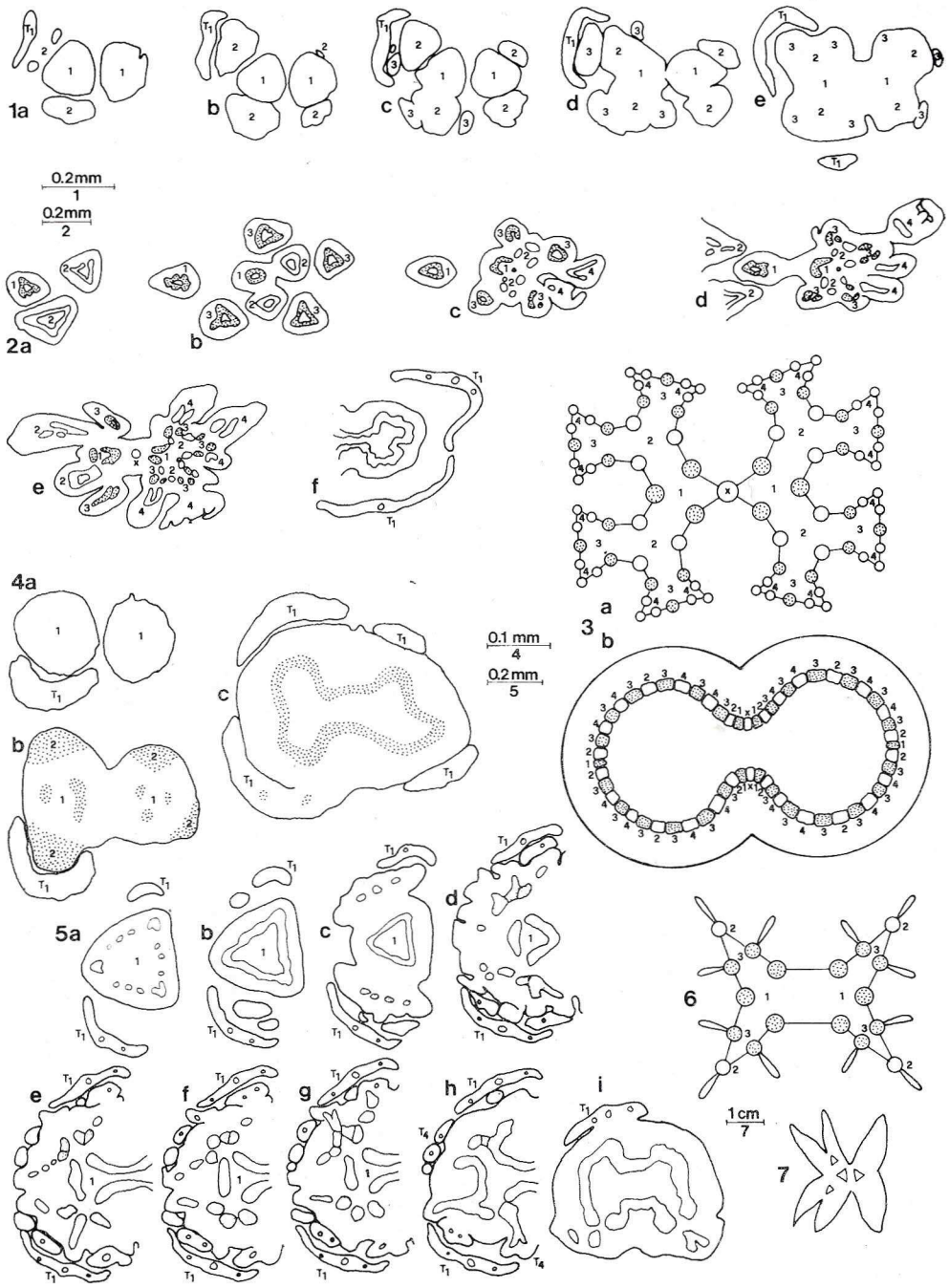
b) Lower level.

Fig. 4. Female inflorescence with primordia of flowers and of cupular valves. Transverse section series. Meristematic tissue, including procambium, dotted.

Fig. 5. Female inflorescence, older bud stage.

Fig. 6. Vascular pattern in the base of the female inflorescence. Schematic figure. Vascular bundles of axes of odd number orders dotted.

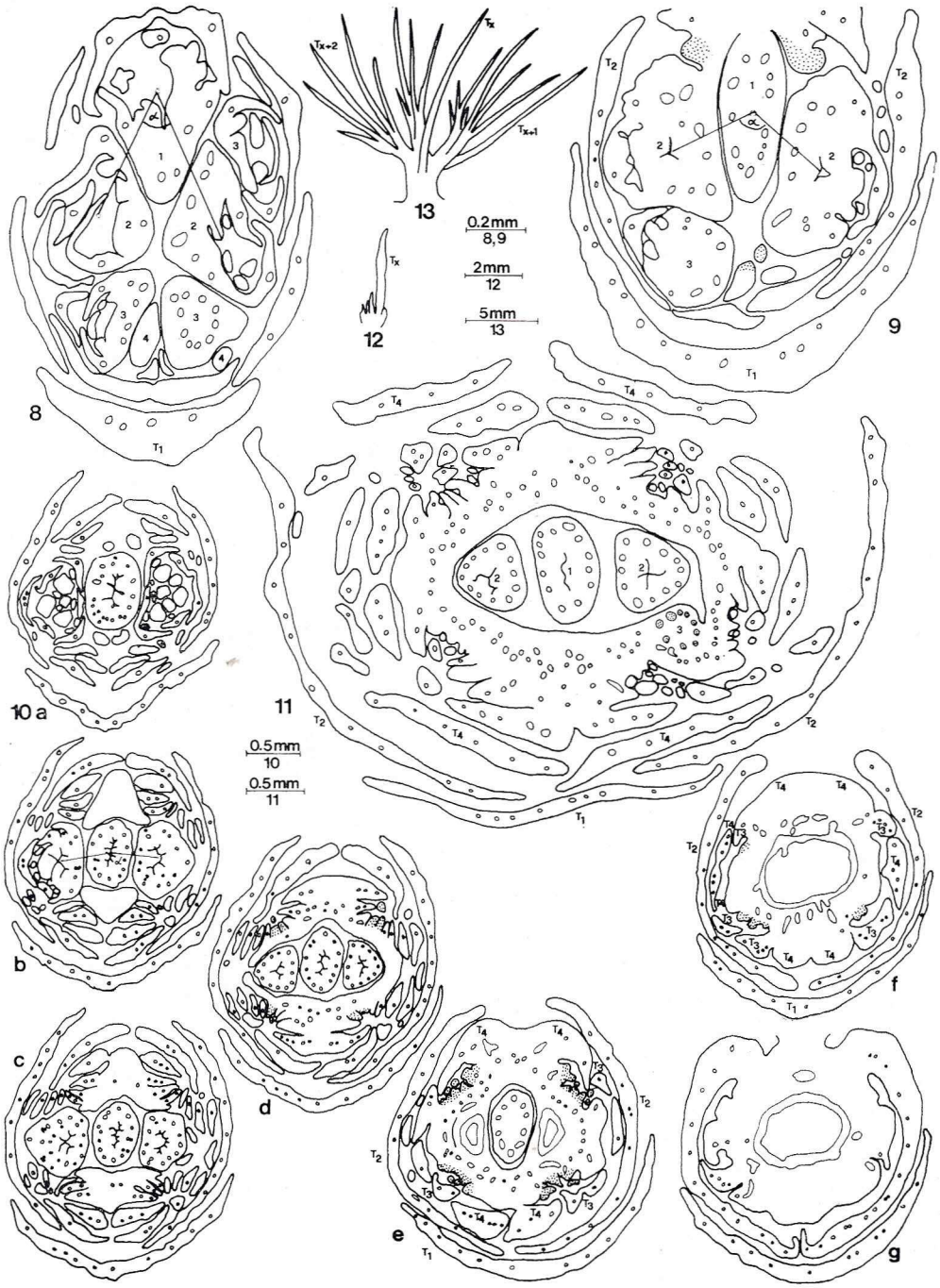
Fig. 7. Open cupule with two additional flowers and doubled corresponding valves, from above. Fruit abscission region marked.



