

Female reproductive structures in Taxales

THOMAS STÜTZEL and IRIS RÖWEKAMP

Lehrstuhl Spezielle Botanik, Fakultät für Biologie, Ruhr-Universität Bochum, Postfach 102148, 44780 Bochum 1

Accepted: February 2, 1998

Summary

The morphology and ontogeny of female reproductive shoots were studied in *Torreya californica* TORR., *Torreya nucifera* (L.) SIEB. et ZUCC. and *Taxus baccata* L. It could be shown that the branching pattern of *Torreya nucifera* is in several aspects intermediate to *Torreya californica* and *Taxus baccata*. The generally assumed and never questioned homology of the biovulate axilar shoots in *Torreya* with the brachyblasts of *Taxus* is now doubted and replaced by an alternative interpretation. In this concept the basic branching unit in both spp. of *Torreya* is the same. From important similarities to *Taxus* it is concluded that the ovule bearing brachyblast in *Taxus baccata* has basically the same branching pattern as fertile annual growth units in *Torreya*. This means that the fertile brachyblasts of *Taxus baccata* are composed of three shoot generations with the arillate seed terminating a lateral axis of third order, while hitherto a position terminal to a lateral axis of second order has been assumed. If the homology of the female reproductive structures is accepted as given here, it will be no longer possible to separate Cephalotaxaceae from Taxaceae on the family level. There unification in a single family may have further consequences for gymnosperm taxonomy.

Key words: Gymnosperms, reproductive biology, *Taxus*, *Torreya*, floral structure

Introduction

The morphology of the reproductive brachyblasts in *Taxus* is very difficult. The descriptions in recent papers and textbooks are mostly based on STRASBURGER (1872) and SCHUMANN (1902). Both did careful and clear morphological and even morphogenetical studies in *Taxus*. HIRMER (1936) gives a detailed analysis of *Torreya* and *Taxus*, but he as well as EICHLER (1889) and all later workers based their interpretation on the never questioned a priori homology of the two- to three-ovulate lateral branchlets („Blühspresse“) of *Torreya* and the fertile brachyblasts of *Taxus* and ignored the position of the reproductive structures within an annual growth unit¹. Thus the female reproductive structures seemed to be very simple and COULTER & CHAMBERLAIN (1917) write: “A general feature of Taxaceae ... is the occur-

rence of very simple strobili, containing usually one ovule, and borne in the axils of leaves of young shoots.” SAHNI (1920) and later FLORIN (1948) stated that taxads lack inflorescences in the female sex and largely on this character FLORIN separates taxads from conifers (Pinales) in his order Taxales. Many taxonomists have adopted these arguments and conclusions, e.g. EHRENDORFER (1991). In the last edition of Englers' Syllabus der Pflanzenfamilien, MELCHIOR (1954) writes: “Die Taxales stellen einen selbständigen Stamm dar. Schon die Gattung *Palaeotaxus* aus der Obertrias hat Blüten mit spiraligen, sterilen Schuppenblättern und einzelnen terminalen Samen, so daß eine Ableitung von einem zapfentragenden Typus mit axillären Samenschuppen nicht zu denken ist.” More recent descriptions of reproductive shoots in *Taxus* are often misleading, ambiguous, or even wrong in important points (e.g. PAGE 1990, p. 348–353), what easily turns out if one tries to construct diagrams or axial schemes from these descriptions. We tried therefore to reinvestigate the “cones” of female *Taxus* plants and to do a comparison with the reproductive branches of female plants of *Torreya californica* and *Torreya nucifera*. This should give some new insights not only in the morphology of these structures, but also in the evolutionary pathways towards

¹ We use the term “annual growth unit” instead of the term “seasonal growth unit” as defined by BRIGGS & JOHNSON (1979). The annual growth units as described here are formed within one year, but comprise two growing seasons. Towards the end of the first season, the bud with all leaves and ovules is initiated, and after a resting period (winter) it comes into its functional phase in the second year.

these structures (character evolution or character state evolution) and towards the taxa (evolution or phylogeny of the taxa).

Materials and methods

Torreya californica TORR., *Torreya nucifera* (L.) SIEB. et ZUCC. and *Taxus baccata* L. were studied during one year continuously in the Botanic Garden of the Ruhr-University of Bochum. In *Taxus* we used several different cultivars which did not show significant differences in those characters, being of interest here. Ramification patterns were analysed in situ as far as possible and documented in diagrams and axial schemes. Special attention was drawn to the position of the reproductive branches in the whole branching system. Reproductive shoots were fixed in FAA and dissected under a stereo microscope. Where necessary additional studies were done by SEM using the critical point drying technique as described by GERSTERBERGER & LEINS 1978.

Results

Torreya californica

The single female plant of *Torreya californica* at the Botanic Garden of the Ruhr-University is about 3 m high and has the habit of a medium sized shrub. The species is generally described as shrub or small tree, but the Botanic Garden of the University of Bonn has a male tree which is about 30 m high and has a trunk of about 45 cm in diameter. The tree has the habit of a well grown *Abies nordmanniana*. The reduced size which is described from natural habits may be the result of the unfavourable conditions of its relict areal.

In spring "flowering"² branches (Figs. 1a, 2a, 4 "spring year x") rise from the terminal bud of a branch from the previous year (Fig. 4 year x-1). Additional flowering branches rise from the axils of mostly two lateral buds, which are formed in the axils of the last or last but two green foliage leaves of the previous season. The ultimate green leaves are reduced in size and thus form intermediates towards the bud scales of the terminal bud. In well growing branches even the last four foliage leaves may bear lateral shoots, but in this case at least the terminal and often also one or more of the distal lateral shoots remain sterile.

The flowering shoot starts with six pairs of decussate brownish bud scales (cataphylls), the basal ones being

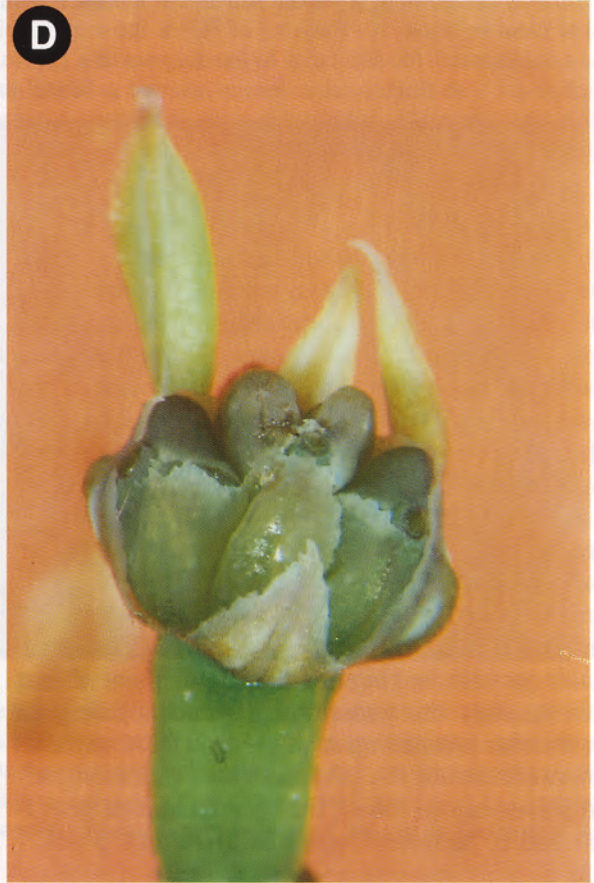
the smallest and the distal the largest ones (Fig. 2a). These cataphylls remain always sterile, branching from their axils has never been observed. Then one to three pairs of fertile leaves follow (pherophylls; term introduced by BRIGGS & JOHNSON 1979, equivalent to the German "Tragblatt") and a terminal bud of 7–15 pairs of opposite leaves. The lowermost two pherophylls may be occasional intermediate in morphology between the largest cataphylls and foliage leaves and then are shorter and have a thin translucent distal margin. The terminal bud has started opening at anthesis, the leaves are still green and the outermost ones have reached about one third of the final length (Fig. 1a). Beginning from the fertile leaves the phyllotaxis changes from decussate to a rather strange pattern, which is called "bijugate" by TOMLINSON & ZACHARIAS (1996, abstract). There are still opposite leaf pairs, but both members of a pair are not initiated exactly at the same time, one appears slightly earlier. It is more obvious that consecutive pairs are not inserted at right angles according to the alternancy rule, but twisted in a way that the phyllotaxis looks alternate at a first glance (Fig. 3b) due to the twining parastiches. To facilitate orientation, the bijugate phyllotaxis is represented as decussate in the diagrams!

