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On the occurrence of non-axillary ovules in *Tetraclinis articulata* (VAHL) MAST. (Cupressaceae s.str.)[1]

With 7 Figures

Summary

The cone morphology in *Tetraclinis* was studied to elucidate the taxonomic position of the genus. A careful analysis of the cone development shows that the characters used as arguments for an affiliation within Callitroideae are superficial and of little taxonomic significance. The developmental patterns indicate a position of *Tetraclinis* within Cupressoideae. *Tetraclinis* displays ovules inserted directly at the distal end of the cone axis and not born in the axil of a seed scale as recently shown for *Juniperus* (SCHULZ et al. 2003) and *Microbiota* (JAGEL & STÜTZEL 2001b). The close relationship between *Tetraclinis*, *Juniperus* and *Cupressus* as suggested by SAXTON (1913) based on embryological data, by GADEK & QUINN (1985) based on biflavones and by GADEK et al. (2000) based on DNS-sequences is supported by the morphological data presented here. Conflicting morphological concepts or morphological trees (e.g. GADEK et al. 2000) are in parts weakly supported and suffer either from ambiguous coding of morphological data or are based on historical morphological errors. To calculate reliable morphological trees, however, requires data of similar quality and cannot be achieved by using data which are tailed to the use in effective diagnostic keys.

Zusammenfassung

Zum Vorkommen von nicht-axillären Samenanlagen bei *Tetraclinis*

Die Zapfenmorphologie von *Tetraclinis* wurde untersucht, um die systematische Stellung der Gattung zu erhellen. Die sorgfältige Analyse der Zapfenentwicklung zeigt, dass die Argumente, die bisher für einen Einschluss in die Callitroideae herangezogen wurden, das Ergebnis von oberflächlicher Betrachtung oder aus anderen Gründen wenig aussagekräftig sind. Die Entwicklungsmuster legen eine Stellung in den Cupressoideae nahe. *Tetraclinis* zeigt am distalen Zapfenende Samenanlagen, die direkt an der Zapfenachse und nicht in der Achsel einer Zapfenschuppe (Deckschuppe) inserieren, wie dies zuvor für *Juniperus* (SCHULZ et al. 2003) und *Microbiota* (JAGEL & STÜTZEL 2001b) gezeigt wurde. Die enge verwandtschaftliche Beziehung zwischen *Tetraclinis*, *Juniperus*, und *Cupressus*, wie sie bereits von SAXTON (1913) auf der Basis von embryologischen Daten und von GADEK & QUINN (1985) auf der Basis von Biflavonen sowie von GADEK et al. (2000) auf der Basis genetischer Analysen postuliert wurde, wird von den hier vorgelegten morphologischen Daten gestützt. Konträre morphologische Ansichten oder Stammbaumrekonstruktionen auf der Basis morphologischer Daten (z. B. GADEK et al. 2000) sind in wichtigen Punkten nur schlecht gestützt, das Ergebnis von zweideutigen oder sogar falschen Kodierungen der Merkmale, die z. T. auf sehr alten historischen Irrtümern basieren. Für die Berechnung verlässlicher morphologischer Stammbäume sind vergleichbar zuverlässige Daten für weitere Gruppen erforderlich. Dies kann nicht erreicht werden, indem Daten, die für die Verwendung in Bestimmungsschlüsseln erhoben wurden, in phylogenetischem Kontext zweitverwendet werden.

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[1] Dedicated to Professor Dr. Dietrich Müller-Doblies, Berlin on the occasion of his 65th birthday.

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Introduction

The monotypic genus *Tetraclinis* is mainly distributed in the Atlas Mountains in northwest Africa. Apart of this main area, some small relict areas exist in Tunisia, the Cyrenaica, Malta and in southeast Spain (TEMPLADO 1975). A fertile fossil record of the Middle Miocene was discovered in Croatia by KOVAR-EDER & KVAČEK (1995). In the "preliminary world list of threatened conifer taxa" by FARJON et al. (1993) it is rated as vulnerable. In Central Europe *Tetraclinis articulata* is not hardy (KRÜSSMANN 1983) and mostly cultivated in the temperate house. Thus, the species is rarely to be found in Botanical Gardens.