General signatures

1, 2, 3	Axes of different orders
T_1, T_2, T_3	Perophylls (subtending phyllomes) of the respective axes
x	Rudimentary axex or residual vascular tissue below rudimentary apex

In serial sections vascular bundles are encircled.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present up to a number of four. Their position is behind the flowers of the second order. Sometimes two of them are united behind the primary flower. If four are present they can be best interpreted as two pairs of stipules (with the median part of the phyllome reduced), representing the two pherophylls (subtending bracts) of the two first flowers of the inflorescence. A similar condition occurs with the bud scales in the vegetative region. These bipartite pherophylls are often suppressed and, if present, they are caducous. The flowers of the higher branching orders do not have pherophylls.

Castanea sativa

In contrast to *Fagus*, the male inflorescences are long, slender catkins with a stiff axis. They are thyrses, mostly without a terminal flower (Codaccioni 1962). The inflorescences of one tree studied contained about 35—100 dichasial partial inflorescences. The first two dichasia originate in the axil of the two transversally positioned prophylls, the following bracts and their dichasia have a spiral arrangement. The first two (transversal) dichasia are often less developed than the following ones. A partial inflorescence often consists of seven flowers with pherophylls. Neighbouring bracts are sometimes more or less united. It is noteworthy that in the axil of the most distal bracts there are rudimentary mounds, apparently floral primordia of the fourth order (Figs. 8, 30). The angle α which is formed by the two straight lines connecting the centre of the primary flower with the centres of the two secondary flowers, is about 50° (Fig. 8).

Quercus robur

The male inflorescences are lax, pendulous catkins, morphologically simple spikes. The pherophylls of the flowers are sometimes bipartite, if present at all. Usually they are lacking.

Figs. 8—13. *Castanea sativa.*

Fig. 8. Young male partial inflorescence. Transverse section. Dichasial angle indicated.

Fig. 9. Young male partial inflorescence with "female" dichasial angle and cupular rudiments. Transverse section. Dichasial angle indicated. Cupular rudiments dotted.

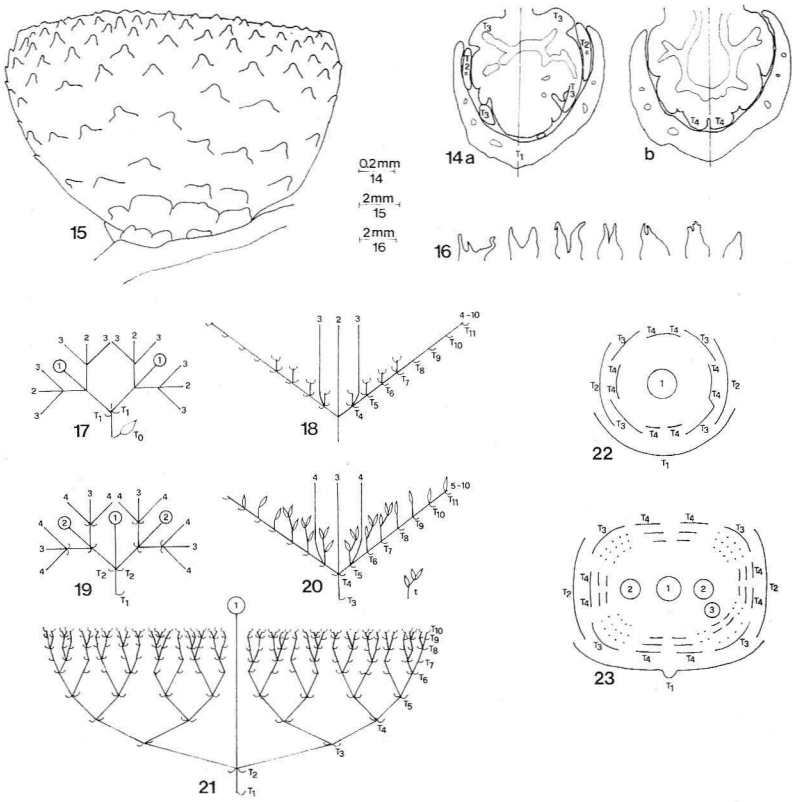
Fig. 10. Young female partial inflorescence with cupule. Transverse section series. Thorn cluster primordia dotted.

a) Level of uppermost parts of cupule.
b) Median parts of neighbouring cupular valves fused. Dichasial angle indicated.
c) Apically converging cupular scale rows visible.
d) Cupular valves fusing around dichasium.
e) Lateral flowers united with cupule, primary flower still separate.
f) Base of the inflorescence.
g) All phyllomes of the inflorescence united with axis.

Fig. 11. Young female partial inflorescence with a supernumerary flower ("3") (cf. Fig. 23). Vascular bundles of the fourth flower dotted.