The ovuliferous lateral branches start with two transversal scales or prophylls (German "Vorblätter"). After the formation of two more leaves in decussate position, the branch is terminated by an unitegmic ovule. The aril forms at anthesis a small ring wall, which is only visible after removing the scale-like leaves (Fig. 3e). The two prophylls are also fertile. From their axils rise shoots, which also form two prophylls and two further scales and then terminate in an ovule. So any of the three ovules is preceded on the same axis by four leaves in two decussate pairs.

This pattern represents the basic bauplan (Fig. 2c and Fig. 2a lowermost lateral branches). Ramifications of higher degree have never been observed, but several variations, which are mostly reductions of the full pattern. The only case, where an extension of the basic pattern could be found is shown in Fig. 2d. The median ovule is surrounded by three leaves instead of two.

Fig. 1. A – reproductive long-shoots of *Torreya californica* at "anthesis" with pollination droplets exposed; B – reproductive brachyblast of *Taxus baccata* with pollination droplet exposed; C – vegetative long-shoot of *Torreya nucifera* from the lower side with several lateral fertile brachyblasts about two months after anthesis, the terminal vegetative bud remains exceptionally dormant and the brachyblast in the uppermost position on the right forms a few reduced leaves from its terminal bud; D – fertile brachyblast of *Torreya nucifera* at the same time as in Fig. c, some of the pherophylls intermediate between cataphylls and foliage leaves.

² The terms "flowering" and "anthesis" are strictly speaking not applicable to gymnosperms. They are used here for the period where the pollination drop is exposed and effective pollination is possible.



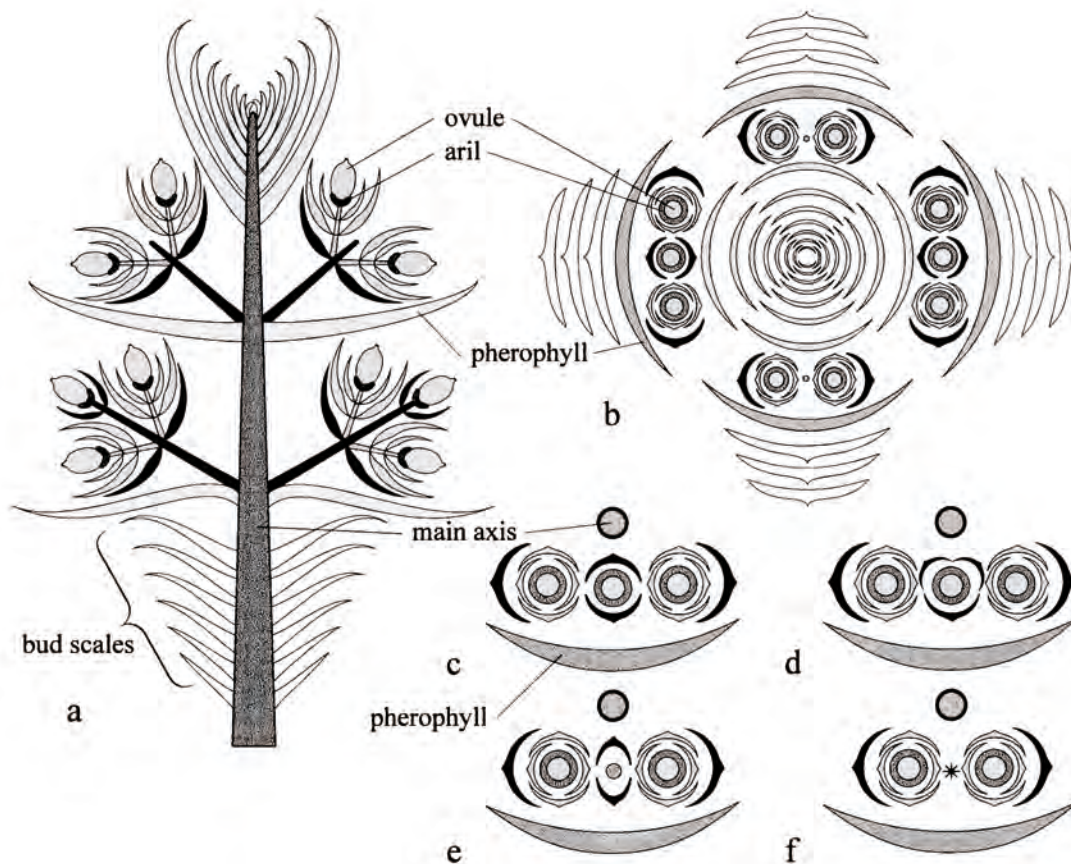


Fig. 2. *Torreya californica*; a – axial scheme of a branch with two pairs of fertile leaves, lateral axis of first order and leaves inserted at them in black; b – diagram of Fig. a, the torsion (bijugate arrangement) of the young foliage leaves in the terminal bud is not represented, the similarity to the diagram of a *Cephalotaxus* cone given by HIRMER (1936 p. 80) is striking; c – cyme like brachyblast with three ovules, leaves inserted at lateral axis of first order in black; d – like Fig. c, but showing the rare situation with three scales around the ovule in median position; e – the common case with the median ovule lacking but its preceding two scales still present; f – median ovule as well as its surrounding scales lacking.

Whenever three leaves surrounding the median ovule have been found, two have been in adaxial position and a single one in abaxial position. This indicates that the formation of these three leaves starts with primordium directed to the main axis. The presence of a third, unpaired scale indicates that the shift from the curious bijugate phyllotaxis to an alternate phyllotaxis might be a minor step. Three leaves and no ovule or more than three leaves never have been observed.

More common are branchlets, where the median ovule and its surrounding two leaves are reduced. It is very common that only the two scales are formed and the median ovule is aborted (Figs. 2e, 3d). Often these two scales are also lacking and the lateral shoot of first order forms only the two prophylls each bearing an ovule with four preceding scales (Fig. 2f). At anthesis often no rudiments of the median ovule or its surrounding two leaves can be found, the apex cannot be detected at all and is “ablasted” sensu EICHLER (1875 vol. 1 p. 52).

The ontogeny of the fertile long-shoot starts in summer with the formation of the bud scales. The primordia of the foliage leaves are formed in September. Counts of the number of leaves in the bud in autumn and early spring and a comparison with the number of green leaves of preceding annual growth units showed about the same variation. It is therefore most likely that all leaves are still present in the overwintering bud and no new leaves are formed during the year before the new bud is initiated. The top view of the bud (Fig. 3b) with all but two cataphylls removed clearly shows the “bijugate” arrangement of the leaves. A lateral view (Fig. 3a) shows in the axils of basal leaves the primordia of the lateral branches, which will form later two to three ovules each (arrow). At this time the first two leaf primordia are still formed (Fig. 3c). The shoot apex is compressed in median direction and somewhat enlarged in lateral direction. So its shape is rather from the circular or elliptical form of typical shoot apex and resembles early stages of the ovuliferous scales in some Pinaceae.

