FLORAL DEVELOPMENT IN TETRACHONDRACEAE AND OLEACEAE – TWO FAMILIES OF BASAL LAMIALES

Diplomarbeit

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CONTENTS

Die vorliegende Diplomarbeit besteht aus zwei Teilen. Der erste Teil umfasst eine detaillierte Studie über die Morphologie, im speziellen die Blütenentwicklungsmorphologie von *Polypremum procumbens* L. (Tetrachondraceae). Der zweite Teil beschäftigt sich mit der Untersuchung der Blütenentwicklung der Oleaceae. Beide Familien sind derzeit in den basalen Lamiales eingeordnet.

TEIL 1: *POLYPREMUM PROCUMBENS* L. (TETRACHONDRACEAE): VOM SAMEN ZUR FRUCHT.

Die Familie Tetrachondraceae umfasst zwei Gattungen mit insgesamt drei Arten: *Tetrachondra* mit *T. patagonica* und *T. hamiltonii*, und *Polypremum* mit *P. procumbens*. Während *Polypremum* sandigen, eher trockenen Untergrund bevorzugt und von den südlichen USA bis Süd-Amerika verbreitet ist (ROGERS, 1986), ist *Tetrachondra* in feuchten Habitaten Neuseelands und Patagoniens zu finden (WAGSTAFF et al., 2000).

Aufgrund ihres speziellen morphologischen Baus und ihrer winzigen Blüten waren die zwei Gattungen schwierig in die bestehende Systematik einzuordnen. SKOTTSBERG (1913) etablierte die Familie Tetrachondraceae, welche sich neuerdings neben den Familien Plocospermataceae, Carlemanniaceae, Oleaceae, Calceolariaceae und Gesneriaceae an der Basis der Lamiales befindet (OXELMAN et al., 1999; WAGSTAFF et al., 2000; OLMSTEAD et al., 2001; BREMER et al., 2001). Diese Stellung innerhalb der basalen Lamiales ist nun sehr gut abgesichert auf Grund der oben genannten Studien. Aber nur einige wenige vergangene Arbeiten beziehen sich eingehend auf die Morphologie, im besonderen auf die Ontogenese der Blüte. Aus diesem Grund möchte ich hier, beginnend mit einer Beschreibung des Samens, der Keimung und dem Keimling auf die vegetativen Merkmale und besonders auf die Blütenentwicklungsmorphologie und Fruchtentwicklung von *P. procumbens* eingehen.

Pflanzenmaterial von *Polypremum procumbens* wurde während einer Sammelreise nach Costa Rica, in Playa Bejemar, Puntarenas, gesammelt. Für die Beobachtung der Blütenentwicklung wurde die Methodik des Rasterelektronenmikroskops (REM) herangezogen. Weiters wurden im Glashaus des botanischen Institutes in Wien aus Samen Pflanzen für die vegetativen Studien herangezogen.

P. procumbens ist eine perennierende krautige Pflanze, die durch eine dekussierte Blattstellung gekennzeichnet ist. Die spitz zulaufenden, an ihren Rändern leicht gezähnten, amphistomatischen Blätter sind über eine häutige Scheide miteinander verbunden. Dieses Merkmal zeigt sich auch in beiden Arten der Gattung *Tetrachondra*. Auch die in die Blattoberfläche eingesenkten Glandelhaare finden sich bei allen drei Arten wieder (Fig. 7a). Das Verzweigungsschema von *P. procumbens* lässt sich wie folgt beschreiben: Aus den Achseln der ersten zwei bis drei Knoten über dem Kotyledonarknoten entwickeln sich jeweils zwei Seitenachsen in dekussierter Stellung. Aus allen darauffolgenden Knoten, außer dem letzten, aus dem sich ein fortsetzendes Dichasium entwickelt, entsteht jeweils nur eine Seitenachse. Die Seitenachsen sind gekennzeichnet durch irreguläre Dichasien. Besonders hervorzuheben ist die Bildung eines zusätzlichen Blattpaares in medianer Position, welches der Blüte vorausgeht, dieses auch *Tetrachondra* zu besitzen scheint (SKOTTSBERG, 1913). Bemerkenswert ist auch die verschiedenartige Orientierung der Blüte im Bezug auf die Hauptachse: sind die Blattpaare an der blütentragenden Achse in gerader Zahl vorhanden, so stehen die zwei Karpelle in transversaler Position; kommen die Blattpaare in ungerader Zahl vor, so sind die Karpelle median orientiert.