Within Cupressaceae s. str., the monotypic genus *Tetraclinis* MAST. was included in the Callitroideae by LI (1953), a classification which was prevalent for a long time (e.g. KRÜSSMANN 1983). In this subfamily, *Tetraclinis* is exceptional because all other members are distributed exclusively in the southern hemisphere while *Tetraclinis* occurs in the mediterranean region. As only argument for this affiliation LI (1953) emphasizes the valvate cone scales of the ripe cones which seem to be similar to the condition in all remaining members of the Callitroideae. In the past few years, the systematic position of *Tetraclinis* was questioned and newly discussed. In trees based on different molecular analyses, *Tetraclinis* came out together with the northern hemispherical Cupressoideae (BRUNSFELD et al. 1994; GADEK et al. 2000). SAXTON (1913) placed *Tetraclinis* also in his Cupressoideae, based on embryological studies, a position within Cupressoideae is also supported by biochemical studies (GADEK & QUINN 1985). The resulting conflict between the morphological approach on the one hand and the molecular and embryological approach on the other hand was widely ignored up to now. While a position of *Tetraclinis* within Cupressoideae seems well supported by most of the more recent studies, the affiliation of *Tetraclinis* within Cupressoideae remained still doubtful.

A survey on the bibliography, however, reveals that the morphological data for *Tetraclinis* itself are far from being consistent and complete. The cone morphology of *Tetraclinis* is in fact very similar to that of e.g *Widdringtonia* in respect to the very short cone axis and the only four (fertile) valvate cone scales. But these characters are weak in indicating basically reduced cones and allowing no clear distinction between Callitroideae and Cupressoideae. Other available data are confusing and often contradictory. This applies especially to the number and position of the ovules within a cone. At a first glance it seems that the (usually) six seeds per cone are born in two groups of three in the axils of the proximal pair of scales, whereas the distal two cone scales are sterile. This impression is underlined by the arrangement of the very wide seed wings (Fig. 1D, Fig. 2). Amongst others, this interpretation was given by KRÜSSMANN (1983) who described the lower seed scales as fertile, bearing two or three seeds each. On the other hand, PABST (1887) assigned one seed to each of the upper two seed scales and two or three to the lower ones. A very doubtful number per cone scale is published by HORA (1981), who indicated two to nine (!) seeds per seed scale without a more precise allocation to cone scales. This would result in a total number of seeds per cone which has never been found by any author and not by us either. Most of the publications do not specify the location of the seeds at all, e.g. PILGER 1926, DALLIMORE & JACKSON 1966, PAGE 1990.

To clarify these systematic and morphological problems, we examined mature and young cones of *Tetraclinis articulata* and studied the morphogenesis. The results are compared with those for other Cupressaceae (JAGEL & STÜTZEL 2001a, b; JAGEL 2002; SCHULZ et al. 2003).

Material and methods

Early developing and ripe cones were collected from cultivated plants at the Botanical Gardens of Düsseldorf and Bonn (North Rhein-Westphalia, Germany). The material was fixed in FAA for at least half a day and then transferred and preserved in 70% alcohol. Young cones were dissected and most of the cone scales removed. For SEM studies they were then dehydrated in FDA and critical point dried and coated with gold-palladium using a Balzers sputter coater. Different cone types were depicted as cone diagrams using CorelDraw 9.0.