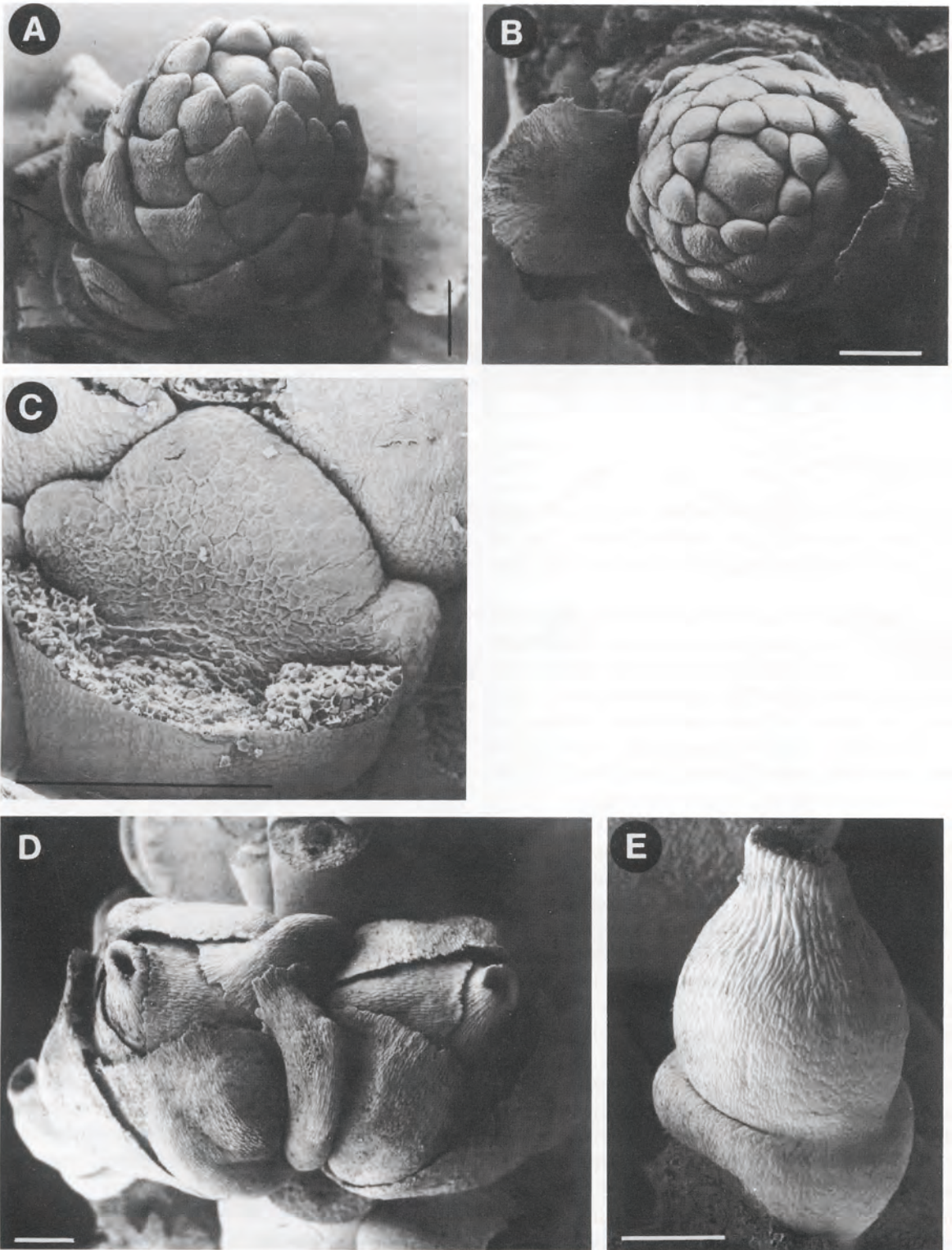


Fig. 3. *Torreya californica*; lateral view of a terminal bud in late November, in the lowermost leaf axils the flattened primordia of the branches like in Figs. 2 c–f can be seen; B – top view of a bud in the same stage showing the “bijugate” phyllotaxis with two leaves opposite, but the next pair appears not at right angle to the first, and both leaves of a pair not appearing exactly at the same time; C – extremely flattened axilar shoot primordium which will develop to a system like Figs. 2 c–f; D – long-shoot at anthesis, in front lateral shoot with the structure of Fig. 2e; E – ovule with basal primordium of the aril at the time of anthesis. Scale bar = 300 μ m.

The tip of the apex is shifted slightly to the right side, what seems to reflect the position of the gap between the next leaves in distal direction.

In the Botanic Garden of the Ruhr-University, only a few ovules continue their development. In the first year, they grow only a few mm and only in the second year after pollination an arillate seed of about 2,5 cm is formed. How and why these seeds are formed is still unclear, because the male plant was in anthesis several weeks later than the female, and there was no overlap during the observation period. It is rather sure that there are no other *Torreya* trees in the region and pollination seems therefore impossible. Up to now we did not find an embryo in the seeds.

Torreya nucifera

The plant in the Botanic Garden of the Ruhr-University are small trees about 4 m high. But the Botanic Garden of the University of Bonn has of this species also trees of about 30 m.

Torreya nucifera shows a similar ramification pattern as *Torreya californica*. But the shoot which raises from the terminal bud generally remains sterile as well as the lateral shoots in the axils of the uppermost leaves. Only in the axils of leaves below, reproductive shoots are formed. These differ from the three sterile shoots at the end of the branch in forming normally no foliage leaves. At anthesis the terminal bud of the reproductive shoots remains completely closed (Fig. 1 d) and later only occasionally a few green leaves are formed. These are markedly smaller and always reach only about half the length of leaves of vegetative shoots. The apex of such a proliferating brachyblast forms either only a very small overwintering bud or the apex degenerates in the same year. Vegetative branching from a brachyblast seems not to occur. If some reduced leaves and an overwintering terminal bud are formed, from this bud only reduced leaves rise and never normal sized leaves like on long-shoots. The growth of the reproductive shoots is therefore limited. *Torreya nucifera* often forms four to eight fertile brachyblast in the distal region of one year old branches (Fig. 4, year x-1). It is important to note that the fertile brachyblasts are not inserted in the axils of consecutive leaves, but some leaves remain sterile between those bearing the fertile brachyblasts (Figs. 1 c, d). In basal parts of the plant and in the inner part of the crown, it often occurs that all overwintering buds give rise to reproductive brachyblasts, including the three at the distal end, which are drawn as vegetative in Fig. 4. In badly growing parts it may even happen that only the terminal bud is formed and produces a brachyblast. In these cases a continuation of the branching system from

such branches does not take place. On the other hand well growing branches in the distal part may form in terminal and lateral position only vegetative long-shoots. Terminal brachyblasts combined with lateral shoots do not occur.

The development of the seeds takes also two years. As the continuation shoot is a sterile long-shoot, flowering brachyblasts are found only in the distal part of long-shoots of year x-1. In long shoots of year x-2 the seeds are still small, and only lateral brachyblasts of long-shoots of year x-3 bear enlarged ripe seeds which reach the same size as in *Torreya californica*.

Taxus baccata

Despite the fact that large *Taxus* trees are rare today, for this taxon it is well known that it may form trees. The ovuliferous brachyblasts are formed in the leaf axils of one year old shoots. Their position in the branching system is therefore the same as in *Torreya nucifera*. Like in *Torreya* vegetative continuation takes only place from the terminal bud of the long-shoot and the axils of adjacent leaves. Further vegetative long-shoots are easily formed in any leaf axil which has not formed a fertile brachyblast if the terminal shoots or buds are removed. Occasionally buds of vegetative brachyblasts occur intermixed with buds of vegetative long-shoots. Long-shoot buds may form green foliage leaves without an intercalated resting period what makes *Taxus* a good plant for trimmed hedges. While in *Torreya* the fertile brachyblasts are restricted to the distal part of the annual growth unit, they are distributed more equally over the whole length of it in *Taxus*. The fertile brachyblasts are mostly concentrated on long-shoots of the previous year. Occasionally a few brachyblasts may be found also on two years old long-shoots and even more rare on older long-shoots.

