Evolution of taxodiaceous Cupressaceae (Coniferopsida)

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Abstract

The evolution of taxodiaceous Cupressaceae has been discussed controversially, because phylogenetic analyses using non-molecular data show major differences to molecular analyses. To solve this problem, we used non-molecular data with a high probability of homology. With these type of data, we could show for the first time in taxodiaceous Cupressaceae that phylogenetic trees of molecular and non-molecular data share the same topology. Investigation of female cone development also contributes to better understanding of morphology and anatomy in taxodiaceous Cupressaceae. Additional developmental, fossil and cone configuration data support the topology constructed by using the molecular and non-molecular data.

Introduction

Taxonomic delimitation

Taxodiaceae has to be included in Cupressaceae because, as widely accepted, Taxodiaceae (= taxodiaceous Cupressaceae) is paraphyletic in relation to Cupressaceae s.str. This is reflected in molecular (Brunsfeld et al. 1994; Gadek et al. 2000; Kusumi et al. 2000; Quinn et al. 2002) as well as in non-molecular investigations (Hart 1987; Farjon et al. 2002; Farjon 2005). *Sciadopitys verticillata* was separated from Cupressaceae s. l. due to several differences (e.g. anatomical differences in Peirce 1936; further differences summarized in Farjon 2005) and its sister-group relationship to Cupressaceae plus Taxaceae including Cephalotaxaceae (Stefanovic et al. 1998; Quinn et al. 2002).

On the basis of detailed developmental studies of female cones (Takaso and Tomlinson 1989: *Cryptomeria*; Takaso and Tomlinson 1990: *Taxodium* and *Glyptostrobus*; Takaso and Tomlinson 1992: *Metasequoia*, *Sequoia* and *Sequoiadendron*; Jagel 2001: *Athrotaxis*; Farjon and Garcia 2003: *Cunninghamia* and *Taiwania*), the following phylogenetic relationships were proposed. *Sequoia*, *Sequoiadendron* and *Metasequoia* (Sequoioideae) form a group defined by the following characters: their cones show no conspicuous ovuliferous scales, and the ovules arise on the cone scale (Takaso and Tomlinson 1992). Two other closely related genera are *Taxodium* and *Glyptostrobus*. In this group the conspicuous ovuliferous scale (= lobate protuberance) arises later in development than in *Cunninghamia*, and after pollination the conspicuous ovuliferous scale closes the cone (Takaso and Tomlinson 1990). The closest relative to *Taxodium* and *Glyptostrobus* is *Cryptomeria* because of its similar cone development (Takaso and Tomlinson 1989). *Cunninghamia* and *Taiwania* are a further pair of closely related taxa. The ovuliferous scale

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in *Cunninghamia* develops as two or three small lobes; each lobe is associated with one ovule (Farjon and Garcia 2003); even if these lobes are absent in *Taiwania*, a small ridge appears as their vestige (Farjon and Garcia 2003). In contrast to *Cunninghamia*, the ovules in *Athrotaxis* are inserted on a conspicuous cushion (= conspicuous ovuliferous scale) which develops later in their development (Jagel 2001). As expected, developmental studies in *Sciadopitys verticillata* reveal major differences to all other taxodiaceous Cupressaceae, e.g. a centrifugal initiation sequence and maturation of the ovules, or an early-developing and conspicuous ovuliferous scale (Takaso and Tomlinson 1991).

Jagel (2001) conducted a comprehensive developmental study of taxodiaceous Cupressaceae excluding *Sciadopitys* and *Taiwania*. Cone development in *Sciadopitys* had been investigated already (Takaso and Tomlinson 1991), and this genus was found to be closely related to Cupressaceae (Quinn et al. 2002). Therefore, *Sciadopitys* is suitable to serve as an outgroup. In our study, we extend the model of Jagel (2001) and relate it to the molecular phylogenetic trees of Kusumi et al. (2000).

Cone configuration

In addition to the development of the female cone, the cone configuration (number of cone scales per cone and number of ovules/pollen sacs per cone scale) constitutes another important character complex for phylogenetic investigations (Schulz and Stützel 2006). Investigations into male and female cone configuration were lacking for the taxodiaceous Cupressaceae, thus were performed in the present study.

Phylogenetic analysis

By comparing morphological, anatomical and cytological data with data from other disciplines, a hypothesis of the evolution of taxodiaceous Cupressaceae has been developed. Often the phylogenetic interpretation developed within a single discipline confirms that of another. The hypothesis concerning the direction of structural evolution in taxodiaceous Cupressaceae that had been developed over several years was recently confirmed by molecular analyses (Gadek et al. 2000; Kusumi et al. 2000; Quinn et al. 2002). However, the results of phylogenetic analyses of non-molecular data (Hart 1987; Gadek et al. 2000; Farjon et al. 2002, Farjon 2005) were contradictory; for certain taxa, e.g. *Neocallitropsis* and *Taiwania* in Gadek et al. (2000), close relations were suggested that had not been assumed from earlier morphological and molecular studies. The molecular analyses are based on single genes (e.g. *matK* and *rbcL* for Cupressaceae in Gadek et al. 2000) or on

specific parts of these genes (methodological approach e.g. in Raupach et al. 2004). Phylogenetic investigations with non-molecular data should be performed using characters with an high probability of homology (e.g. Wägele 2005). Regarding this criterion, a phylogenetic analysis and a comparison of the results of molecular and non-molecular analyses could be conducted.

Materials and methods

Cone configuration

In our study, female and male cones were collected from several trees (except for *Taiwania cryptomerioides*, of which only a single plant was available) and various positions on the trees (Table 1). Usually the cone configuration has been presented by a cone diagram (e.g. Eichler 1878). However, in taxodiaceous Cupressaceae male and female cones have a large number of cone scales; thus cone diagrams would be too complex. Formulas as introduced by Eichler (1878) to describe flowers are not suitable for gymnosperms, because there are no different organ categories such as calyx, corolla, androecium, and gynoecium but only scales with ovules or pollen sacs. However, the scales can be numbered consecutively from basal to distal, and for a given series the number of pollen sacs or ovules can be added. This leads to formulas of the following type (see also Tables 2 and 5):

$$[S_1 - S_n]^a [S_{n+1} - S_o]^{b-c} [S_{o+1} - S_p - (S_q)]^d \ldots [S_{u+1} - S_v]^e.$$

S_1–S_n are the n most basal cone scales that all have a pollen sacs/ovules, and

S_{n+1}–S_y are the following cone scales which may have b or c pollen sacs/ovules, etc.