Schon im ersten Jahr trägt die Pflanze zahlreiche kleine weiße Blüten. Diese sind tetramer (inklusive dem Androeceum), aber durch ein dimeres Gynoeceum gekennzeichnet. Dieser Blütenaufbau ist auch bei *Tetrachondra* beschrieben. Mit Hilfe des Rasterelektronenmikroskops (REM) wird nun auf die Blütenentwicklung von *P. procumbens* eingegangen. Die Kelchanlagen entstehen gleichzeitig am Blütenvegetationskegel in diagonaler Position. Später verwachsen sie zu einer kurzen Kelchröhre und die Kelchlappen zeichnen sich durch eine ab-

steigende Aestivation aus (Fig. 4a – i). Alternierend, in orthogonaler Stellung entwickeln sich die Kronblattanlagen. Auch die Petalen fusionieren zu einer Kronröhre (späte Sympetalie) und die abgerundeten Kronlappen sind tellerförmig ausgebreitet. Der Schlund der Kronröhre ist durch viele Perlschnurhaare bedeckt. Alternierend zu den Petalen entwickeln sich zeitgleich die Staubblätter, die in weiterer Folge in die Kronröhre eingefügt sind. Im erwachsenen Zustand neigen sich die Antheren über die Narbe und öffnen sich noch in geschlossenen Blüten. Die Bildung von Perlschnurhaare und die über die Narbe gebeugten Antheren in der geschlossenen Blüte geben einen Hinweis auf Autogamie dieser Art. Die Blüten der Gattung *Tetrachondra* besitzen zwar keine solche Haare, aber auch SKOTTSBERG (1913) beschreibt die über die Narbe geneigten, offenen Antheren in der geschlossenen Blüte und weist auf eine eventuelle Autogamie in *T. patagonica* hin. Das Gynoecium bildet sich aus zwei transversal stehenden Karpellen. Aus diesem entwickelt sich bei *P. procumbens* eine Kapsel, die sich zuerst lokulizid und später noch septizid öffnet, hingegen bei *Tetrachondra* entsteht eine Klausenfrucht, wie man sie bei den Boraginaceae findet.

Beide Gattungen sind sich in ihren Merkmalen sehr ähnlich, auch letztere molekularbiologische Untersuchungen unterstützen diese nahe Verwandtschaft (JENSEN, 2000; OXELMAN et al., 1999). Die Familie Tetrachondraceae wird an die Basis der Lamiales zu den Plocospermataceae, Carlemanniaceae, Oleaceae, Calceolariaceae und Gesneriaceae gestellt (OXELMAN et al., 1999; WAGSTAFF et al., 2000; OLMSTEAD et al., 2001; BREMER et al., 2001).

Um die Ontogenese der Blüte als ein zusätzliches Merkmal in die Systematik einzubringen, spricht die Vierzähligkeit für diese oben genannten Verwandtschaftsverhältnisse. Hingegen die Orientierung der Blüte ist doch eine andere als in nahe verwandten vierzähligen Familien Carlemanniaceae, Oleaceae und Calceolariaceae. Der Kelch entsteht in diagonaler Position, während in den Oleaceae und auch Calceolariaceae ein orthogonal orientierter Kelch vorkommt. Innerhalb der Oleaceae gibt es nur eine Ausnahme, die dasselbe Entwicklungsmuster des Kelches aufweist, *Nyctanthes arbor-tristis*. Dieses Merkmal könnte sich als ein homologes nun innerhalb der Oleaceae geformt

haben und in der etwas abgeleiteteren Familie der Tetrachondraceae wieder aufgetreten sein.

Ein weiterer Trend ist in der Entwicklung des Androeceums zu finden. Carlemanniaceae, Oleaceae und Calceolariaceae als sehr basale Familien sind durch ein dimeres Androeceum gekennzeichnet. Nur innerhalb des etwas abgeleiteteren Tribus Oleinae der Oleaceae finden sich auch Gattungen und Arten mit vier Staubblättern. Diese Tetramerie des Androeceums zieht sich durch viele Familien der Lamiales. Somit könnte sich die Tetramerie des Androeceums aus der Dimerie, und nicht umgekehrt, wie von ENDRESS (1999) dargestellt, entwickelt haben.

TEIL 2: BLÜTENENTWICKLUNG DER OLEACEAE

Die Familie der Oleaceae umfasst derzeit 25 Gattungen mit rund 200 Arten, welche sowohl alt- als auch neuweltlich, vom temperaten Klima bis in die Tropen verbreitet sind. Einige Arten werden als Nutz- und Zierpflanzen in weiten Teilen der Welt kultiviert (Olivenbaum, Flieder, Liguster,...).

Die Oleaceae wurden in die Scrophulariales (CRONQUIST, 1981), Oleales (TAKHTAJAN, 1986) aber auch Gentianales (HUBER, 1991) eingeordnet. Heute findet man die Familie an der Basis der Lamiales, gemeinsam mit Plocospermataceae, Carlemanniaceae, Tetrachondraceae and Calceolariaceae (OXELMAN et al., 1999; OLMSTEAD et al., 2001; BREMER et al., 2001).