The rather large pollination droplets are formed in spring (Fig. 1 b). The ovule is surrounded by a number of scales and at a first glance, the ovule seems to terminate an unbranched brachyblast. This brachyblast starts with a number of bud scales, the first two being in transversal position as prophylls in gymnosperms and dicotyledons generally are. The following scales change their phyllotaxis more or less rapidly from the 180° divergence to the spiral arrangement with about 137° divergence (Fig. 6 a) and are more or less lanceolate. The ovule is surrounded by always three pairs of decussate leaves which are much larger than the bud scales, overlapping a little bit with their margins and are broadly obovate to obtuse. Below the ovule and its surrounding three leaf-pairs a small apex with two to four leaves can be found. In September the buds of female brachyblasts

Torreya californica

Torreya nucifera

Taxus baccata

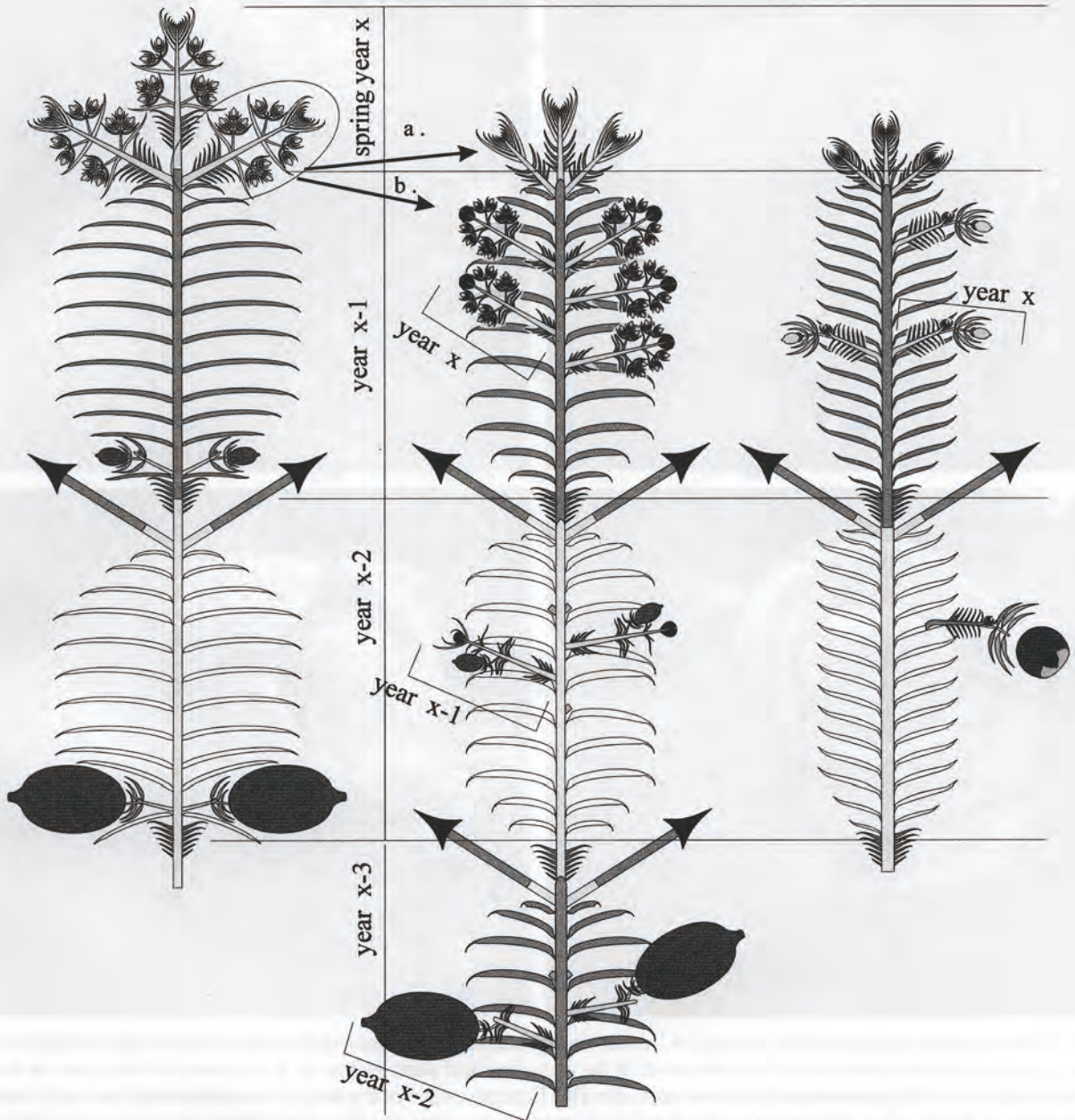


Fig. 4. Ramification patterns and correlations in shoot morphology between *Torreya californica*, *Torreya nucifera* and *Taxus baccata*. All schemes representing the situation at anthesis of the youngest fertile shoots. In *Taxus*, the arillate seeds have still been dispersed and the brachyblasts mostly fallen off in spring and are therefore drawn as separate units.

still show the three decussate leaf-pairs and the primordium of the ovule shortly before the initiation of the integument (Fig. 5a). Outside the three decussate leaf pairs in the gap between one leaf of the outermost and one of the second pair an apex with two leaves can be seen (lower left corner in Fig. 5a). The first leaf of this apex is addorsed to the ovule and its surrounding leaves. The position of this leaf is variable in different buds, so it is

more lateral in Fig. 5b. As lateral shoots always should start with prophylls in transversal position, it is very unlikely that this small apex is lateral to an axis terminated by the ovule. Furthermore, there are no transitions between the relatively thick and fleshy decussate leaf pairs and the spirally arranged thin scales preceding them. The margin of one of these thin scales can be seen in Fig. 5a behind the small apex. Since STRASBURGER