Scales that occur in some cones and lack in others are in parentheses. The number of pollen sacs/ovules increases towards positions marked in boldface; the scales in boldface display the maximum numbers of pollen sacs/ovules; then the number decreases again. For an example, see *Taiwania cryptomerioides* in Table 2 and Fig. 1.

For each taxon, 30 male and 30 female cones were dissected; presentation of the cone formula includes only frequent configurations (see Schulz and Stützel 2006). Male and female cones in taxodiaceous Cupressaceae are more variable in numbers of cone scales per cone and of ovules per cone scale than in *Chamaecyparis*; therefore, all configurations with a minimum frequency of 13.3% (4/30) were included.

Phylogenetic analysis

Our phylogenetic tree (Fig. 4) is based on 16 characters (see "Character coding" below). Phylogenetic

Table 1. Species analysed, collecting locations (BG = botanical garden) and dates

Species	Location (date)
Sciadopitys verticillata	BGBochum (10.04.00/16.04.00/14.01.05)
Cunninghamia lanceolata	BGBochum (10.01.00/13.03.00/12.02.04/02.04.04); BGDüsseldorf (03.02.01)
Taiwania cryptomerioides	BGDüsseldorf (12.02.00/25.02.02/07.03.02/26.02.05)
Athrotaxis cupressoides	BGBonn (11.04.00/12.07.00/09.11.00/08.08.01/04.03.02/11.10.02/ 01.10.03/25.02.04); Pinetum Blijdenstein Hilversum (06.09.04)
Athrotaxis laxifolia	BGBonn (09.11.00/04.03.02/26.02.04); BGDüsseldorf (28.07.00/15.08.00); BGFreiburg (09.02.04)
Athrotaxis selaginoides	BGBonn (11.04.00/12.07.00/09.11.00/25.02.04); BGGünterstal (11.02.00)
Metasequoia glyptostroboides	BGBochum (19.01.99/01.02.99/16.02.99/12.02.04); BGFreiburg (09.02.04); MHannover (15.05.99)
Sequoia sempervirens	BGDüsseldorf (18.08.00/10.02.05); BGBochum (19.07.00/15.03.05); BGBonn (30.07.99/03.08.00); BGFreiburg (11.02.00)
Sequoiadendron giganteum	BGBochum (04.07.00/12.07.00/19.07.00/07.01.04/22.03.04); BG Dortmund (20.02.99)
Cryptomeria japonica	BGBochum (10.02.99/26.07.99/12.02.04); Castrop-Rauxel: private garden (06.02.04)
Taxodium distichum	BGBochum (28.03.99/30.04.99/10.04.04) Palmengarten Frankfurt (05.03.99)
Glyptostrobus pensilis	BGBochum (27.07.00/31.07.00/11.08.00/20.02.04); BGBonn (30.07.99/ 03.08.00/26.02.04)

Table 2. Female cone formula

Taxon	Female cone formula
Sciadopitys verticillata	$[1\text{–}2]^0$ $[3\text{–}4]^{0\text{–}1}$ $[5\text{–}6]^{2\text{–}5}$ $[7]^{3\text{–}5}$ **[8–14]**$^{5\text{–}10}$ $[15\text{–}21]^{8\text{–}6}$ $[22\text{–}24]^{7\text{–}4}$ $[25\text{–}27]^{5\text{–}4}$ $[28]^{4\text{–}2}$ $[29]^2$ $[30]^{2\text{–}1}$ $[31\text{–}32]^1$ $[33\text{–}35]^{1\text{–}0}$ $[36\text{–}40(\text{–}52)]^0$
Cunninghamia lanceolata	$[1\text{–}20]^0$ $[21\text{–}23]^{0,2}$ $[24\text{–}29]^{0,2,3}$ **[30–40]**$^{2\text{–}3}$ $[41\text{–}47(\text{–}51)]^{3\text{–}2,0}$ $[52\text{–}54]^{2,0}$ $[55\text{–}72]^0$
Taiwania cryptomerioides	$[1\text{–}2]^0$ $[3]^{0\text{–}1}$ $[4\text{–}5]^{0\text{–}2}$ **[6–15]**^{2} $[16]^{2,0}$ $[17\text{–}19]^{2\text{–}0}$ $[20]^{1\text{–}0}$ $[21\text{–}25]^0$
Athrotaxis cupressoides	$[1\text{–}6]^0$ $[7]^{0,2,5}$ $[8]^{2\text{–}5}$ $[9]^{3\text{–}5}$ **[10–13]**$^{4\text{–}6}$ $[14]^{6\text{–}3}$ $[15]^{5\text{–}3}$ $[16]^{4\text{–}2}$ $[17]^2$ $[(18)]^{2\text{–}1}$ $[(19\text{–}20)]^{1\text{–}0}$ $[(21\text{–}24)]^0$
Athrotaxis laxifolia	$[1\text{–}5]^0$ $[6]^{0,3}$ $[7\text{–}8]^{0,4\text{–}6}$ $[9]^{5\text{–}6}$ **[10–16]**$^{5\text{–}7}$ $[17\text{–}18]^{7\text{–}4}$ $[19]^{6\text{–}4}$ $[20\text{–}21]^{6\text{–}5,3\text{–}2}$ $[(22\text{–}30)]^{5\text{–}1}$
Athrotaxis selaginoides	$[1\text{–}8]^0$ $[9]^{0,3\text{–}4}$ $[10]^{0,4\text{–}7}$ **[11–21]**$^{4\text{–}8}$ $[22\text{–}23]^{6\text{–}3}$ $[24]^{6\text{–}2}$ $[25\text{–}36]^{5\text{–}0}$
Metasequoia glyptostroboides	$[1]^0$ $[2]^{0\text{–}3}$ $[3]^{2\text{–}5}$ $[4\text{–}5]^{4\text{–}6}$ **[6]**$^{5\text{–}6,0}$ $[7]^{6\text{–}4,0}$ $[8]^{4\text{–}0}$ $[9]^2$ $[(10\text{–}14)]^0$
Sequoia sempervirens	$[1]^0$ $[2]^{0,2\text{–}3}$ $[3]^{2\text{–}4}$ $[4]^{4\text{–}5}$ **[5–15]**$^{5\text{–}6}$ $[16\text{–}18]^{5\text{–}3}$ $[19]^{3\text{–}2,0}$ $[20\text{–}21(\text{–}28)]^0$
Sequoiadendron giganteum	$[1\text{–}2]^0$ $[3]^{0,1,4}$ $[4]^{1\text{–}5}$ $[5]^{4\text{–}6}$ $[6]^{5\text{–}6}$ $[7\text{–}10]^{5\text{–}7}$ **[11–27]**$^{6\text{–}8}$ $[28\text{–}30]^{7\text{–}5}$ $[31\text{–}34]^{6\text{–}4}$ $[35\text{–}36]^{6\text{–}3}$ $[37]^{5\text{–}3,0}$ $[38\text{–}39]^{4\text{–}2,0}$ $[40]^{3\text{–}2,0}$ $[41(\text{–}48)]^0$
Cryptomeria japonica	$[1\text{–}18]^0$ $[19\text{–}23]^{0,2\text{–}3}$ **[24–35]**$^{2\text{–}3}$ $[36\text{–}38]^{2,0}$ $[39\text{–}42(\text{–}55)]^0$
Taxodium distichum	$[1\text{–}2]^0$ $[3\text{–}8]^{0,2}$ **[9–16]**^{2} $[17(\text{–}22)]^{2,0}$ $[(23\text{–}27)]^0$
Glyptostrobus pensilis	$[1\text{–}14]^0$ $[15\text{–}18]^{0,2}$ $[19\text{–}23]^{0\text{–}2}$ **[24–26(–27)]**^{2,0} $[(28\text{–}34)]^0$