Fig. 12. Thorn cluster of young cupule, from the side.

Fig. 13. Thorn cluster of mature cupule, from abaxial.



Figs. 14—16. *Quercus robur.*

Fig. 14. Young female flower. Transverse sections (cf. Fig. 22).

Fig. 15. Mature cupule.

Fig. 16. Variability of pherophylls of female flowers.

Figs. 17—18. *Fagus sylvatica.*

Fig. 17. Diagram of inflorescence with cupule.

Fig. 18. Tentative diagram of ramification pattern of a cupular valve.

Figs. 19—20. *Castanea sativa.*

Fig. 19. Diagram of partial inflorescence with cupule.

Fig. 20. Tentative diagram of ramification pattern of a cupular valve. t = thorn cluster.

Figs. 21—22. *Quercus robur.*

Figs. 21. Tentative diagram of ramification pattern of a cupule.

Fig. 22. Empirical diagram of a young cupule (cf. Fig. 14).

Fig. 23. *Castanea sativa.* Diagram of female partial inflorescence with a supernumerary flower and five cupular valves (cf. Fig. 11).

Cupule and Female Inflorescences

The female inflorescences of the *Fagaceae* are also usually catkins or heads of a thyrsic or dichasial structure. In contrast to the male inflorescences each flower or each dichasium is surrounded by a cupule. At anthesis, the cupule is still inconspicuous, but later it develops considerably and plays a role in protection as an often massive and armed envelope of the fruits.

Castanea sativa

In the axils of the proximal phyllomes of a flowering shoot male catkins are produced (thyrses with usually seven-flowered dichasia and a dichasial angle of about 50°, see above). In the axils of the more distal phyllomes androgynous catkins are formed, each with about 35 partial inflorescences, thus, a lower number than in the male catkins. They often bear two female, usually 3-flowered, partial inflorescences

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Figs. 24—29. *Fagus sylvatica.*

Figs. 24—25. Male inflorescences.

Fig. 24. Stage with floral primordia (× 150).

Fig. 25. Young inflorescence (× 130).

Fig. 26—29. Female inflorescences.

Fig. 26. First dichasial branching (× 140).

Fig. 27. Second dichasial branching (× 140).

Fig. 28. Formation of the first scales on the cupular valves, from above (× 140).

Fig. 29. Slightly older stage, from the side (× 160).

Figs. 30—35. *Castanea sativa.*

Fig. 30. Male partial inflorescence (× 80).

Figs. 31. Male partial inflorescence with "female" dichasial angle (× 70).

Figs. 32—35. Female partial inflorescences.

Fig. 32. First dichasial branching (× 160).

Fig. 33. Formation of the cupular valves (× 130).

Fig. 34. Similar stage as Fig. 33 (× 130).

Fig. 35. Part of young cupule with initiation of field of thorn clusters. Scales and flowers removed (× 75).

Figs. 36—41. *Quercus robur.* Female flowers.

Fig. 36. Floral and cupule primordium from above (× 130).

Fig. 37. About the same stage, from the side (× 130).

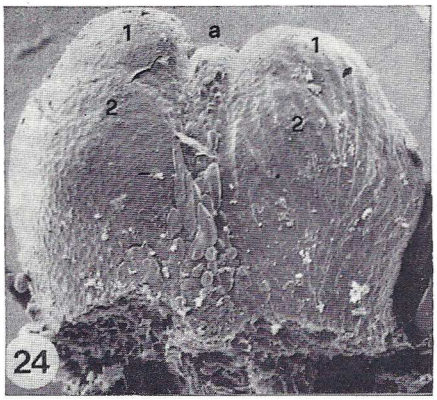
Figs. 38—41. Four young flowers and cupules showing variability of early primordium formation pattern (fusion of bracts of the same or of subsequent axial orders).

Fig. 38. (× 80).

Fig. 39. (× 75).

Fig. 40. (× 80).