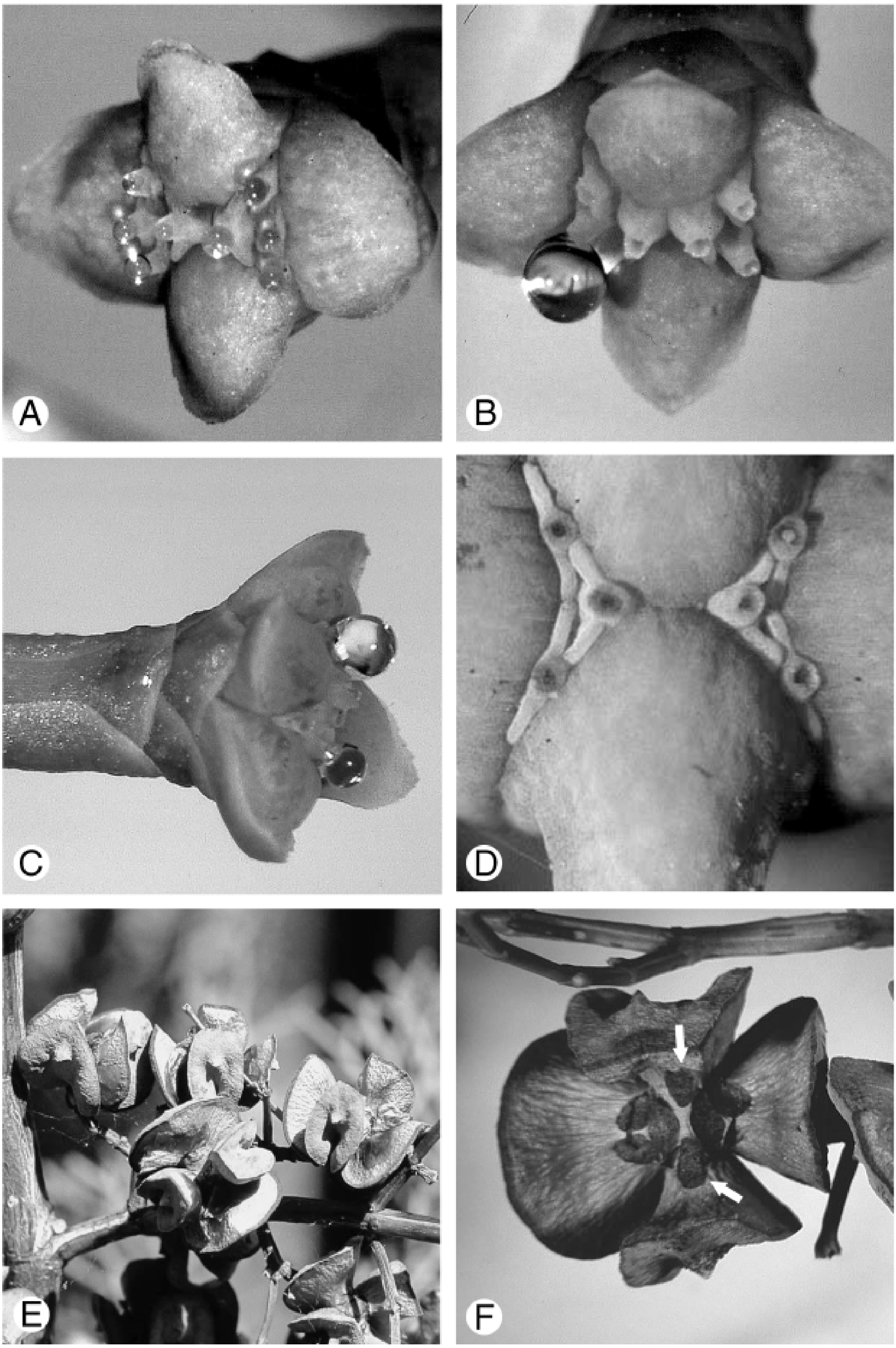
Results

The ovulate cones of *Tetraclinis* are formed terminally on short shoots. Just at the beginning of the cone formation, the reproductive shoots are bent down into a horizontal (plagiotropic) position. Thus, the pollination droplets are exposed in this direction as well. The last two pairs of leaves below the cone are transitional between vegetative leaves and cone scales being much shorter than normal vegetative leaves. The cone itself consists always of two pairs of scales. At pollination, the cone scales are already swollen at the base. The tips of the cone scales are thus spreading and give the flowering cone a star-like appearance in top view. This is unusual within the Cupressoideae, and apart from *Tetraclinis* only found in *Juniperus* sect. *Sabina*. At the distal end of the cone, no terminal piece ("columella", see also JAGEL & STÜTZEL 2001a) is developed, and normally no trace of the end of the cone axis can be found. But sometimes a rudimentary and undifferentiated apex could be found in younger developmental stages hidden between the inner ovules (Fig. 3). The shape of this rudiment resembles the situation in the cones of *Widdringtonia schwarzii* (see JAGEL 2002). The seed scales as well as the scale leaves are decussate, although in some publications they are described as arranged in whorls of four (e.g. DALLIMORE & JACKSON 1966; KRÜSSMANN 1983; PAGE 1990; GADEK et al. 2000). The decussate arrangement is proved by developmental studies of the cone apex and can be detected even from mature stages under a dissecting microscope. The strange habit results from a regular alternation of a long and a very short internode.

Pollination in both individuals studied occurred at a quite different time. The plant in the Botanical Garden of Bonn developed pollination droplets at the beginning of November in 1999 in the temperate house. The youngest developmental stages of these cones had been found in July of the same year. Thus, the cones had passed a resting period of some months as it is the usual case within the Cupressaceae. On the other hand the plant in the Botanical Garden of Düsseldorf flowered already at the beginning of August in 2001, at a time, when it had been removed from the greenhouse to the open air. Unfortunately, the earliest developmental stages of these cones have not been observed by us, but they have obviously not passed such a long resting period. Although the cultivating conditions of both plants are quite similar, the differences in pollination time should be best regarded as a cultivation artefact. In its natural range in Spain the pollination of *Tetraclinis articulata* takes place between September and November (TEMPLADO 1975).