Square brackets = position of ovules within the cone. Superscript = number of ovules in a certain position within the cone. Values in parentheses = cone scale not present in all cones. Values without parentheses = cone scale present in all cones. Boldface = highest number of ovules within the cone.

Table 3. Absolute and average numbers for female cone, ovule and scale configuration

	Scales		Ovules per scale		Ovules per cone		Basal sterile scales	
	Absolute number	Average number	Absolute number	Average number	Absolute number	Average number	Absolute number	Average number
Sciadopitys verticillata	40–52	46	1–11	5.10	118–218	153	2–5	4
Cunninghamia lanceolata	47–72	61	1–3	2.61	26–95	60	18–32	25
Taiwania cryptomerioides	20–25	23	1–2	1.87	17–33	28	2–6	4
Athrotaxis cupressoides	18–24	21	1–7	3.13	35–64	47	2–7	6
Athrotaxis laxifolia	21–30	23	1–9	4.94	67–130	89	3–9	6
Athrotaxis selaginoides	24–36	26	1–9	5.00	67–148	90	5–12	8
Metasequoia glyptostroboides	18–28	24	1–7	4.00	17–70	44	1–6	3
Sequoia sempervirens	21–28	24	1–7	4.71	55–96	80	0–5	1
Sequoiadendron giganteum	41–48	45	1–10	5.89	183–267	218	1–5	3
Cryptomeria japonica	42–55	48	1–5	2.69	30–54	43	17–24	20
Taxodium distichum	17–27	21	1–2	2.00	15–42	28	1–9	5
Glyptostrobus pensilis	25–34	30	1–2	1.71	7–19	12	13–22	17

Average values rounded to integers; ratio values rounded to 2 decimal places.

Table 4. Absolute numbers, average numbers and ratios for female cone scales and ovules

	Distal sterile scales		Fertile scales		Average number of sterile scales (proximal + distal)	Fertile/ sterile scales	Ovules/ scales
	Absolute number	Average number	Absolute number	Average number			
Sciadopitys verticillata	5–19	13	16–34	30	17	1.76	3.33
Cunninghamia lanceolata	6–25	14	13–36	23	39	0.59	0.98
Taiwania cryptomerioides	1–9	5	9–18	15	9	1.67	1.22
Athrotaxis cupressoides	0–4	2	10–20	15	8	1.88	2.24
Athrotaxis laxifolia	0–1	0	13–25	18	6	3.00	3.87
Athrotaxis selaginoides	0–2	0	14–31	18	8	2.25	3.46
Metasequoia glyptostroboides	6–14	10	6–17	11	13	0.85	1.83
Sequoia sempervirens	1–9	5	13–21	17	6	2.83	3.33
Sequoiadendron giganteum	0–10	6	32–43	37	9	4.11	4.84
Cryptomeria japonica	7–18	11	12–20	16	31	0.52	0.90
Taxodium distichum	1–6	3	9–20	14	8	1.75	1.33
Glyptostrobus pensilis	0–11	7	4–10	7	24	0.29	0.40

Average values rounded to integers; ratio values rounded to 2 decimal places.

analysis was conducted with PAUP*4.0b10 (Swofford 2002) using exact (branch-and-bound) search. For finding the shortest (MP) trees, the search was performed with 'furthest', 'asis', 'simple', 'maxmini', and 'kmaxmini' taxon addition sequences. For this phylogenetic analysis, we used only characters with states that had been investigated in most of the species; consequently, there are no more than two absent character states in the data set. Characters with a low probability of homology were excluded. A character with a low probability of homology is the leaf form, for example, because it is often an adaptation to environmental conditions. Where character variability was not ascertainable, characters were excluded. For example,

the variability of 'form of ray cells in cross section' (Peirce 1936) was not ascertainable because it varied considerably within a taxon. The data set contains information from cytological, anatomical, morphological, and other investigations (non-molecular data). For statistics such as CI (= consistency index), RI (= retention index), and RC (= character rescaled CI), all parsimony-informative characters were used. The ingroup includes all taxodiaceous Cupressaceae after Farjon (1998). The only appropriate outgroup is *Sciadopitys verticillata*, because it is both conspicuously different from the ingroup and the closest relative of the latter. The morphological distance between taxodiaceous Cupressaceae and other conifer families

Table 5. Male cone formula

Taxon	Male cone formula
Sciadopitys verticillata	$\mathbf{[1–57(–88)]^2}$
Cunnighamia lanceolata	$\mathbf{[1–30]^3}$ $[31–52(–60)]^{3–2}$ $[(61–83)]^2$
Taiwania cryptomerioides	$\mathbf{[1–7]^3}$ $[8–10]^{3–2}$ $[11–12(–17)]^2$
Athrotaxis cupressoides	$\mathbf{[1–21(–26)]^2}$
Athrotaxis laxifolia	$\mathbf{[1]^{3–2}}$ $[2–28(–58)]^2$
Athrotaxis selaginoides	$\mathbf{[1–23]^{3–2}}$ $[24–39(–59)]^2$
Metasequoia glyptostoboides	$\mathbf{[1–7]^3}$ $[8–12]^{3–2}$ $[13–24(–33)]^2$ $[(34–39)]^{2–1}$
Sequoia sempervirens	$\mathbf{[1–12]^{4–3}}$ $[13–14]^3$ $[15(–25)]^{2–1}$
Sequoiadendron giganteum	$\mathbf{[1–10]^{4–3}}$ $[11–12(–13)]^3$ $[(14–16)]^{3–2}$ $[(17–20)]^2$
Cryptomeria japonica	$[1–2]^0$ $[3]^2$ $[4]^{2–3}$ $[5–7]^3$ $\mathbf{[8–16]^{3–4}}$ $[17–19]^3$ $[(20–21)]^{3–2}$ $[(22–26)]^2$
Taxodium distichum	$[1]^{5–6}$ $\mathbf{[2-4]^{7–5}}$ $[5–7]^{6–4}$ $[8]^{6–3}$ $[9(–17)]^{4–1}$
Glyptostrobus pensilis	$[1–2]^{1–2}$ $[3–4]^{2–3}$ $\mathbf{[5–10]^{3–4}}$ $[11(–13)]^{3–2}$ $[(14)]^2$ $[(15–19)]^{2–1}$