Fig. 41. 3, 4: Pherophylls of axis of the corresponding order (× 65).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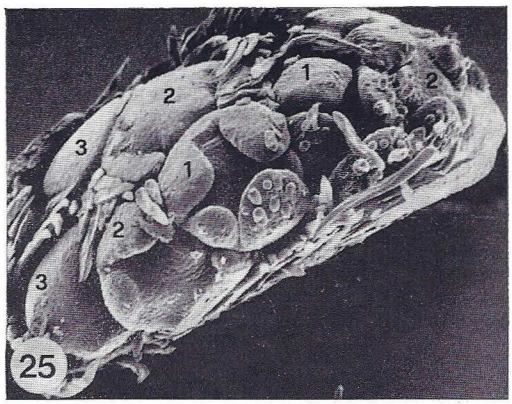
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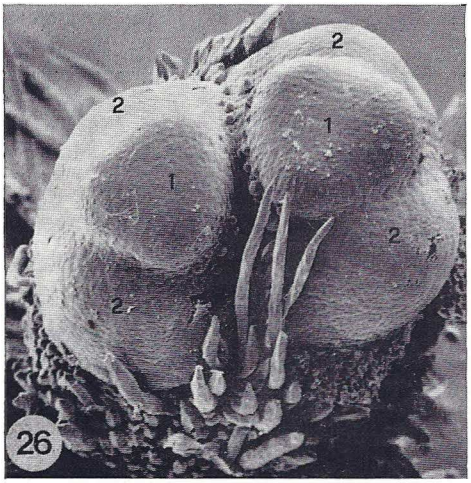
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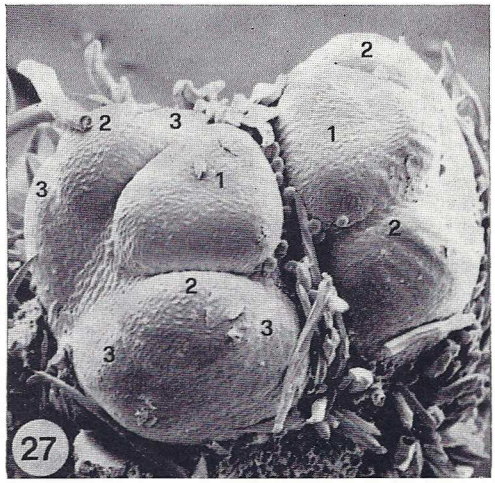
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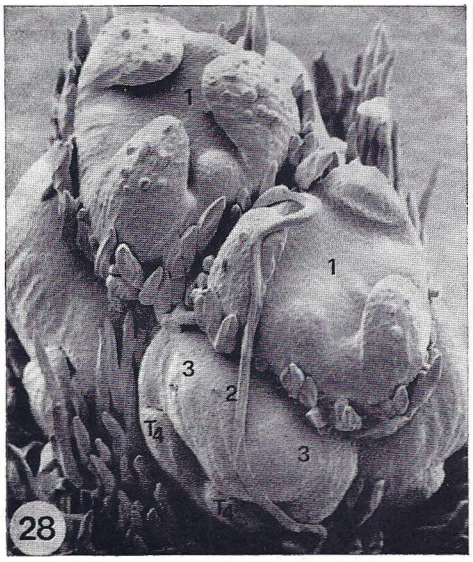
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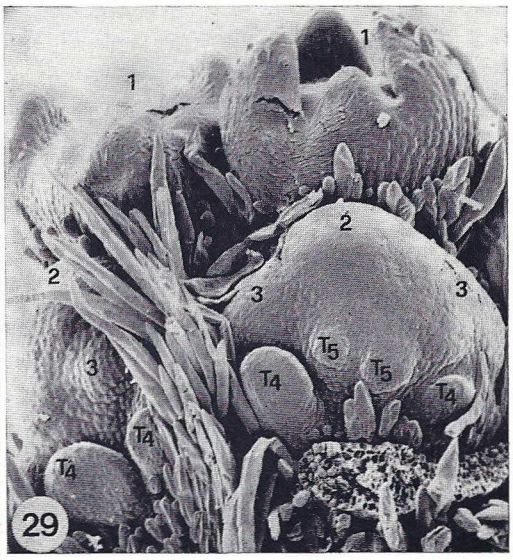
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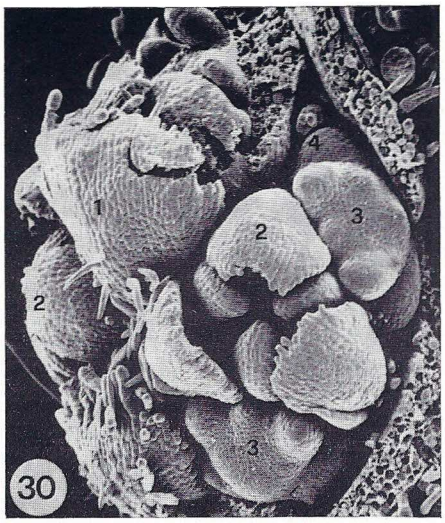
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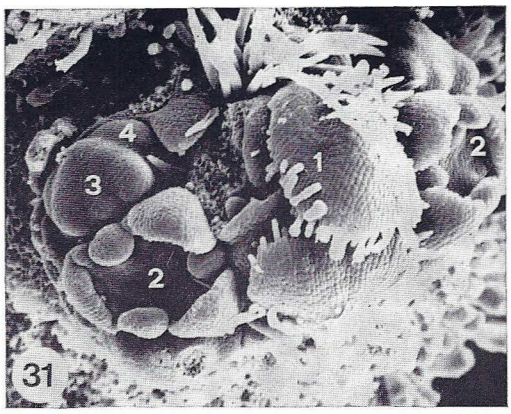
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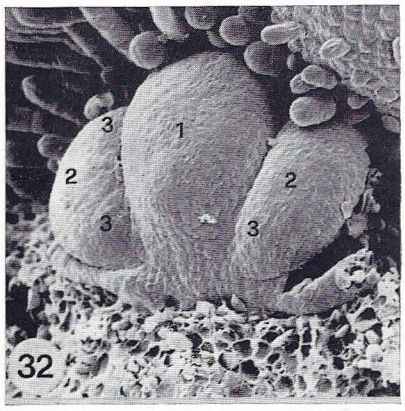
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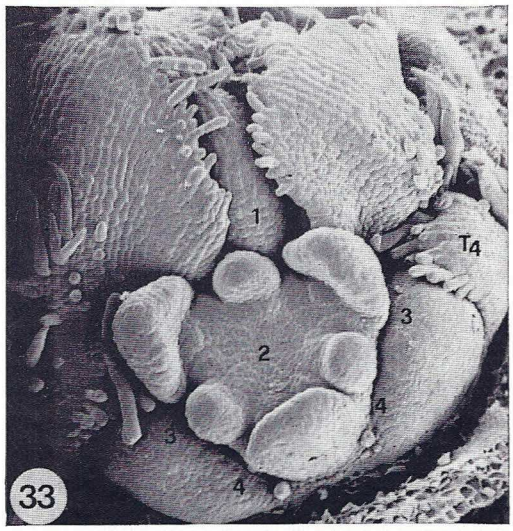
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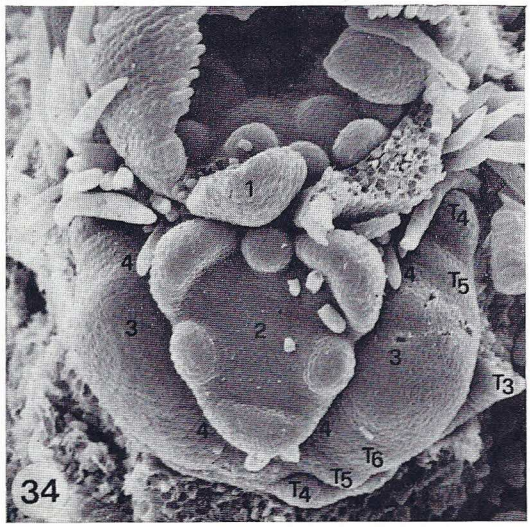
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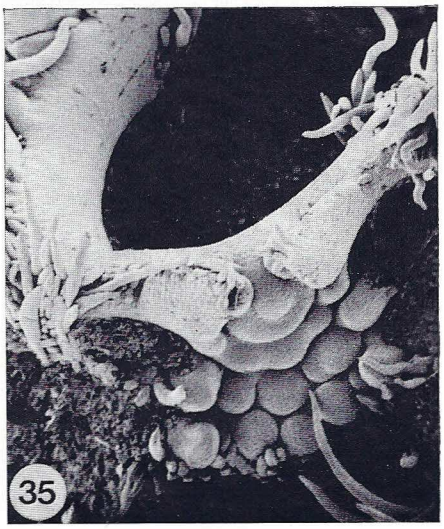
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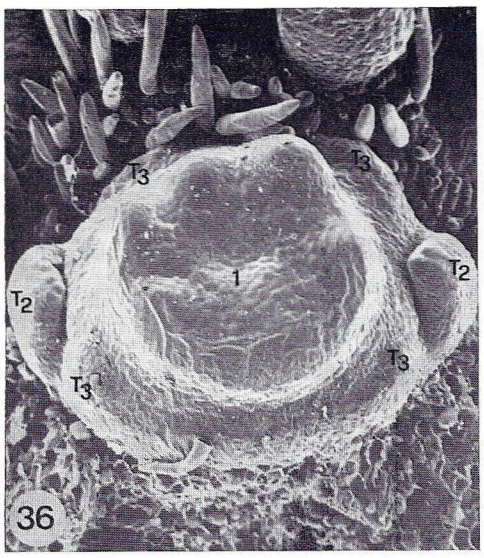
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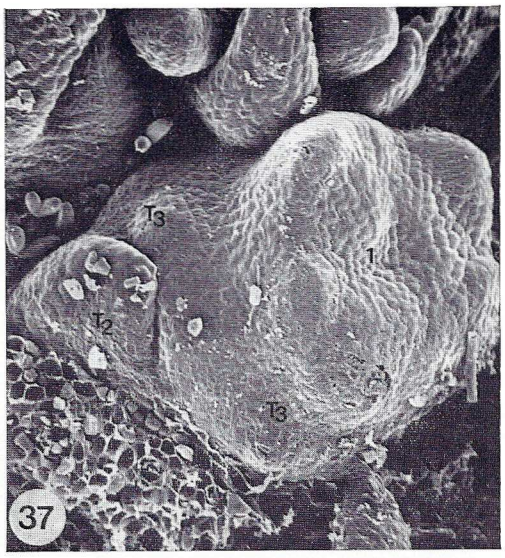
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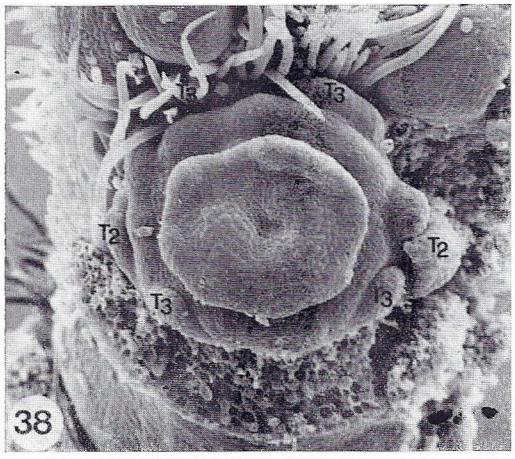
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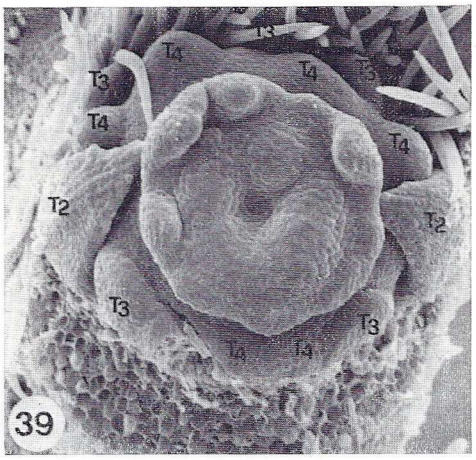
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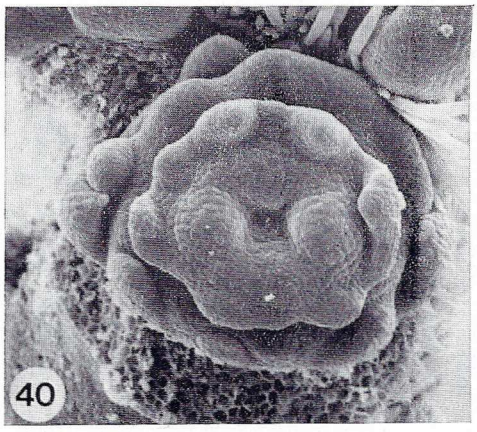
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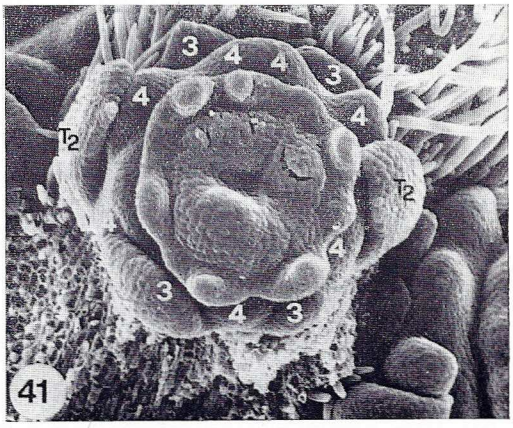
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in the axil of the two (transverse) prophylls, and male partial inflorescences in the axil of the following (spiral) bracts. There are no purely female catkins. The dichasial angle of a female partial inflorescence is about 165° (Fig. 10b), thus, it deviates considerably from that in the male partial inflorescence (50°).