Twigs with flowering cones were collected in the Botanical Garden of Bonn and transported to the Ruhr-University in Bochum. Being put into a vase, the ovules developed pollination droplets again. At first each ovule formed a single pollination drop (Fig. 1A). In later stages the pollination droplets increased and finally fused with the droplets of the neighbouring ovules (Fig. 1B, C). Such a fusion of pollination droplets has been observed in other genera of Cupressaceae, e.g. in *Cupressus* (JAGEL & STÜTZEL 2001a) and *Juniperus* sect. *Sabina* (SCHULZ et al. 2003), *Fitzroya*, and some others (JAGEL 2002). This feature is so far known only from within Cupressaceae s.l. and probably represents an advantage in catching the pollen grains, due to the much larger diameter of the droplets which allows a more effective exposition of the droplet. The fusion is not a pruning artefact and can be observed in situ in the Botanical Garden, too.

Most of the cones of *Tetraclinis articulata* develop a total number of six ovules (Fig. 4A_1). The development of such cones is shown in Fig. 5A–C. The innermost ovules of the cone develop first (marked with "1"), followed by two ovules at each side of the cone (marked with "2"). These four ovules develop more or less simultaneously, and they are significantly younger than the first two ones. In some cases more than six ovules are formed, and an additional ovule appears between one pair (Fig. 4B_1) or between each pair (Fig. 4C_1) of the younger ovules. The developmental lead of the first two ovules is maintained until pollination (Fig. 1A, B). In very rare cases, one can find cones with eight ovules in a different arrangement. Compared to the most frequent type with six ovules, two additional ovules develop in median position to the uppermost scales (Fig. 1F, arrows). The scars remaining


A
B
C
D
E
F

◀ Fig. 1
Tetraclinis articulata

A — Cone at the beginning of pollination. The droplets are separated from each other; B, C — Cone at pollination time with fused, much larger pollination drops; D — Young cone after pollination time. The seed wings are orientated in the same direction; E — Mature cones; F — Rarely found type of mature cone with seed scars in the axils of the uppermost pair of cone scales

after seed shed of the two most distal ovules are at right angle to the scars of the other ones. As cones with more than six ovules have been rare in both examined plants (and seem to be rare in the species at all) we could not find early developmental stages of such cones.

The mature cones of *Tetraclinis articulata* (Fig. 1E) are best described as having a cube-like shape in the closed state and are orientated more or less erect. The inner cone scales are slightly narrower than the outer ones. The outer surface of the cone scales is prominently concave, and the original leaf tip forms a backward-curved hook in the distal third of the scale. The seeds have very broad wings which are broader than the seed itself (Fig. 2). The relative position of the wings in a transversal section is shown for all seeds in the cone in Fig. 4, second column. Due to the saddle, shaped insertion of the fertile cone scales, the wings are elongated proximally (Fig. 6B). After seed shed, a narrow ellipsoidal scar remains on the cone axis, which can easily be seen in older cones due to its dark colour (Fig. 1F). The orientation of these scars within the different cone types is shown in Fig. 4, third column.

Discussion

The contradictory information in literature about the position of the ovules or seeds seems to be based on interpretations of the orientation of the seed wings in the ripe cone. These observations do not consider the morphogenesis of the cone nor the seed scars in the ripe cones although these features are obviously essential for the understanding of the seed cone in *Tetraclinis articulata*.

Looking at the most frequent cone type with six ovules, one might assume that they are grouped by three in the axils of the last but one whorl of cone scales. A position of any ovule or combination of ovules in the axils of the uppermost whorl would lead to a constant asymmetric arrangement what is in full contrast to the highly symmetric architecture of the cone. But if interpreted as groups of three, this