Square brackets = position of pollen sacs within the cone. Superscript = number of pollen sacs in a certain position within the cone. Values in parentheses = cone scale not present in all cones. Values without parentheses = cone scale present in all cones. Boldface = highest number of pollen sacs within the cone.
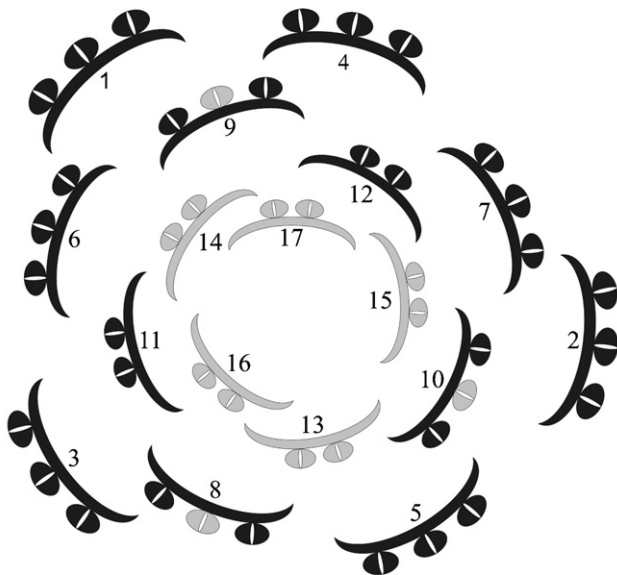

Fig. 1. Male cone diagram of *Taiwania cryptomerioides*; the corresponding formula is: $[1–7]^3$ $[8–10]^{3–2}$ $[11–12(–17)]^2$. Black = elements that are always present; grey = elements that are present only in some cases.

(e.g. Taxaceae, Pinaceae) is too large to ascertain homology of characters.

The usefulness of phylogenetic bootstrapping is limited by the number of characters and the size of the data matrix, respectively (e.g. Soltis and Soltis 2003; Wägele 2005). Bootstrap values of data sets with many characters are not comparable with bootstrap values of data sets with only very few characters. Our data set contains only 16 characters (see below, and Table 7); therefore, we did not calculate bootstrap values.

Character states were mapped on the phylogenetic tree (Fig. 4). We have mapped the cone scale on the phylogenetic tree of Kusumi et al. (2000) to illustrate cone scale evolution in taxodiaceous Cupressaceae (Fig. 2).

Character coding

Char. 1 – rays in wood (Peirce 1936; Yu 1948): 1(0) max. 10 cells high; 1(1) max. 24 cells high; 1(2) max. 60 cells high.

Char. 2 – crassulae in wood (Peirce 1936): 2(0) pronounced to indistinct; 2(1) distinct.

Char. 3 – number of pits on tracheid side of crossfield (Peirce 1936): 3(0) only 1; 3(1) max. 4; 3(2) max. 6.

Char. 4 – transverse walls in wood parenchyma (Peirce 1936): 4(0) entire or pitted, but never thick; 4(1) thick, with numerous pits.

Char. 5 – papillae on pollen (Ueno 1951): 5(0) (almost) absent; 5(1) present.

Char. 6 – archegonial position within female gametophyte (Gadek et al. 2000): 6(0) all apical; 6(1) some apical, some lateral, or all lateral.

Char. 7 – pollination droplets (Jagel 2001): 7(0) not fused; 7(1) fused.

Char. 8 – orientation of flowering female cones (Jagel 2001): 8(0) pendant; 8(1) horizontal or slightly downwards; 8(2) vertically upwards.

Char. 9 – flat conspicuous ovuliferous scale (e.g. Jagel 2001; Fig. 2): 9(0) arising on cone scale and not closing the cone; 9(1) absent; 9(2) arising in axillary position and not closing the cone.

Char. 10 – distal adaxial swelling on cone scale (e.g. Jagel 2001; Fig. 2): 10(0) present; 10(1) absent.

Char. 11 – insertion of ovules (e.g. Jagel 2001; Fig. 2): 11(0) on cone scale; 11(1) axillary.