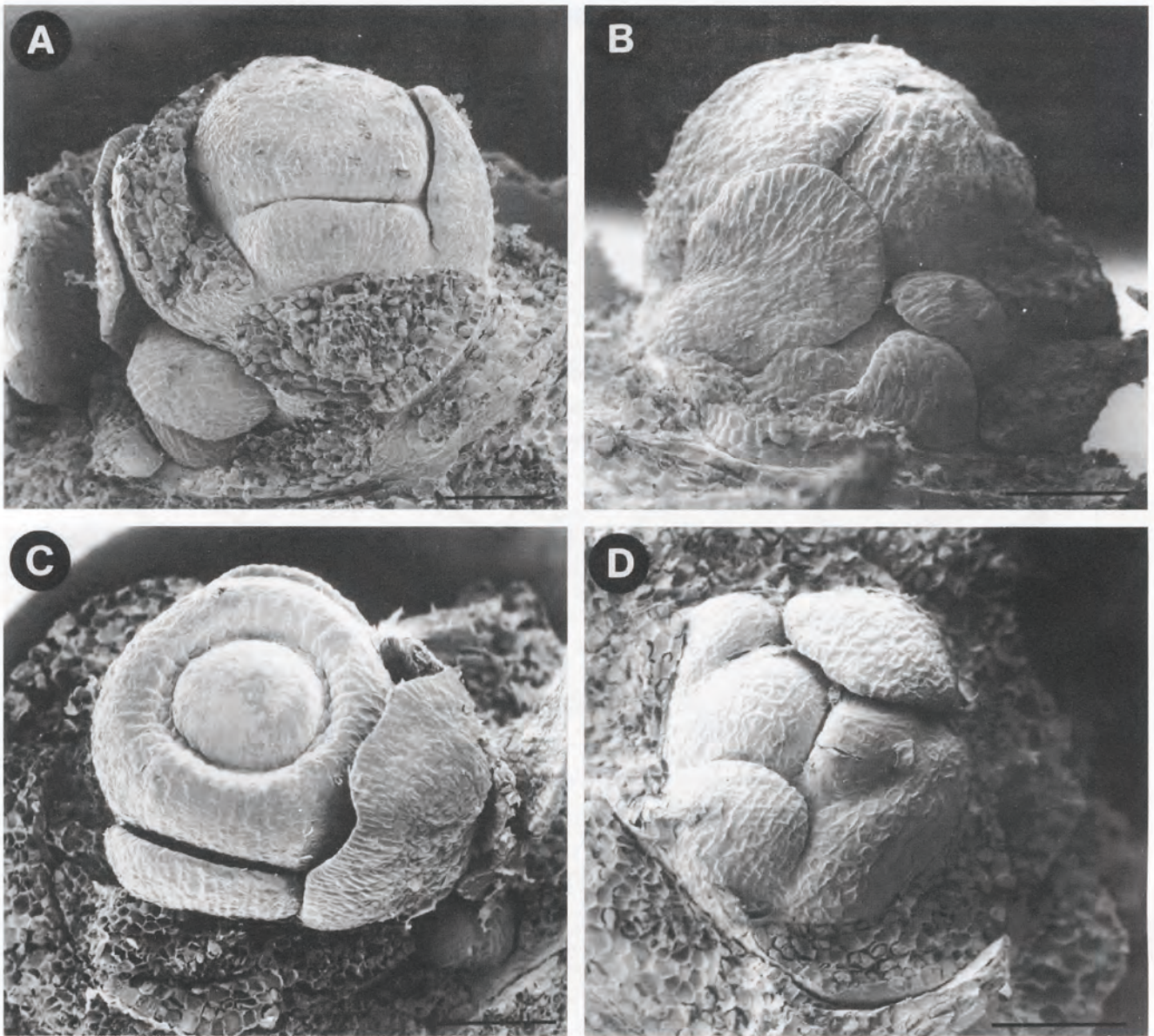


Fig. 5. *Taxus baccata*, brachyblasts in autumn; A – ovule shortly before the initiation of the integument, on the left side one leaf of the second pair and in front one of the outermost of the decussate leaf pairs removed, in the lower left the apex of the first order axis of the brachyblast with two leaf primordia; B – like Fig. a but none of the six leaves surrounding the ovule removed, the distal part of the first leaf of the apex terminating the main axis is distorted and seems to belong to the axis terminated by the ovule; C – ovule in a stage about three weeks older than in Fig. a showing the formation of the integument, D – first stage of the formation of the lateral shoot bearing the ovule, the lateral apex is at this stage smaller than the apex of the main axis (left hand). Scale bar = 100 μ m.

(1872) the small apex is therefore regarded as the apex of the brachyblast and the ovule together with its three pairs of decussate leaves as a single, unbranched lateral axis of second order. The development of the seeds takes only one summer and ripe seeds are shed in autumn of the same year as they were pollinated and about 12 months after the initiation of the ovule.

Discussion

In most details, our results confirm those of earlier workers. Only the diagram of *Torreya californica* given by HIRMER (1936 p. 85) could not be supported. Two pairs of decussate leaves surrounding a sterile terminal axis between the two lateral ovules never could be found. We

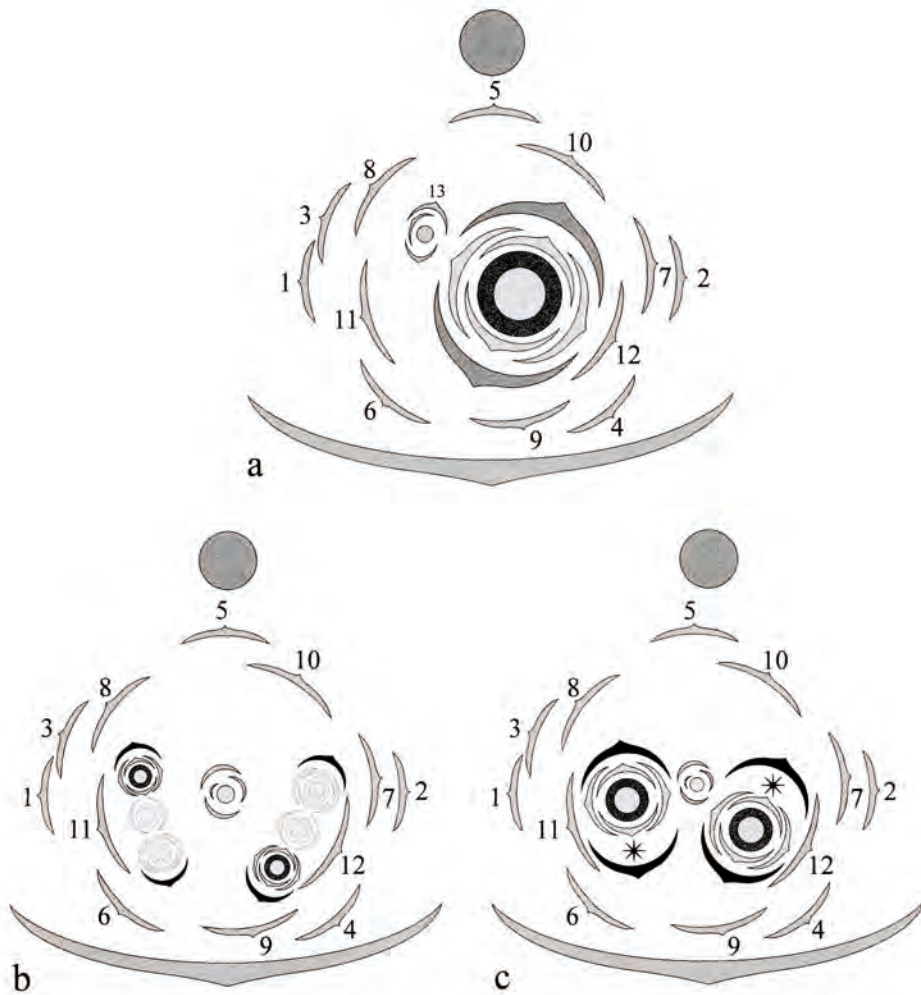


Fig. 6. *Taxus baccata*; a – empirical diagram, after a variable number of scales follow the ovule surrounded by always three pairs of exactly decussate leaves and a small apex which does not develop further; the rules of phyllotaxis suggest that the ovule is lateral and the small apex is terminal to the axillary brachyblast; b – theoretical diagram based on the comparison with *Torreya*, all parts which are lacking in comparison to *Torreya* with dotted outline and bright grey; c – like Fig. b, the ablasted apex marked by an asterisk, the leaves formed by this apex drawn in black.

believe that the two additional leaves have not been reported, but have been added to explain that the apex from which they originate is a normal vegetative apex, and to support the homology with a conifer strobilus. The important difference between the interpretation given in Fig. 4 and the interpretation of all earlier workers is that we do not compare the three-ovulate lateral branch of *Torreya californica* with the fertile brachyblast of *Taxus*, but the fertile long-shoot of *Torreya californica*. While none of the earlier workers gave any argument for the traditional homologisation, we have three important arguments on which our homologisation is based:

1. The three- or two-ovulate branchlets of both species of *Torreya* branch directly from the prophylls. In *Taxus*

a number of always sterile cataphylls follows the always sterile prophylls as it is the case in fertile long-shoots of *Torreya californica*, the fertile brachyblasts of *Torreya nucifera* and in all vegetative shoots of all Taxaceae.