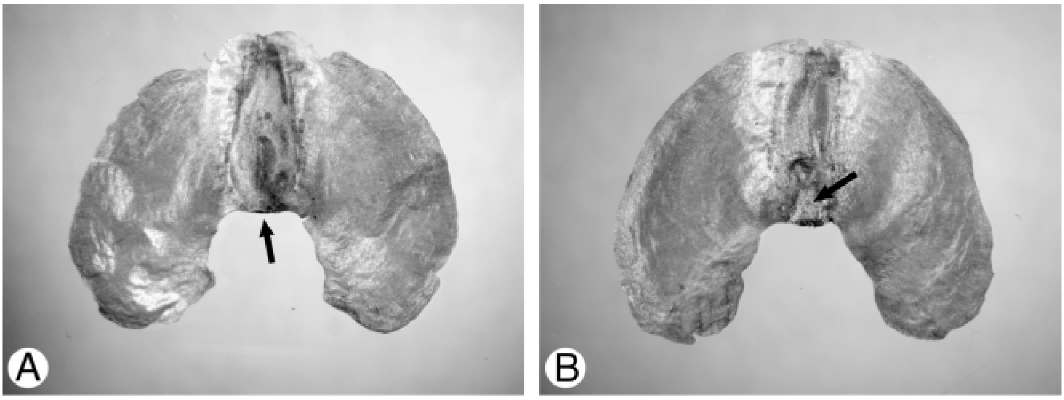


Fig. 2
Tetraclinis articulata

Mature seeds. A — Seed of an uppermost ovule with the scar showing same orientation as the wings; B — Seed born in the axil of a last but one cone scale with the scar orientation in a right angle to the wings. The arrows indicate the abscission scars

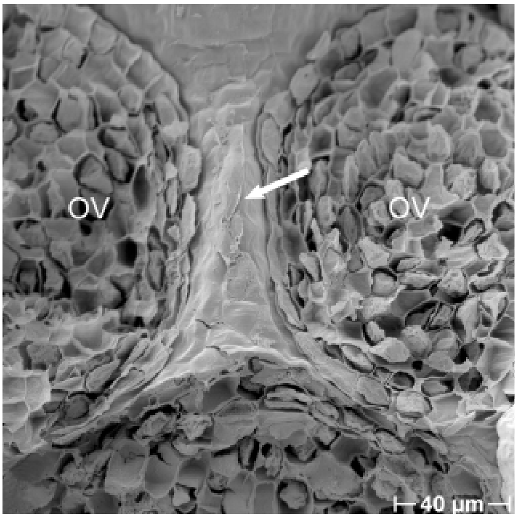


Fig. 3
Tetraclinis articulata

Rudimentary and undifferentiated apex (arrow) in a younger developmental stage hidden between the two most distal ovules (OV) (removed)

would imply at the same time a centrifugal initiation sequence for the ovules within a row. This would be in contrast to the centripetal initiation sequence which has been proved for all Cupressaceae hitherto investigated (JAGEL 2002). In genera with a seemingly centrifugal formation (*Chamaecyparis*), it could be shown that the pattern is centripetal, e.g. derived from a basipetal sequence of several rows of ovules following a centripetal pattern within the row (JAGEL & STÜTZEL 2001a). Furthermore, we could not yet find any species in which the difference in size between the ovules of a single row was as prominent in early stages as in *Tetraclinis* (Fig. 5A).

Sometimes the ovules are grouped to four. In this case (Figs. 5D–F) the fourth ovule is in median position basal to the first ovule to develop. This might be interpreted as two rows of ovules in the axil of one scale with either the first row consisting of three ovules and the second one with a single one or vice versa. As the first (most distal) row is generally best developed and displays the largest number of ovules, one can hardly assume, that the first row comprises only a single ovule. In case the first (distal) row is regarded as being composed of three ovules, the initiation sequence is wrong in comparison to the other genera of the family.

The scar that is left after seed shed gives additional and convincing evidence, that the ovules in groups of three or four are not axillary to the same cone scale. Looking at the scars left after seed shed, e.g. in *Cupressus sempervirens* (Fig. 6A, Fig. 7), one can see that all the scars of a single row are parallel and at right angle to the insertion zone of the subtending scale. Subsequent rows exhibit exactly the same orientation. In *Tetraclinis*, however, the scar of the larger distal ovule is at right angle to the other ones (Fig. $4A_3$, $4B_3$, $4C_3$). This ovule can hardly be axillary to the same scale as the more basal ovules. The sometimes formed fourth ovule, however, has its scar parallel to the lateral ones and is therefore part of a group of three in the axil of the last but one whorl of cone scales. As a single ovule in the axil of a cone scale is always positioned in median position to the scale (SCHULZ et al. 2003), the distal pair of ovules cannot be regarded as axillary product of the distal cone scales and cannot be confined to any of the cone scales.