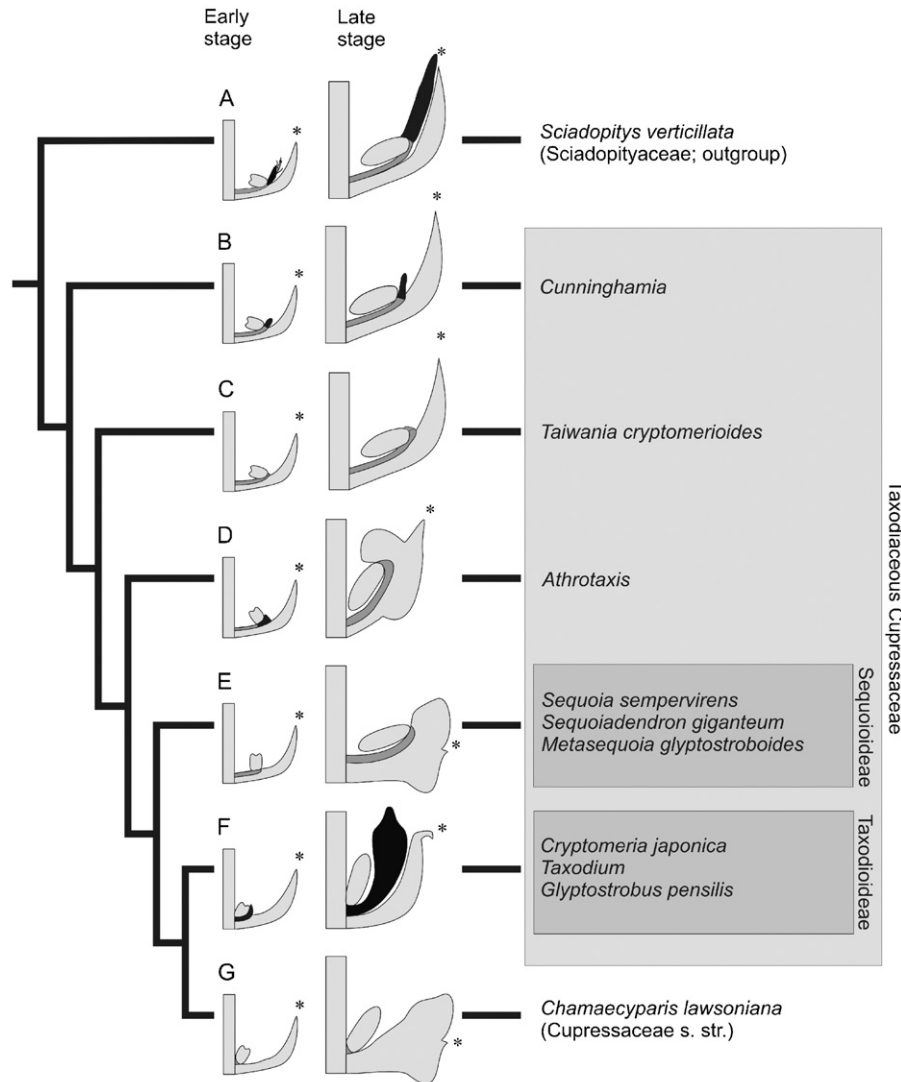Char. 12 – orientation of micropyle (Sorger 1925; Jagel 2001; see Fig. 2): 12(0) ovule turned, so that

Fig. 2. Bract and ovuliferous scale development (B, D–F from Jagel 2001) mapped onto phylogenetic tree of Kusumi et al. (2000). * = tip of female cone scale; light grey = cone axis, bract and ovule; black = conspicuous ovuliferous scale (recognizable); dark grey = adnate ovuliferous scale (interpreted).

micropyle points to cone axis at time of maturation; 12(1) ovule not turned, so that micropyle points to cone scale tip at time of maturation.

Char. 13 – proliferation of female cones (Masters 1882; Lemoine-Sébastian 1968; Fig. 3A, B): 13(0) proliferating; 13(1) not proliferating.

Char. 14 – cone configuration of male cones (Table 5): 14(0) on male cone, number of pollen sacs per cone scale decreases from proximal to distal; 14(1) on male cone, number of pollen sacs per cone scale first increases, then decreases from proximal to distal.

Char. 15 – seeds: 15(0) without additional structure close to hilum; 15(1) with an additional structure close to hilum (arrow in Fig. 3C).

Char. 16 – chromosomes (Farjon 2005 after Li 1989): 16(0) no Stebbins type 1A chromosomes; 16(1) Stebbins type 1A chromosomes.

Glossary

Frame homology: A group of details forming a complex homologous pattern (character) or being physically combined. Within such a pattern, not all details have to be homologous in different organisms (Wägele 2005).

Ovuliferous scale: An axillary appendage that bears one or more ovules (simplified after Farjon 2005). Conspicuous ovuliferous scale: a conspicuously visible ovuliferous scale. An ovuliferous scale can also be assumed (interpreted) due to the ovule position.

Probability of homology: Either the estimated probability that a real homology has been recognized correctly or that a homology evolved (Wägele 2005).

Crassulae: Ridge-like thickenings of the compound middle lamellae in tracheids of certain conifers. Normally appear near bordered pits.
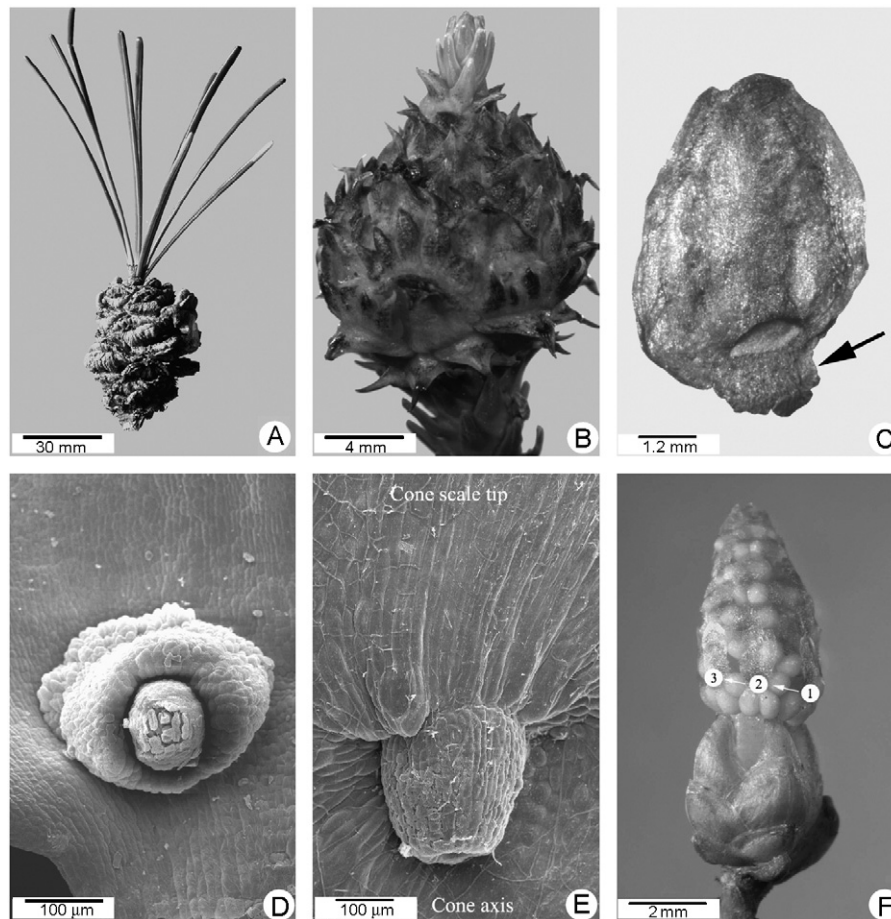
Fig. 3. (A) *Sciadopitys verticillata*, proliferating female cone. (B) *Cryptomeria japonica*, proliferating female cone. (C) *Cunninghamia konishii*, seed with additional structure close to hilum (arrow). (D) *Cunninghamia lanceolata*, ovule with weakly developed ovuliferous scale. (E) *Taiwania cryptomerioides*, aborted ovule. (F) *Metasequoia glyptostroboides*, mature male cone with bijugately arranged scales; only one cone scale (1, 2, 3) visible, second scale (1′, 2′, 3′) on backside of cone.