Each female dichasium is surrounded by a cupule. The cupule in an advanced stage of development is a thorny, thick envelope of all the fruits of a dichasium. At maturity it opens by dehiscing into four valves. The thorns on the outside of the valves are arranged in clusters. Regions of thorn clusters alternate with regions of scales. The arrangement of the thorn clusters and scale groups forms a regular pattern.

Partial inflorescences before anthesis studied with the SEM and with serial transverse sections reveal the following structure: The pherophylls of the central flower and the two pherophylls of the two lateral flowers are represented by broad bracts. The summit of the young cupule consists of four mounds in two pairs near the median plane (Fig. 10a). Four somewhat irregular scales on the adaxial side of the two pherophylls of the second order can be viewed as the four pherophylls (third order) of the four apices of the cupule (Fig. 10e, f). In addition, each of them has two lateral neighbours, constituting eight pherophylls of the fourth order (Fig. 10f). They are the outermost part of 8 arcs of scales which converge acropetally in pairs. Between the arcs there are horizontal rows of thorn cluster primordia (Fig. 35). Each row is associated with a pair of bracts belonging to a pair of arcs. The developmental sequence of the thorn clusters is acropetal. Each thorn cluster in itself has a dichasial appearance in that it begins its ramification by a tripartition (Fig. 35).

At fruit maturity the cupule splits into four valves. It dehisces exactly in the median and in the transverse plane. Therefore, each valve has a group of thorn clusters in the middle region and each lateral part bears a row of scales. The minute scales are, however, hidden by the large thorn clusters.