2. Previous workers state that the ovule in *Taxus* is always preceded by three pairs of decussate leaves, but they cannot explain why always three pairs occur and never more or less. In our concept, the unit formed by the three pairs of leaves and the ovule in *Taxus* are homologous to the three ovulate lateral branch of *Torreya*. The only difference to *Torreya* is that terminal as well as one lateral ovule are aborted (Fig. 6b). This implies that the three pairs of leaves belong to two different shoot generations. The outermost two are homologous to the fertile prophylls in the three ovulate

branchlets in *Torreya*, but in *Taxus* only one of them is fertile bearing a lateral branchlet with two decussate pairs of leaves as in *Torreya*, the other prophyll being sterile.

3. If this way of homologisation is accepted, the position of the reproductive shoots within the branching system will be very similar in all Taxaceae. *Torreya californica*, *Torreya nucifera* und *Taxus baccata* form a transition series with *Torreya nucifera* being intermediate between the other two species in several aspects. *Torreya californica* shows the most simple branching pattern with long-shoots bearing at their base ovuliferous brachyblasts of a very fixed structure. *Torreya nucifera* shows a higher degree of shoot differentiation. Those shoots, which occur in *T. californica* as reproductive long-shoots are in *T. nucifera* always sterile long-shoots (arrow a in Fig. 4). More basal shoots of the same ramification pattern as the long-shoots in *T. californica* occur as lateral brachyblasts (arrow b in Fig. 4). Therefore the fertile brachyblasts in both species of *Torreya* are not homologous. The branching pattern of *Taxus baccata* is basically the same as in *Torreya nucifera*. Especially the position of the fertile brachyblasts is very similar to *Torreya nucifera* and we therefore believe that the brachyblasts of *Torreya nucifera* are homologous to the brachyblasts of *Taxus baccata* and not to the brachyblasts of *Torreya californica*.

In our concept, the three ovulate units in *Torreya* are regarded as a very fixed unit. Any ovule is preceded by exactly two pairs of leaves. If the ovule and two surrounding bracts are regarded as a fixed unit, the branching pattern of the ovuliferous brachyblast will be the same as in cymes in flowering plants. In Angiosperms besides real cymes, cyme-like structures with inflorescences instead of flowers occur e.g. in Asteraceae and Euphorbiaceae. This indicates, the exclusive branching from prophylls may be a primitive character. The high emphasis we put in this character to discard the homology of the three ovulate branchlets in *Torreya* with the fertile brachyblasts of *Taxus* seems therefore well justified.

Earlier workers have regarded the occurrence of a third ovule in the lateral units of *Torreya californica* as abnormal with the argument that a strobilus is generally not terminated by an ovule. We do not homologize these units with a strobilus but the whole shoot on which they are inserted. For us the frequent occurrence of the median ovule is therefore normal and fulfils the complete bauplan, while two ovulate units are regarded as reductions.

Both species of *Torreya* show intermediate forms in shoot architecture and branching patterns, which to our mind clearly show that the correlations really are as described here. These intermediates are sterile shoots in distal position in *T. californica* and late development of

foliage leaves from the terminal bud in some of the brachyblasts in *T. nucifera*. On the other hand the fertile brachyblasts in *T. californica* branch from the axils of the prophylls, while it forms a number of sterile cataphylls in *T. nucifera* first. This excludes a direct homology of the brachyblast in *T. californica* and *T. nucifera* and supports the homologisation presented here. The observed variability in the position of the fertile brachyblasts in *Torreya nucifera* is relatively high and the case represented in Fig. 4 is only one of several. But it must be stated that the female plants in the Botanic Garden of the Ruhr-University are far from the habit of well grown trees. If we would have such trees, the study probably would concentrate on lower branches which are easy to reach. Studies in natural sites with focus on the zone where most flowers and seeds are formed are needed to get more detailed insights in the typical architecture of *Torreya*. Nevertheless we feel that our data are sound enough to support the interpretation given here.

According to our concept, the structure of the brachyblasts of *Taxus* becomes even more complicated than it still was. Like in *Torreya nucifera*, the brachyblast starts in *Taxus* with a number of cataphylls, but the terminal bud not only generally but always stops further development after the formation of the reproductive lateral branches. Even if the homologisation of the whole brachyblast of *Torreya nucifera* with the whole brachyblast of *Taxus* is accepted, two different possibilities for the homologisation of the ovuliferous lateral branches with its three pairs of preceding leaves are existing. This becomes clear when analysing which parts of the basal, cyme-like unit of *Torreya* have to be maintained and which ones have to be omitted to reach a situation similar to *Taxus baccata*. Starting with a structure like Fig. 2a it is possible to omit both lateral ovules and their preceding two decussate leaf pairs. The other possibility is to omit the terminal ovule including its single pair of preceding leaves and one of the lateral ovules with both preceding leaf pairs. The latter alternative seems to be the better one because of two reasons. First, the terminal ovule is often lacking in *Torreya*. Often no remnants of the apex between the two lateral ovules can be found at all. It is known from *Fedia* (Valerianaceae) that an apex can disappear completely morphologically and ontogenetically. This may occur only, if lateral branches are formed in the axils of the uppermost leaves without being separated from the main apex by any leaves (PHILIPSON 1947, WEBERLING 1961). This precondition is always fulfilled in *Torreya*, because the primordia of the leaves preceding the median ovule are inserted at right angle to the prophylls and therefore never separate the terminal apex from the lateral ones. It can therefore easily happen that the meristematic tissue of the median apex even together with first leaf primordia is incorporated into the lateral

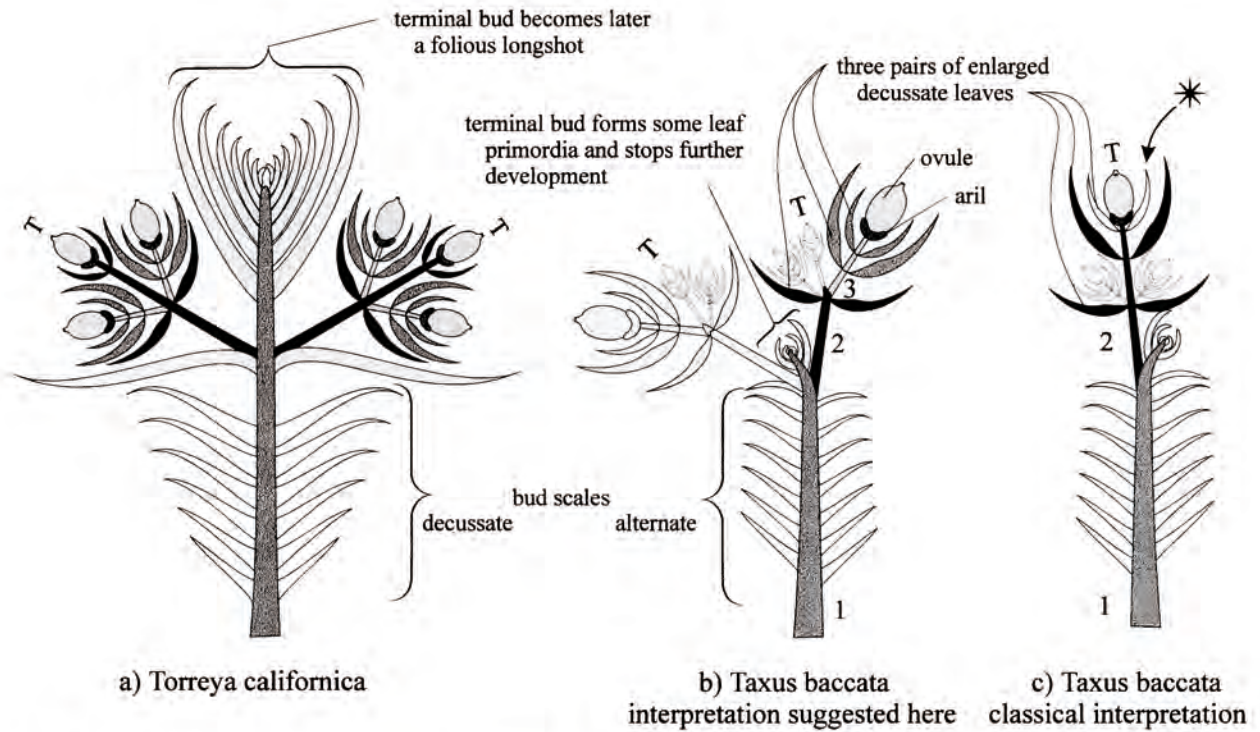


Fig. 7. Axial schemes for *Torreya* and the two interpretations for *Taxus baccata*.