Results

Phylogenetic analysis

Maximum parsimony analysis of the non-molecular data set with all taxodiaceous Cupressaceae after Farjon (1998) yielded a single tree independent of the taxon addition sequence (Fig. 4), in which Taxodioideae (*Taxodium, Glyptostrobus* and *Cryptomeria*) and Sequoioideae (*Metasequoia, Sequoia* and *Sequoiadendron*) are monophyletic (length = 26 steps; consistency index, CI = 0.77; retention index RI = 0.89; rescaled consistency index, RC = 0.69).

Cone configuration

The configuration of the female cones reveals a uniform pattern. Female cones of taxodiaceous Cupressaceae have proximally from 0 (e.g. *Sequoia*) up to 32 (e.g. *Cunninghamia*) sterile cone scales. Within the cone

the number of ovules per cone scale increases from the proximal to the middle position (e.g. up to eight ovules in *Athrotaxis selaginoides*), then decreases again towards the distal end. Distally the cone has up to 25 (*Cunninghamia lanceolata*) sterile cone scales (Tables 2–4).

In contrast, the male cones of taxodiaceous Cupressaceae have proximally no sterile cone scales, except *Cryptomeria japonica*. Most of the taxa (except *Cryptomeria, Taxodium* and *Glyptostrobus*) have proximally the highest number of pollen sacs per cone scale (e.g. four in *Sequoia*). Usually the number of pollen sacs decreases from the proximal to the distal position within the cone (e.g. to one in *Taxodium*). In Taxodioideae (*Cryptomeria, Taxodium* and *Glyptostrobus*), the number of pollen sacs increases from the proximal position of the cone (e.g. to four in *Glyptostrobus*), then decreases (e.g. to one in *Glyptostrobus*) (Tables 5 and 6).

Our non-molecular tree (Fig. 4) shows the same topology as the molecular tree of Kusumi et al. (2000),
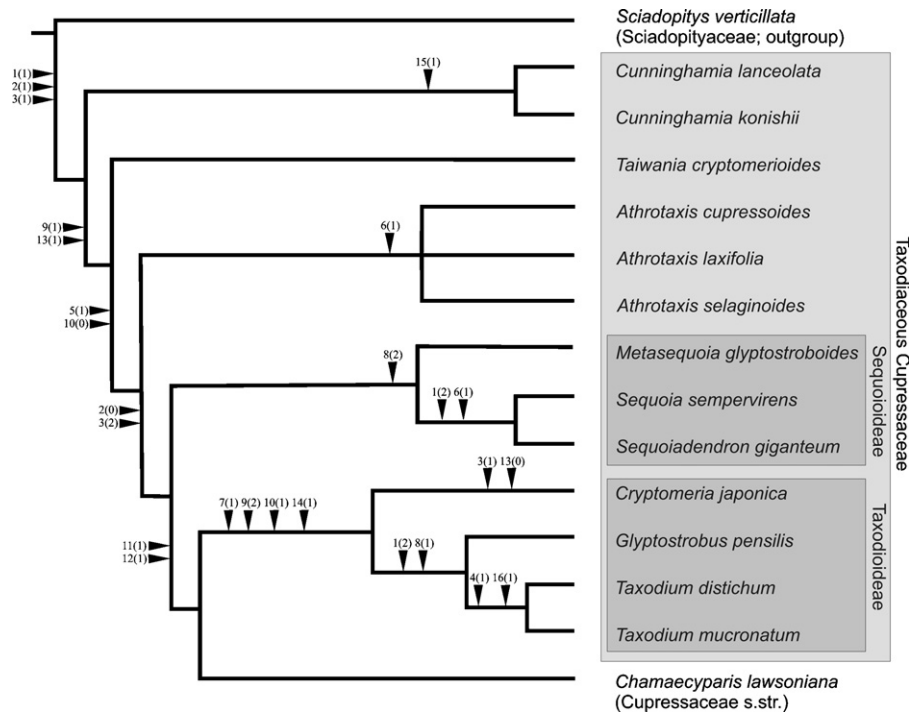
Fig. 4. Phylogenetic tree based on exact search (branch-and-bound) using non-molecular data. Tree length 26 steps; CI = 0.77; RI = 0.89; RC = 0.69 (including 16 parsimony-informative characters). Black triangles = character states.

Table 6. Absolute numbers, average numbers and ratios of the male cone scale and pollen sacs

	Scales		Pollen sacs per fertile scale		Pollen sacs per cone		Pollen sacs/ scales	Pollen sacs/ ovules
	Absolute number	Average number	Absolute number	Average number	Absolute number	Average number		
Sciadopitys verticillata	57–88	72	1–2	2	114–175	143	1.99	0.93
Cunninghamia lanceolata	52–86	65	2–4	3	135–234	183	2.82	3.05
Taiwania cryptomerioides	12–17	15	2–4	3	31–44	38	2.53	1.36
Athrotaxis cupressoides	21–27	24	2	2	42–54	48	2.00	1.02
Athrotaxis laxifolia	28–61	41	2–4	2	56–121	83	2.02	0.93
Athrotaxis selaginoides	39–59	48	1–5	2	84–125	104	2.17	1.16
Metasequoia glyptostroboides	24–39	35	1–4	2	58–87	77	2.20	1.75
Sequoia sempervirens	15–25	19	1–6	3	45–76	58	3.05	0.73
Sequoiadendron giganteum	12–20	16	1–6	3	42–64	53	3.31	0.24
Cryptomeria japonica	19–27	23	1–4	3	53–77	63	2.74	1.47
Taxodium distichum	10–17	13	1–8	5	40–85	59	4.54	2.11
Glyptostrobus pensilis	11–19	15	1–5	3	27–44	38	2.53	3.17

Average values rounded to integers; ratio values rounded to 2 decimal places.

except for the *Athrotaxis* species, which appear as a polytomy. Taxodioideae (*Cryptomeria*, *Taxodium* and *Glyptostrobus*) and Sequoioideae (*Metasequoia*, *Sequoia* and *Sequoiadendron*) each form monophyletic groups (Table 7).