Still younger partial inflorescences studied by SEM and transverse section series supplement the picture. They show that the median region of the partial inflorescence is higher and somewhat further developed than the lateral parts (Fig. 10). The four parts of the cupule have, therefore, an oblique position and their four mounds in the transverse sections are not their central apices, but more lateral parts (towards the median plane of the whole partial inflorescence) (Fig. 34). On both sides of the two lateral flowers a mound originates soon after floral initiation (Fig. 32). Each of these four mounds, in turn, develops two lateral mounds (Figs. 33, 34). Around the three flowers, therefore, a system of twelve mounds is formed which, consequently, is raised by a ring wall around the three flowers. Further organs develop on the outer flank of the ring wall which differentiate into the previously mentioned scales and thorn clusters. The position and developmental sequence of the three flowers, twelve mounds and further organs reveals them to be a dichasial branching system.

Of further interest are intermediate forms between male and female partial inflorescences (already found by Eichler 1878). They occur (1) on androgynous cat-

kins between female and male partial inflorescences and (2) as basal partial inflorescences on male catkins immediately below androgynous ones along the flowering shoot. They show cupular rudiments and/or an intermediate dichasial angle.

The first example (Fig. 9) shows a partial inflorescence from an androgynous catkin. The flowers are male, but (1) there are only four of them, (2) there is a rudimentary cupule with irregular mounds and many scales, (3) the dichasial angle is intermediate of ca. 115°. The second example shows a basal partical inflorescence from a transitional catkin (Fig. 31). The dichasial angle is the same as in female partial inflorescences. There are no cupular rudiments: Instead of a cupule four flowers of the third order and eight apices of the fourth order are present. There are but few remarks on the thorns in the literature. Čelakovský (1890) figures a thorn cluster which he calls "Stachelblatt" (spiny leaf). Forman (1966) points to branched thorns in *Chrysolepis chrysophylla*. Since such a cluster is three-dimensionally branched, it is best interpreted as a part of a cymose branching system in which each thorn represents a modified bract. Often recaulescent subtending thorns are present, and always on the lowest order branch (Figs. 12, 13).

Fagus sylvatica

The female inflorescence consists of two flowers which are surrounded by a four-valved cupule. The valves are congenitally free, in contrast to *Castanea sativa*. There are no thorns, only scales. Serial sections and SEM-micrographs show that each floral primordium is flanked by two mounds (Figs. 4, 26) which, in turn, each produce two lateral mounds (Fig. 27). Also in *Fagus sylvatica*, the dichasial pattern is extended into the cupular valves. This is also shown again by the vascularization (Fig. 6) which resembles that of the male inflorescence to some extent. In each valve there are three main bundles which seem to be correlated with the three main mounds. The slender, almost filamentous, scales are arranged in about eight more or less horizontal, and alternating rows. The lowermost scales originate on the axes of the third order and may be subdivided (Figs. 5, 28, 29).

The lowermost bracts at the base of the cupular valves represent most probably the two pherophylls of the two flowers. They are often bilobed, bipartite or tripartite and seem to correspond to similar organs in the male inflorescences.

Quercus robur

The female inflorescences are simple spikes. As in the other species described here, the bracts are often bipartite, sometimes even tripartite (Fig. 16). The cupule in *Quercus* does not open by valves at maturity, as it surrounds only part of the fruit in a cup-like manner. In *Quercus robur* it contains about ten irregular horizontal rows of scales. The scales of the upper rows become successively smaller and more numerous than those of the lower rows (Fig. 15).

Each floral primordium is accompanied by two transversal prophylls (Figs. 14, 22, 36—41). Subsequently a ring wall is initiated around the floral primordium which constitutes the cupule primordium. The further development shows some variation,

but a certain pattern can be recognized as follows: On the ring wall four scales arise in a diagonal position, i.e. two on each side of a transversal prophyll (Figs. 36, 37). On the next heigher level eight (or less) scales arise, alternating with the four of the previous level (Figs. 38—41). It seems, therefore, that the scales on subsequent (irregular) whorls on the cupule represent bracts of axes of subsequent orders in a compact dichasial branching system.

Discussion

Male Inflorescences

The male inflorescences of the *Fagaceae* are — with the exception of *Fagus* and *Nothofagus* — simple spikes or thyrses. Nothofagus has single flowers or 2- or 3-flowered dichasia in the axils of foliage leaves. In contrast, in *Fagus*, the much condensed and several-flowered heads have been interpreted in different ways: (1) as a catkin composed of cymes (Eichler 1878; Čelakovský 1890), (2) as a thyrse (Reece 1938), (3) as a dichasium with a primary terminal flower (or a reduced thyrse composed of two dichasia) (Prantl 1887; Brett 1964), or (4) as a dichasium without a primary terminal flower (= two dichasia) (Palibin 1935; Hjelmqvist 1948).

The present ontogenetic investigations have clearly shown that — for the material examined — the fourth interpretation is correct. The apex of the first order branch of the inflorescence may be present as a reduced bulge between the two first flowers. One of the two first flowers may slightly dominate the other one in size and, therefore, simulate a single primary flower.

Female Inflorescences

The female inflorescences of the *Fagaceae* are also spikes or thyrses. In *Fagus*, two-flowered dichasia (or two-flowered spikes), and in Nothofagus, two- or three-flowered dichasia or single flowers are produced in the axils of the foliage leaves.

Careful and detailed ontogenetic investigations in *Fagus grandifolia* led Macdonald (1979b) to conclude that the two flowers of an inflorescence are not two lateral, but one lateral and one terminal flower. The main reason for his conclusion was that one flower was more advanced in development than the other.

It seems to us, however, that his figures do not support his new interpretation. Our results in *Fagus sylvatica* clearly show that both flowers are of the same axial order. Macdonald did not consider that the two lateral flowers of a dichasium (or the flowers of a 2-flowered spike) do not need to be initiated simultaneously, but can arise one after the other, since they are two subsequent flowers along their axis of origination. Therefore, it would not be expected that there should be absolute symmetry between the two flowers.

In his figures, MacDonald labels three bracts below the two flowers as "B_1", one of them constituting the pherophyll of the lateral flower and two of them constituting the pherophylls of the cupular valves. However, as mentioned, the number of the bracts varies, and even his Fig. 3 shows a fourth appendage, neglected by him, which would not fit in the framework of his interpretation.

Previous Interpretations of the Cupule

Various morphological interpretations of the fagaceous cupule have previously been put forward:

(1) The cupule is composed of fused bracts. The apical parts of the bracts remain free and form scales or thorns (le Maout 1844; Payer 1857).