We therefore are convinced that the most distal two ovules are not axillary to any of the cone scales, but are parts of a seed scale (ovule bearing brachyblast) terminating the cone axis (see SCHULZ et al. 2003). The two ovules take the position and display the shape of the insertion zone, which is expected for a third whorl of leaves. This interpretation explains also why they are ahead in development in comparison to the other ones. The meristem in the axils of the cone scales must first be formed, the meristem of the cone axis is still present. The ovular scars are always transversal to the axis to which the ovule belongs. The axillary ovules are part of an axillary short shoot (seed scale) and have there scars at right angle to the leaf base of the cone scales. The ovules of the terminal short shoot for the same reason have their scars parallel to the leaf base of the preceding cone scales (Fig. 6B). The decussate arrangement of the cone scales is probably the reason why this pattern has not been recognized earlier. In cones with spiral arrangement of the cone scales, the ovules of the terminal short shoot would never be placed in perfectly

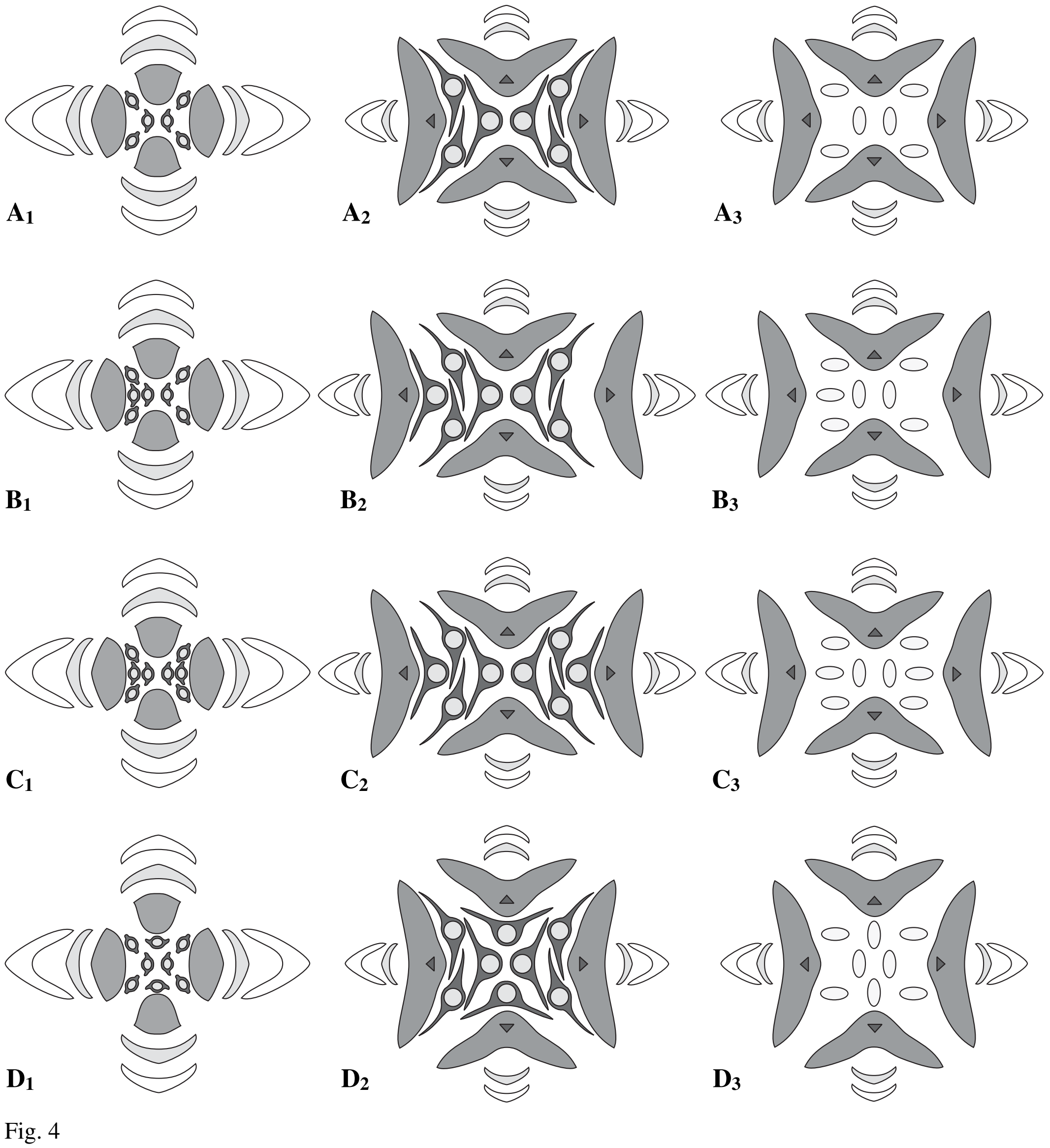
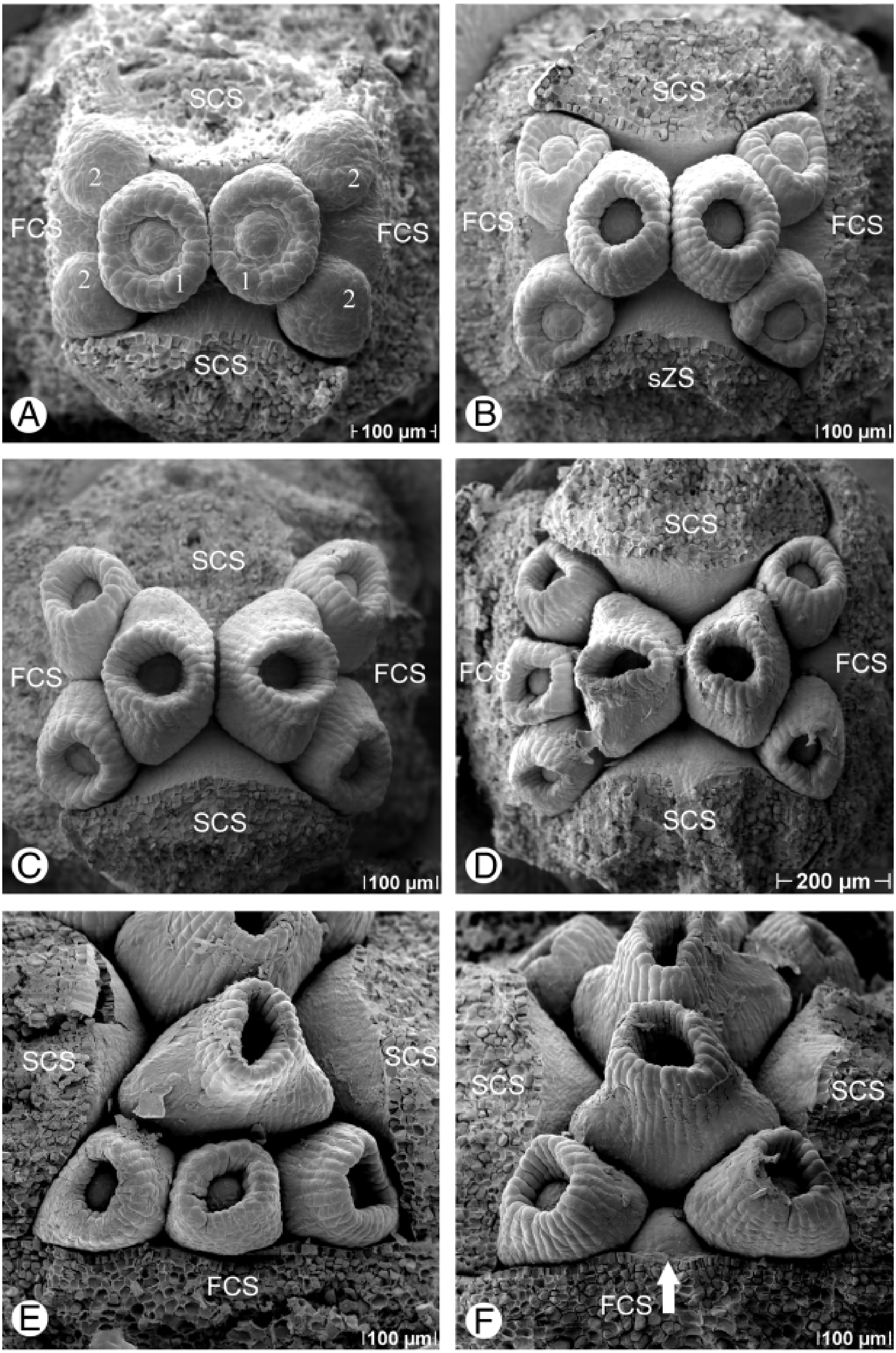