Discussion

In most of Cupressaceae s. str. and Taxodioideae, the ovules develop in the axil of a cone scale, but never on the cone scale (Fig. 2F, G). In Cupressaceae s. str. the

Table 7. Data matrix

	Character number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Sciadopitys verticillata	0	0	0	0	0	?	0	?	0	1	0	0	0	0	0	0
Cunninghamia lanceolata	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0
Cunninghamia konishii	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0
Taiwania cryptomerioides	1	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0
Athrotaxis cupressoides	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0
Athrotaxis laxifolia	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0
Athrotaxis selaginoides	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0
Metasequoia glyptostroboides	1	?	?	?	1	0	0	2	1	0	0	0	1	0	0	0
Sequoia sempervirens	2	0	2	0	1	1	0	2	1	0	0	0	1	0	0	0
Sequoiadendron giganteum	2	0	2	0	1	1	0	2	1	0	0	0	1	0	0	0
Cryptomeria japonica	1	0	1	0	1	0	1	0	2	1	1	1	0	1	0	0
Taxodium distichum	2	0	2	1	1	0	1	1	2	1	1	1	1	1	0	1
Taxodium mucronatum	2	0	2	1	1	0	1	1	2	1	1	1	1	1	0	1
Glyptostrobus pensilis	2	0	2	0	1	0	1	1	2	1	1	1	1	1	0	1
Chamaecyparis lawsoniana	?	?	?	?	1	0	0	?	1	0	1	1	1	0	0	?

Characters and character states numbered as in the text; ? = state unknown.

cone scale (here corresponding to a bract) corresponds to a leaf in its entirety, and the ovules are the sole remnants of a short shoot (Schulz et al. 2003). In Taxodioideae, only the bract corresponds to a leaf, and the ovuliferous scale represents the short shoot. In contrast, in taxodiaceous Cupressaceae (except Taxodioideae) the ovules develop on the cone scale (e.g. Takaso and Tomlinson 1992), and the rest of the ovuliferous short shoot can be regarded as adnate or congenitally fused to the cone scale (Jagel 2001). In *Cunninghamia*, *Athrotaxis* and Taxodioideae a conspicuous ovuliferous scale is formed (part of the short shoot; Fig. 2B, D, F), whereas in *Taiwania* (usually) and Sequoioideae a conspicuous ovuliferous scale is not recognizable (Fig. 2C, E). However, due to the ovules on the cone scale it can be assumed that the part from the adaxial base, up to the insertion of the ovules, belongs to the ovuliferous scale (= short shoot) (Jagel 2001). Consequently, the short shoot in *Cunninghamia* and *Athrotaxis* is represented by the free distal part of the ovuliferous scale (= conspicuous ovuliferous scale) and the adnate basal part of the ovuliferous scale (interpreted). In contrast, the short shoot in *Taiwania* and Sequoioideae is without the conspicuous part of the ovuliferous scale. In Taxodioideae, the short shoot is only represented by the conspicuous part of the ovuliferous scale (= lobate protuberance).

The homology of the flat conspicuous ovuliferous scale in *Sciadopitys*, *Cunninghamia*, and the Taxodioideae has been discussed intensively. All three groups share probably the same frame homology: the (conspicuous and interpreted part of the) ovuliferous scale corresponds to a short shoot, only to different extent. However, there is no detailed homology of the flat

conspicuous ovuliferous scale of *Cunninghamia* and Taxodioideae, because the development of the conspicuous ovuliferous scale in the groups between *Cunninghamia* and Taxodioideae (e.g. Sequoioideae, *Taiwania*) is suppressed.

Cunninghamia is the only representative of Cupressaceae s. l. that shows both a flat conspicuous ovuliferous scale and ovules on the cone scale (Fig. 2B), similar to *Sciadopitys* (Takaso and Tomlinson 1991; Fig. 2A). This character state is most likely plesiomorphic; therefore it cannot support the relationship between *Cunninghamia* and *Sciadopitys* but does not disprove it either. The conspicuous ovuliferous scale of *Sciadopitys* arises earlier in the development than that of *Cunninghamia*. However, the comparison between *Araucaria* (P. Knopf and T. Stützel, in prepartion), *Sciadopitys* (Takaso and Tomlinson 1991) and *Cunninghamia* (Farjon and Garcia 2003) shows different times of development of the flat conspicuous ovuliferous scale. From *Araucaria* via *Sciadopitys* to *Cunninghamia*, the conspicuous ovuliferous scale arises gradually later in development. As a result, it can be concluded that the time of development has changed during evolution.

The high number of ovules per cone scale in *Sciadopitys* (up to 11), and the low number in the primitive taxodiaceous Cupressaceae such as *Cunninghamia* (3) and *Taiwania* (2) seem unexpected. However, the Sciadopityaceae have several fossil representatives, e.g. *Sciadopitys yezo-koshizakae* (Ohsawa et al. 1991), *Sciadopitys cretacea* (Ogura 1932), *Sciadopitys tertiaria* (Florin 1963), *Sciadopityostrobus* (Saiki 1992) and *Parasciadopitys* (Yao et al. 1997). As *Parasciadopitys* (Yao et al. 1997) has five ovules and *Sciadopitys verticillata* up to 11, the character state '11 ovules' is

probably derived within fossil Sciadopityaceae. Many character states of *Sciadopitys verticillata* are probably synapomorphies of the Sciadopityaceae, e.g. the pseudo-needles (e.g. Hille 2002; Farjon 2005), perhaps the centrifugal sequence of ovule development (Takaso and Tomlinson 1991), and the chromosome number of 2n = 20 (Li 1988). An evolutionary interpretation is difficult because of the assumption that *Sciadopitys verticillata* is probably a derived species, and the fact that it is the only representative of a formerly diverse family. However, both *Sciadopitys* and *Cunninghamia* have a high number of male and female cone scales (Tables 2 and 5).

The genera *Cunninghamia* and *Taiwania* have a cone scale in which the distal adaxial part does not form a swelling and the ovules arise on the cone scale. In *Taiwania*, sometimes primordia arise on the cone scale in the same position as the primordia of the lobes (= ovuliferous scale) in *Cunninghamia* (Farjon and Garcia 2003). Our study has confirmed these results, and in addition we occasionally found a short and thin conspicuous ovuliferous scale in *Cunninghamia* (Fig. 3D). Moreover, a weak swelling is visible close to aborted ovules in *Taiwania* (Fig. 3E). These findings display a reduction from the conspicuous ovuliferous scale in *Cunninghamia* to *Taiwania*. The relationship is also reflected in the fossil species *Parataiwania*, which contains four ovules with small lobate protuberances (= conspicuous ovuliferous scales) and shows many similarities with *Taiwania* (Nishida et al. 1992). Even the cone configurations of male and female cones in *Cunninghamia* and *Taiwania* are very similar; only the number of cone scales is lower in *Taiwania* (Tables 2 and 5). All things considered, the cones of *Taiwania* are probably a reduced form of the cones in *Cunninghamia*. Alternative to the relationship presented here (Fig. 4), it is also conceivable that *Cunninghamia* and *Taiwania* form a monophyletic group (Farjon et al. 2002, Farjon 2005).