(2) The valves are modified prophylls, the scales or thorns emergences (Eichler 1878).

(3) The cupule is an intercalary formation of the floral axis below the flower. Thereby the appendages of the cupule are either phyllomes (bracts) (Schacht 1856; Baillon 1875; Čelakovský 1887, 1890, 1893; Prantl 1887; Tognini 1894; Büsgen 1925; Troll 1926; Bagda 1948; Hjelmqvist 1948), or

(4) emergences (Forman 1964, 1966; Soepadmo 1968).

(5) The four valves are differentiated from the modified basal part of the axis which bears the flowers at the end as a reduced inflorescence, the appendages being stipules (van Steenis 1953 for *Nothofagus*). Therefore, morphologically (but not evolutionarily) this model coincides with (3).

(6) The cupule is composed of sterile compact axes of the next higher order subsequent to the flowers of the highest order in the dichasium (Palibin 1909, 1935; Berridge 1914; Lendner 1916; Reece 1938; Langdon 1947; Raud 1961; Brett 1964; Abbe 1974; Puri & Agarwal 1976; Macdonald 1979b). Brett interprets the cupule of *Fagus* and *Castanea* with this model, however, he does not exclude that *Quercus* is constructed according to model (3).

The New Interpretation of the Cupule

None of the former interpretations of the morphological nature of the fagaceous cupule is satisfactory in the light of the present investigations. Ontogenetic analysis shows that the arrangement of the appendages (scales and thorns) is more orderly than it appears in the mature state. At least in early development there are more or less regular patterns of a certain symmetry. These patterns resemble those of the richly branched cymes in male inflorescences.

It seems, therefore, that number (6) is the best of the previous interpretations of the cupule, but not yet fully elaborated. The female flowers together with their cupule represent a highly complex cymose branching system. Each cupular valve corresponds not just one branch of the dichasial system, but is itself an entire cymose (dichasial-monochasial) branching system. Within the cupule the axes of the different orders remain extremely short and congenitally united by a rapid ramification. The entire ramification system forming the cupule remains compact ("Coenosom"). Minute mounds on the top of the valves, as occurring in *Fagus*, *Castanea* and *Castanopsis*, are probably the last remains of the apices of the branches, and in other genera investigated *(Nothofagus, Trigonobalanus, Chrysolepis, Lithocarpus, Quercus)* they were no more distinctive (Fey 1981).

Highly branched, compact cymose systems are also known from *Moraceae* and *Urticaceae*, as demonstrated by the classic work of BERNBECK (1932). Also in these groups, either axes (flowers) or bracts (pherophylls) may be suppressed, due to the rapid sequence of origin of branching orders. The rudimentary cupule in some *Myricaceae* is interpreted by MACDONALD (1979a, 1980) as consisting of two reduced and modified lateral branches of the inflorescence.

Castanea sativa

The cupule of *Castanea* has already been described in the first section in such a way as to elucidate its cymose structure. The most important points are discussed here:

(1) The ripe cupule dehisces into four valves, if it encloses three flowers (which is the usual condition). If (occasionally) a fourth flower develops, five valves are formed, as expected in a dichasial system (Figs. 11, 23).

(2) Each valve is tripartite in two respects:

(a) The median part bears thorn clusters, whereas the two lateral parts bear scales.

(b) On the top it bears three mounds which apparently represent rudimentary shoot apices. This suggests that each valve is composed of at least three axes (one of the third and two of the fourth order).

(3) Transitional morphs between male and female partial inflorescences suggest that a partial inflorescence of three female flowers including their cupule is homologous with a male partial inflorescence consisting of at least seven flowers plus eight reduced axes. KAUL & KAUL (1981) point to correspondences in male and female partial inflorescences in other *Castaneoideae* without giving a precise interpretation of the nature of the cupule.

(4) The lowermost scales of a female partial inflorescence may be interpreted as pherophylls of lateral branches of the first up to the fourth order. It is probable that the other scales are pherophylls of branches of still higher orders. The thorn clusters are dichasially or dichotomously branched and are subtended themselves by a thorn which can be interpreted as a pherophyll.

The following two models seem to offer a reasonable explanation (Figs. 19, 20):

(1) Each cupular valve consists of three axes. The central (main) axis bears thorn clusters, the two lateral ones bear scales. The thorn clusters are again cymose branching subsystems.

(2) Each cupular valve consists of many axes of subsequent higher orders. Each scale and each thorn is a pherophyll of an axis of a higher order.

Model (2) has the advantage of being cymose throughout, whereas in model (1) the cymose region of the lowermost and of the highest orders of the branching system is interrupted by a "racemose" region.

Fagus sylvatica

As in *Castanea*, a richly branched cymose system makes up the cupular valve (and the whole partial inflorescence). This is shown by the following features:

(1) The cupular valves are arranged in a dichasial pattern, as in *Castanea*. If supernumerary flowers occur, they are accordingly more numerous (Fig. 7).

(2) In young stages, SEM-micrographs show each cupular valve as consisting of an elongate ridge with three mounds on the top. This again suggests a complex primordium, consisting of at least three axes. Apparently the system branches so quickly that the precocious lateral axes inhibit the development of the corresponding pherophylls. This feature is also present in the homologous male inflorescences. The same condition occurs in certain *Urticales*, where the compact dichasial inflorescence system does not produce pherophylls in the lower branching orders (Bernbeck 1932).

(3) Anatomically the vascular pattern points to the cymose structure of the cupular valves.

(4) Male dichasia usually contain 14 to 15 (in the extreme up to 23) flowers. This could further support the interpretation of the cupule as consisting of several axes.

(5) Occasionally male flowers are produced on the top of the cupular valves (Cole 1923). This is not surprising, if the valves are modified branching systems.

Again, model 2 (as described for *Castanea*) has the best fit for interpretation of the cupule of *Fagus* (Figs. 17, 18). In this model the appendages on the cupule represent pherophylls and are homologous to the scales and main thorns of the cupule of *Castanea*.

Quercus robur

The cupule consists of a cup without valves. However, it is not radially symmetric, but medianly monosymmetric. This is shown by transverse sections in young stages (Fig. 14) (see also Macdonald 1979b for *Quercus macrocarpa*). On the ring wall of the young cupule bracts are formed acropetally in horizontal rows. According to the position of the bracts of the lower rows it can be surmised that also in *Quercus* the seemingly highly simplified cupule represents a cymose branching system with a dichasial pattern in the lower branching orders (Fig. 21). Each of the approximately ten horizontal rows of scales is the place of origin of a further branching order. This is also reflected by the increasing number of scales in each ring from bottom to top of the cupule and by the lack of a regular phyllotactic pattern (in contrast to Sattler 1973 for *Quercus rubra*). This feature differs from what one would expect of an uniaxial structure, but fits well with the model of a congested cymose branching system.