apical meristems. In no case the terminal ovule was present and both or one of the lateral ones were lacking in *Torreya*. It is therefore easier, to assume that the ovule which generally lacks in *Torreya* always lacks in *Taxus* and in addition one of the two, which are always present in *Torreya* instead of assuming that the single ovule remaining in *Taxus* is the first to be reduced in *Torreya*. Second, three pairs decussate leaves are required for *Taxus*. If both lateral ovules were omitted, the remaining terminal ovule would be preceded by only two decussate pairs (black in Fig. 2c). To fulfil the *Taxus* bauplan, a third pair of leaves would have to be inserted, which has no equivalent in *Torreya* (Fig. 7c, marked with asterisk). If a lateral ovule is assumed, the outermost pair represents the prophylls of the cyme-like structure (black in Fig. 6b). The terminal apex is "ablasted"³ as it is often the case in *Torreya*, and in the axil of one prophyll a lateral shoot bearing two leaf pairs and the ovule is formed (grey in Fig. 6b, the "ablasted"

ovules and leaves with dotted outline; in 6c the "ablasted" apex marked by an asterisk). If this case is assumed for *Taxus*, all three leaf pairs will have their equivalent in *Torreya*, but they will belong to two different branches. In a brachyblast in *Taxus* bearing two ovules, each ovule has three preceding pairs of leaves and both arise from the axils of different cataphylls, the aborting apex with its few leaf primordia more or less between them (Fig. 6c; 7b, uniformly grey branch left hand). Our interpretation is in full congruence with the occurrence of even three ovules on a brachyblast as reported and presented in a diagram by HIRMER (1936 p. 85). The branching of a brachyblast from three (or two) of the middle cataphylls as described and drawn by PILGER (1926 p. 203 Fig. d) has obviously never been described anywhere else neither earlier nor later and seems doubtful to us mainly because the position within the branching system remains unclear. We could imagine this pattern only, if the terminal bud of a vegetative shoot would have been transformed to a fertile brachyblast, which is usually not the case.

The transition series from *Torreya californica* to *Taxus baccata* as presented here, implies that proliferating cones are the plesiomorphic condition and typical conifer cones the derived situation. This is in conflict to the classical approach, but recent studies (SCHWEITZER

³ The term is used by EICHLER (1875) for structures, which have dissapeared completely during the phylogeny, they are expected from comparative studies, but cannot be detected by ontogenetic studies while aborted structures are formed in early morphogenesis and do not undergo further development.

1996) show, that proliferating cones are very frequent in fossil material. SCHWEITZER therefore suggests, that proliferating cones may be the primitive condition (SCHWEITZER, pers. communication). It may be, that the classical approach was not mainly supported by any concepts for character state evolution or by outgroup comparisons, but mainly influenced by the fact that the better known and common situation is the non proliferating cone of Pinaceae.

In none of the species under study we could find a structure, which could be interpreted without difficulties as a sporophyll. The ovules are initiated terminal on lateral axis of different order and due to the fact that the ultimate leaves preceding the ovule are always exactly decussate, the ovule cannot be regarded as closer attached to one of them. It may be still too early to discuss this old problem anew, but it may be stated that in recent gymnosperms undoubtedly macrosporophylls are only reported for Cycads.

Conclusions

From a comparative study of the reproductive shoots of *Torreya californica*, *Torreya nucifera* and *Taxus baccata* it is concluded that the fertile brachyblasts of *Taxus* are formed of three instead of only two shoot generations. For this result, it was essential to take the position of the reproductive shoots within the whole branching system into consideration as emphasized for angiosperms many times by TROLL (1964) and WEBERLING (1983). The homologisations suggested here are completely different from the classical concept. In contrast to the classical concept, we gave explicit arguments for the basis of homologisation as used here. This does not necessarily guarantee that the interpretation as given here must be correct. Further investigations are needed to test this hypothesis. These have to include not only well grown plants from natural sites, but have to put the same emphasis in a comparison of male structures. These studies should give additional support for the concept presented here or as a minimum give no contradictions to it.

If the concept of homologisation as presented here is correct, this might have important taxonomic consequences. The significant differences in the basic structure of the female cones of *Cephalotaxus* and *Torreya* as seen in the past do not exist any more, because now the long-shoot of *Torreya californica* as a whole and not the three ovulate branchlet has to be regarded as equivalent to a strobilus. It will probably become impossible to maintain their separation in two distinct orders (FLORIN 1948) or even subclasses (EHRENDORFER 1991).

Acknowledgements

We gratefully acknowledge the help by Prof. H. SCHWEITZER. He explained us the significant changes and advances in palaeobotany and corrected several of our erroneous interpretations of recent and older papers in palaeobotany. Furthermore he gave valuable ideas how to compare conifer cones. We are grateful to the Botanic Garden of the Ruhr-University of Bochum which supplied most of the material for this study and to the Botanic Garden of the University of Bonn where we had access to very large trees of male plants of *Torreya californica* and *T. nucifera*.

References

- BRIGGS, B. & JOHNSON, L. (1979): Evolution in Myrtaceae – evidence from inflorescence structure. *Poc. Linn. Soc. New South Wales* **102**: 157–272.
- COULTER, J. M. & CHAMBERLAIN, C. J. (1917): *Morphology of Gymnosperms*. 2nd Edn., University of Chicago Press, Chicago (Reprint 1982).
- EHRENDORFER, F. (1991): Gymnospermae, Nacktsamer. In: SITTE, P., ZIEGLER, H., EHRENDORFER, F., & BRESINSKY, A.: *Lehrbuch der Botanik für Hochschulen*. Fischer, Stuttgart, 712–730.
- EICHLER, A. W. (1875): *Blüthendiagramme*. Verlag Engelmann Leipzig.
- (1889): Coniferae (Zapfenbäume oder Nadelhölzer). In: ENGLER, A. & PRANTL, K. (eds): *Die natürlichen Pflanzenfamilien II. Teil*, Leipzig, 111–113.
- FLORIN, R. (1948): On the morphology and the relationships of the Taxaceae. *Bot. Gaz.* **110**: 31–39.
- (1954): The female reproductive organs of conifers and taxads. *Biol. Rev.* **29**: 367–389.
- GERSTERBERGER, P. & LEINS, P. (1978): Rasterelektronische Untersuchungen an Blütenknospen von *Physalis philadelphica*, Solanaceae. *Anwendungen einer neuen Präparationsmethode*. *Ber. Deutsch. Bot. Ges.* **91**: 381–387.
- HIRMER (1936): *Die Blüten der Coniferen*. *Bibliotheca Botanica* **114** (1): 1–100.
- MELCHIOR, H. & WERDERMANN, E. (1954): *Englers' Syllabus der Pflanzenfamilien*. Geb. Borntraeger, Berlin.
- PAGE, C. N. (1990): Taxaceae. In: KUBITZKI, K. (ed.): *The families and genera of vascular plants*. Springer Verlag, Berlin Heidelberg New York, 348–353.
- PHILIPSON, W. R. (1947): Studies in the development of the inflorescence III. The thyrses of *Valeriana officinalis*. *Ann. Bot.* **11**: 409–416.
- PILGER, R. (1926): Coniferae. In: ENGLER, A. (ed.): *Die natürlichen Pflanzenfamilien*, 2nd ed., Bd. **13**. Reprint 1960 Duncker & Humblot, Berlin, 121–403.
- SAHNI, B. (1920): On certain archaic features in the seeds of *Taxus baccata*, with remarks on the antiquity of the Taxineae. *Ann. Bot.* **34**: 117–133.
- SCHUMANN, K. (1902): Über die weiblichen Blüten der Koniferen. *Verh. Bot. Ver. Prov. Brandenburg* **44**: 5–80.