In *Athrotaxis*, the ovules are situated on a whitish cushion (= conspicuous ovuliferous scale), which is different from the greenish bract during pollination time (Jagel 2001). This fact supports the interpretation of Jagel (2001) that the basal adaxial part of the cone scale in taxodiaceous Cupressaceae (except Taxodioideae) is an adnate part of the ovuliferous scale. The distal adaxial swelling of the bract which closes the cone is a character of *Athrotaxis*, Sequoioideae and the Cupressaceae s. str. (Fig. 4: character state 10(0)).

It has long been discussed whether *Athrotaxis laxifolia* is a natural hybrid between *A. selaginoides* and *A. cupressoides* or a separate species. The hybrid hypothesis is supported by an intermediary leaf form of *A. laxifolia*, no distinct area between that of both parents (Elliott 1951; Farjon 1998), intermediary pollination time (Jagel and Stützel 2001), and results of molecular investigations (Isoda et al. 2000). Although cytological investigations (Gulline 1952) cannot support the hybrid hypothesis, many researchers regard *A. laxifolia* as a natural hybrid (Curtis 1956; Clifford and Constantine 1980; Gray 1998; Hill 1998; Isoda et al. 2000; Jagel and Stützel 2001). In our study, we can support this hypothesis by intermediary cone configurations in *Athrotaxis laxifolia* between those of both parents in male as well as female cones (Tables 2 and 5).

Monophyly of Sequoioideae (*Metasequoia*, *Sequoia* and *Sequoiadendron*) is shown in molecular (Brunsfeld et al. 1994; Gadek et al. 2000; Kusumi et al. 2000) as well as in non-molecular trees (Fig. 4). It is supported by the following complex synapomorphy: The ovule develops on the cone scale, a conspicuous ovuliferous scale is not present, and the distal adaxial part of the bract forms a swelling which closes the cone as in *Athrotaxis* (Fig. 2E). The trend revealed in *Taiwania* and *Athrotaxis* continues, as the conspicuous ovuliferous scale is completely reduced.

Within taxodiaceous Cupressaceae, *Metasequoia* is distinct by an opposite phyllotaxis, except for bijugately arranged cone scales in adult male cones (Fig. 3F). This character state caused the sister-group relationship of *Metasequoia* and Cupressaceae s. str. in Farjon et al. (2002) and Farjon (2005). However, the 'leaf arrangement' character has a weak probability of homology. For example, in *Juniperus squamata* the leaf arrangement within a short branchlet changes from 'opposite' to 'in whorls of 3' (Schulz 2001). Thus, the above-mentioned synapomorphy of ovule position in Sequoioideae has a higher probability of homology than phyllotaxis. Therefore, monophyly of Sequoioideae (Brunsfeld et al. 1994; Gadek et al. 2000; Kusumi et al. 2000; Fig. 4) is more probable than the sister-group relationship between *Metasequoia* and Cupressaceae s. str. as in Farjon et al. (2002) and Farjon (2005).

Monophyly of Taxodioideae (*Taxodium*, *Glyptostrobus* and *Cryptomeria*) is apparent in molecular (Gadek et al. 2000; Kusumi et al. 2000) and non-molecular trees (Farjon et al. 2002, Farjon 2005; Fig. 4). A synapomorphy of Taxodioideae and Cupressaceae s. str. is the presence of ovules that arise in axillary position and do not change their position or orientation during development (Fig. 4: character state 11(1)). Only in some derived groups the ovules arise terminally or alternate with the cone scales (Schulz et al. 2003). In Taxodioideae, a synapomorphy is a flat conspicuous ovuliferous scale that arises as an outgrowth after ovule development (= lobate protuberance) and closes the cone (Fig. 4: character state 9(2)). Fossil records from Lemoigne (1967) support the sister-group relationship of Taxodioideae and Cupressaceae s. str. These fossils have oppositely arranged scale leaves (typical for Cupressaceae s. str.) and cones with teeth (= conspicuous ovuliferous scale) as in *Cryptomeria*. The close relationship

between extant *Taxodium* and *Glyptostrobus* is also supported by the fossil genus *Glyptodium*, which is described as intermediary (Boyd 1992). Moreover, they appear as a clade in molecular (Gadek et al. 2000; Kusumi et al. 2000) as well as in non-molecular trees (Farjon et al. 2002, Farjon 2005; Fig. 4).

Despite several data from morphological, anatomical, cytological, and other comparative investigations of taxodiaceous Cupressaceae, less data remain for phylogenetic investigations. In several comparative studies within taxodiaceous Cupressaceae, the number of taxa used has been too low for phylogenetic conclusions. Data sets with many absent character states can support 'wrong' topologies. A multiplicity of homoplasies in the non-molecular trees of Gadek et al. (2000), Farjon et al. (2002) and Farjon (2005) is caused by non-homologies or by characters with a low probability of homology, such as 'leaf form' (Farjon et al. 2002 and Farjon 2005). Leaf form is an adaptation to environmental conditions, and not as fixed as cone structure. Another problem is the scoring of character states in non-molecular data sets for phylogenetic use. If the variabilities of character states are not ascertainable, they cannot be used for phylogenetic analysis (e.g. 'form of pit aperture' in Peirce 1936).

The topologies of the molecular (Gadek et al. 2000; Kusumi et al. 2000) and the non-molecular tree (Fig. 4) are almost identical. Developmental investigations, fossil records and the cone configuration support several clades in the topology. Extant taxodiaceous Cupressaceae form a small group of relict species, whereas fossil taxodiaceous Cupressaceae were widely distributed and diverse in the Mesozoic (Stewart and Rothwell 1993) – many more species are extinct than extant. The remaining question is: In what way will information about fossil taxodiaceous Cupressaceae affect topology? Using fossil taxa for phylogenetic investigations is possible. However, a significant number of descriptions is based on isolated organs or even fragments (Miller 1999). This inevitably leads to a tree of organs instead of a tree of clades, and a more or less complete morphological dataset is available for fossils in few cases only (e.g. *Sewardiodendron*; Yao et al. 1998).

Acknowledgements

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