Conclusion

Several morphological interpretations of the puzzling cupule in *Fagaceae* exist in the previous literature. The most acceptable among them is that the cupular valves represent the outermost modified, sterile branches of the cymose partial inflorescence.

In this paper an ontogenetic analysis shows that this interpretation has to be modified. Each cupular valve does not represent just one single branch but an entire cymose sterile branching system including axes of several orders ("Coenosom").

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References

Abbe, E. C. (1974): Flowers and inflorescences of the "*Amentiferae*". Bot. Rev. **40**: 159—261.

Bagda, H. (1948): Morphologische und biologische Untersuchungen über Valonea-Eichen (*Quercus macrolepis* Ky.). im Haci-Kadin-Tal bei Ankara. Comm. Fac. Sci. Univ. Ankara **1**: 89—125.

Baillon, H. (1875): Recherches organogéniques sur les Amentacées. C. R. Assoc. Franç. Avanc. Sci. **4**: 756—771.

Bernbeck, F. (1932): Vergleichende Morphologie der Urticaceen- und Moraceen-Infloreszenzen. Bot. Abh. **19**.

Berridge, E. M. (1914): The structure of the flower of the *Fagaceae*, and its bearing on the affinities of the group. Ann. Bot. **28**: 509—526.

Brett, D. W. (1964): The inflorescence of *Fagus* and *Castanea*, and the evolution of the cupules of the *Fagaceae*. New Phytol. **63**: 96—118.

Büsgen, M. (1925): Cupuliferae. In: Kirchner, L., Loew, E., & Schroeter, C.: Lebensgeschichte der Blütenpflanzen Mitteleuropas, II, **1**: 1—253, Stuttgart.

Čelakovsky, L. (1887): O morfologickém významu kupuly (čišky) u pravých Kupulifer. Sitzungsber. Königl. Böhm. Ges. Wiss. Prag, Math.-Naturwiss. Cl. **1886**: 604—618.

— (1890): Ueber die Cupula von *Fagus* und *Castanea*. Jahrb. Wiss. Bot. **21**: 128—162.

— (1893): Ueber die Blüthenstände der *Quercus ilicifolia* und die Eichelcupula. Oesterr. Bot. Z. **43**: 272—277.

Codaccioni, M. (1962): Recherches morphologiques et ontogéniques sur quelques Cupulifères. Rev. Cytol. Biol. Végét. **25**: 1—208.

Cole, L. W. (1923): Teratological phenomena in the inflorescences of *Fagus silvatica*. Ann. Bot. **37**: 147—150.

Eichler, A. W. (1878): Blüthendiagramme, 2. Theil. Leipzig.

Fey, B. S. (1981): Untersuchungen über Bau und Ontogenese der Cupula, Infloreszenzen und Blüten sowie zur Embryologie bei Vertretern der *Fagaceae* und ihre Bedeutung für die Systematik. Diss. Univ. Zürich.

Forman, L. L. (1964): *Trigonobalanus*, a new genus of *Fagaceae*, with notes on the classification of the family. Kew Bull. **17**: 381—396.

— (1966): On the evolution of cupules in the *Fagaceae*. Kew Bull. **18**: 385—419.

Hjelmqvist, H. (1948): Studies on the floral morphology and phylogeny of the *Amentiferae*. Bot. Not., Suppl., **2**, 1.

Kaul, R. B., & Kaul, M. N. (1981): Homologies between staminate and pistillate inflorescences in the *Fagaceae*. XIII. Int. Bot. Congress, Sydney, Abstr. 283.

Langdon, L. M. (1947): The comparative morphology of the *Fagaceae*. I. The genus *Nothofagus*. Bot. Gaz. **108**: 350—371.

Lendner, A. (1916): Sur la cupule des Fagacées. Bull. Soc. Bot. Genève, Sér. 2, **8**: 161—166.

Macdonald, A. D. (1979a): Development of the female flower and gynecandrous partial inflorescence of *Myrica californica*. Can. J. Bot. **57**: 141—151.

— (1979b): Inception of the cupule of *Quercus macrocarpa* and *Fagus grandifolia*. Can. J. Bot. **57**: 1777—1782.

— (1980): Organogenesis of the female reproductive structure of *Myrica pensylvanica*. Can. J. Bot. **58**: 2001—2006.

Maout, E. le (1844): Leçons élémentaires de Botanique, 2. Paris.

Palibin, J. V. (1909): Sur la cupule des *Fagus*. Bull. Soc. Bot. Genève **1**: 359.

— (1935): Sur la morphologie florale des Fagacées. Izv. Akad. Nauk SSSR, Otd. Mat. Nauk **1935**: 349—381.

Payer, J.-B. (1857): Eléments de Botanique. Paris.

Prantl, K. (1887): Beiträge zur Kenntnis der Cupuliferen. Bot. Jahrb. Syst. **8**: 321—336.

Puri, V., & Agarwal, R. M. (1976): On accessory floral organs. J. Ind. Bot. Soc. **56**: 95—114.

Raud, G. (1961): Etude morphologique et anatomique de la bogue du châtaignier. Bull. Soc. Bot. France **108**: 130—158.

Reece, P. C. (1938): Morphology of the flowers and inflorescences of the *Fagaceae*. Ph.D. Thesis, Cornell University.

Sattler, R. (1973): Organogenesis of flowers. Toronto.

Schacht, H. (1856): Lehrbuch der Anatomie und Physiologie der Gewächse, 2. Berlin.

Soepadmo, E. (1968): A revision of the genus *Quercus* L. subgen. *Cyclobalanopsis* (Oersted) Schneider in Malesia. Gardens' Bull. Singapore **22**: 355—427.

Steenis, C. G. G. J. van (1953): Results of the Archbold Expeditions: Papuan *Nothofagus*. J. Arnold Arboret. **34**: 301—374.

Tognini, F. (1894): Ricerche di morphologia ed anatomia sul fiore feminile e sul frutto del Castagno (*Castanea vesca* Gaertn.). Atti Ist. Bot. Univ. Pavia II, **3**: 1—35.

Troll, W. (1926): Über die weiblichen Partialinfloreszenzen von *Pasania* Miq. und *Quercus* L. Ber. Deutsch. Bot. Ges. **44**: 290—295.

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