- SCHWEITZER, H. (1996): *Voltzia hexagona* (BISCHOFF) GEINITZ aus dem mittleren Perm Westdeutschlands. *Palaeontographica B* **239**: 1–22.
- STRASBURGER, E. (1872): Die Coniferen und die Gnetaeen. Fischer, Jena.
- TOMLINSON, P. B. & ZACHARIAS, E. (1996): Phyllotaxis and phenology in *Cephalotaxus*, *Torreya* and *Amentotaxus*. *Am. J. Bot.* **86** (7): 67 (abstract).
- TROLL, W. (1964): Die Infloreszenzen. Fischer, Stuttgart.
- WEBERLING, F. (1961): Die Infloreszenzen der Valerianaceen und ihre systematische Bedeutung. *Abh. Akad. Wiss. Lit. Mainz, Nat. Wiss. Klasse Nr. 5*: 153–281.
- (1983): Fundamental features of modern inflorescence morphology. *Bothalia* **14**: 917–922.

Buchbesprechung

WISSKIRCHEN, R. & HÄUPLER, H.: **Standardliste der Farn- und Blütenpflanzen Deutschlands**. Mit Chromosomenatlas von F. ALBERS. – Herausgegeben vom Bundesamt für Naturschutz. – Verlag Eugen Ulmer: Stuttgart 1998. – 765 S., DM 148.–, ISBN 3-8001-3360-1.

Die lange erwartete umfassende Nomenklaturliste der Farn- und Blütenpflanzen Deutschlands liegt nun als kompaktes 765-seitiges Werk vor. In einleitenden Kapiteln werden die methodischen Grundlagen der Erarbeitung dieser Liste erläutert und eine Anleitung zu deren Gebrauch gegeben. Die Einleitung wird durch ein Verzeichnis der zahlreichen Mitarbeiter an der Checkliste, eine Literaturübersicht zu den einleitenden Kapiteln und Übersichten der Abkürzungen und Fachbegriffe abgeschlossen.

Den Hauptteil der Arbeit macht natürlich eine übersichtliche Darstellung der derzeit gültigen wissenschaftlichen Namen von über 4.000 Pflanzensippen Deutschlands aus. Umfangreiche, aber nicht immer vollständige Aufzählungen von Synonymen folgen, und es wird in abgekürzter Form der Gebrauch der zitierten Namen in wichtigen europäischen Standardwerken, z. B. „Flora Europaea“, „Hegi“ und „Rothmaler“, angegeben. Weiterhin werden deutsche Bezeichnungen für die Pflanzensippen genannt, bekannte Typuskollektionen zitiert und überprüfte bibliographische Angaben mit einem Stern gekennzeichnet. Die Zitate der Originalveröffentlichungen und der Autorennamen sind standardisiert. Besonders wertvoll sind zahlreiche kritische Kommentare und Bestimmungshinweise, besonders zu schwierigen Sippen. Hierbei zählt sich die enge Zusammenarbeit mit vielen Fachkollegen und Spezialisten aus. Ohne eine eigene Meinung zu komplizierten taxonomischen Problemen zu meiden, scheuen sich die Autoren aber auch nicht, offene Fragen und unbefriedigende Lösungen klar anzusprechen oder sogar, wie z. B. bei *Oenothera*, gegensätzliche Auffassungen gegenüberzustellen. So ist dieses Werk eine hervorragende Quelle, die die Vielzahl taxonomischer Probleme aufzeigt und den dringenden Forschungsbedarf auf diesem scheinbar in Mitteleuropa „beackernten“ Forschungsgebiet deutlich macht.

Die Gestaltung des Gesamtbandes, besonders aber das Layout der Artenliste, ist ausgezeichnet. Die Nutzung verschiedener Schrifttypen, die farbige Absetzung von Synonymen, Unterarten und Anmerkungen, aber auch die graue Unterlegung von Aggregaten sind sehr gelungen und tragen zur Übersichtlichkeit der Liste bei.

Ein Chromosomenatlas der Farn- und Blütenpflanzen aus Deutschland schließt den speziellen Teil ab. Diese gleichfalls

gründlich erarbeitete Zusammenstellung stellt eine wertvolle Bereicherung der „Standardliste“ dar, zeigt aber auch die großen Lücken und den entsprechenden Forschungsbedarf auf diesem Gebiet in Deutschland. Das umfangreiche Literaturverzeichnis zum speziellen Teil der Arbeit ist eine wichtige Quelle für den Einsteiger in taxonomisch-systematische Forschungen zur zentraleuropäischen Flora, um sich einen Überblick zum Bearbeitungsstand auf diesem Gebiet zu verschaffen. Den Abschluß bildet ein Gesamtregister der wissenschaftlichen Namen, in dem die anerkannten Namen fett gedruckt sind und bei Synonymen auf den jeweiligen gültigen Namen verwiesen wird.

Natürlich werden auch die Grenzen der „Standardliste“ schnell deutlich. So ist die Zahl der überprüften Originalzitate relativ gering und bezieht sich meist auf häufige, leicht zugängliche Quellen oder auf Sippen, die von Spezialisten und Monographen bearbeitet worden sind. Aber gerade die alten, schwer zugänglichen Monographien und Zeitschriften machen Probleme, und es wäre wünschenswert, hier eine größere Vollständigkeit zu haben. Natürlich ist dem Rezensenten klar, daß bei der zeitlichen und personellen Ausstattung des Projekts, welches zur Erarbeitung der „Standardliste“ führte, eine solche „Vollständigkeit“ unmöglich war. Hier wäre ein sinnvoller Ansatz für ein Nachfolgeprojekt zur „Flora Deutschlands“ gegeben, der auch Arbeiten zur weiteren, bisher ungenügenden Sippentypisierung umfassen sollte. Unverständlich bleibt, warum bei zahlreichen Synonymen bibliographische Angaben völlig fehlen, so z. B. bei *Leontodon hyoseroides* WELW. ex RCHB. (S. 288), dem Basionym von *Leontodon hispidus* ssp. *hyoseroides* (RCHB.) MURR, bei *Scirpus germanicus* (PALLA) LINDM. (S. 527) oder vielen Synonymen der *Ulmus*-Arten (S. 532). Hier bleibt dem Benutzer unklar, ob die entsprechenden Arten oder Kombinationen überhaupt gültig veröffentlicht worden sind. In anderen Fällen fehlt ein Zitat des Basionyms eines gültigen Namens völlig, z. B. bei *Picris hieracioides* ssp. *villarsii* (JORD.) NYMAN (S. 364).

Diese kritischen Anmerkungen schmälern aber den Wert dieses wichtigen Grundlagenwerkes nicht, das ohne Zweifel eine unentbehrliche Informationsquelle und Datengrundlage für alle Ämter, Organisationen und Forschungseinrichtungen in Biologie, Forst- und Landwirtschaft und Naturschutz werden wird, die mit Pflanzennamen zu tun haben. Die „Standardliste“ sollte in keiner entsprechenden Bibliothek fehlen. Der Preis ist angemessen und für hiesige Verhältnisse nicht zu hoch.

U. BRAUN, (Halle/Saale)