Fig. 4
Tetraclinis articulata

A–D — Diagrams of different cone types. First column (1): at pollination time, second column (2): at ripeness; third column (3): ripe cones after seed shed showing the orientation of the seed abscission scars. A — most frequently found type with six ovules/seeds, B — Type with three ovules/seeds on one of the last but one cone scales, C — Type with three ovules/seeds on the last but one seed scales each, D — Type with fertile uppermost seed scales
Colours of the scales: white: normal scale leaves; light grey: transitional leaves; dark grey: cone scales; black: backward-curved hook on the backside of the scone scales indicating the tip of the scale primordium

median position to a lower cone scale as it is the case in *Tetraclinis*, and therefore could not be mixed up with those being axillary to a scale. As the seed wings are formed very late, their orientation does not reflect the developmental pattern. They obviously fill the available space and this leads to an orientation which obscures the bauplan.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◀ Fig. 5
Tetraclinis articulata

Cone development. A–C — Development of the most frequently found cone type with six ovules per cone. The innermost ovules of the cone develop first (in A marked with “1”), followed by two ovules at each side of the cone (in A marked with “2”). D–F — Cone with three ovules in the axils of both last but one cone scales, the median one on the right side is aborted in an early stage of development as can be seen from Fig. F (arrow). A–D — top view, E, F — lateral view
FCS = fertile cone scale, SCS = sterile cone scale

With ovules inserted directly at the cone axis and not axillary to any cone scale, *Tetraclinis* displays the same phenomenon as *Juniperus* sect. *Juniperus* (SCHULZ et al. 2003) or some cone types in *Microbiota* (JAGEL & STÜTZEL 2001b). The morphology of the cones therefore fits perfectly for Cupressoideae and such a phenomenon could not be found within the Callitroideae. A closer affinity be tween *Tetraclinis* and *Chamaecyparis* is pro-

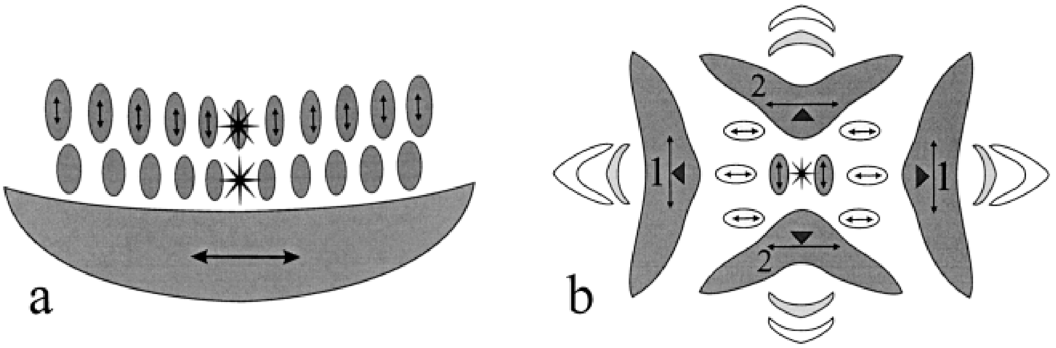

Fig. 6
Scheme of development and orientation of seed scars in *Cupressus sempervirens* (A) and *Tetraclinis articulata* (B)

In *Cupressus* the scars remain after seed shed are elongated at right angle to the insertion zone of the fertile cone scale in all rows of ovules. If a row of ovules is regarded as a lateral axis bearing ovules instead of leaves, the insertion zone is enlarged always transversal to the axes the organs are inserted on. If the bauplan of *Cupressus* applies to *Tetraclinis*, the uppermost two ovules cannot be axillar to whorl 1 because of the wrong orientation of the abscission scar. The scar has in this case the orientation which would be expected for a third whorl of leaves. It is therefore suggested that these ovules take the position of an additional whorl of leaves and are inserted directly at the cone axis. This interpretation goes in line with other important developmental characters

Fig. 7
Cupressus sempervirens

Adaxial side of a mature seed scale after seed shed. The scars are orientated in a right angle to the insertion zone of the subtending scale posed by ALVIN et al. (1982) on the base of comparative studies of the cuticules, but they question the monophyly of Cupressoideae and Callitroideae and end up with intermingled genera of both groups. It seems that *Tetraclinis* is best placed in the core group of Cupressoideae, but the position of *Tetraclinis* within Cupressoideae remains still problematic. While BRUNSFELD et al. (1994) have *Tetraclinis* sistered to *Thuja* and *Thujopsis*, it appears sistered to *Platycladus* and *Microbiota* in the analyses by GADEK et al. (2000). Further studies must clarify in addition, whether there are other taxa misplaced in Callitroideae or Cupressoideae. At present, it seems best to regard ovules inserted directly at the cone axis and continuing the phyllotaxis of the cone scales as a special feature of reduced cones. Such reductions might be expected as parallelisms, but the evidence yet available indicates that it is a developmental tendency restricted to the core Cupressoideae *(Cupressus, Juniperus, Platycladus, Microbiota, Tetraclinis)* and may be an apomorphy for them as well. In *Cupressus* and *Platycladus* the transitions series probably does not include the extremely reduced cones with non axillary seeds but both genera show the same tendencies in the variation of the cone morphology as *Juniperus*, *Tetraclinis* and *Microbiota* and therefore seem to form a well defined monophyllum.

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