Auch die molekularsystematischen Verwandtschaftsverhältnisse innerhalb der Familie wurden kürzlich durch eine Arbeit von WALLANDER & ALBERT (2000) geklärt. Obwohl die Familie als monophyletisch erscheint, ist sie durch eine Vielfältigkeit an morphologischen Merkmalen gekennzeichnet. Besonders im Blütenaufbau und in der Blütenentwicklung zeigen einige Gattungen Abweichungen vom Grundbauplan. Frühere Studien befassten sich eingehend mit dem Auffinden eines solchen Grundbauplans der Oleaceen-Blüte (EICHLER, 1875; TORGÅRD,1924; WEBER, 1928).

In der vorliegenden Studie wurde die Blütenentwicklung von 15 Arten aus 10 Gattungen mit Hilfe des Rasterelektronenmikroskops untersucht: (1) zur Klärung des Blütenbaus innerhalb der Familie, (2) zur Diskussion dieses morpho-

logischen Charakters bezüglich der neuen intrafamiliären Systematik und (3) zur Diskussion des Blütenbaus der nächst verwandten Familien.

Folgendes bestimmtes Muster der Blütenentwicklung zieht sich durch die ganze Familie:

KELCH – tetramer, monozyklisch, in orthogonaler Stellung

KRONE – tetramer, monozyklisch, in diagonaler Stellung

ANDROECEUM – dimer/tetramer, monozyklisch, in transversaler Orientierung

GYNOECEUM – dimer und monozyklisch, in medianer Orientierung.

Abweichungen im Kelch findet man vor allem in den basalen Triben in den Gattungen *Nyctanthes*, *Jasminum* und *Menodora*, welche einen pleiomeren Kelch ausbilden. In einigen Arten von *Fraxinus*, *Forestiera* und *Priogymnanthus* kann der Kelch auch abortiert sein. Tendenz zu einer pleiomeren Korolle ist in den Gattungen *Nyctanthes*, *Jasminum*, *Menodora* und *Schrebera* zu erkennen, wobei es bei *Fraxinus* und *Forestiera* wieder zu Ausfällen derselben kommen kann.

Dieses oben geschilderte Schema des Blütenbaus stimmt nur in Teilen mit jenen aus vergangenen Studien überein (EICHLER, 1875; TORGÅRD,1924; WEBER, 1928).

(1) EICHLER (1875) charakterisierte den Kelch als dimer und dicyclisch. Die monozyclische Korolle als tetramer und sowohl das Androeceum als auch Gynoeceum als dimer und monozyklisch.

(2) TORGÅRD (1924) hingegen beschrieb den Grundbauplan, wie man ihn in *Fraxinus dipetala* erkennt: S_{2+2}, C_2, A_2, G_2. Die tetramere Krone soll daher durch Spaltung aus den zwei primären Kronblattprimordien entstanden sein.

(3) WEBER (1928) stellte den Bauplan der Blüte als durchwegs dimer und dicyklisch dar (inklusive Androeceum und Gynoeceum).

Die Ergebnisse aus den Studien der Blütenentwicklung machen einen dizyklischen Aufbau, wie ihn WEBER (1918) beschreibt, unwahrscheinlich. Die Primor-

dien eines Organs werden zeitgleich in einem Wirtel angelegt. Es findet keine topographisch verschobene und chronologisch spätere Insertion weiterer Primordien statt, die auf Dizyklie hinweisen würde.

Auch die Dimerie des Perianths wird durch die Ergebnisse dieser Studie widerlegt. Ontogenetisch entsteht ein ganz klar vierzähliger, monozyklischer Kelch (cf. *Fontanesia*, *Syringa*, *Ligustrum*, *Chionanthus*, *Olea*, *Phillyrea*). Sogar in *Jasminum* wurden teratologische Formen mit einem tetrameren Kelch gefunden. Die Krone wird schon von EICHLER (1875) als tetramer und monozyklisch beschrieben. Meine Ergebnisse sind mit denen Eichlers konform. Kein Hinweis in ontogenetischer Hinsicht wurde hinsichtlich Dimerie in der Krone gefunden.

Das Androeceum wird als durchwegs dimer und monozyklisch beschrieben, das auch mit den Ergebnissen der aktuellen Studie übereinstimmt. Ausnahmen bilden Gattungen des Tribus Oleeae, vor allem innerhalb des Subtribus Oleinae, die ein tetrameres Andoeceum ausbilden. Weiters finden sich in einigen Gattungen/Arten innerhalb der Oleeae teratologisch vier Stamina.

INTRAFAMILIÄRE VERWANDTSCHAFTSVERHÄLTNISSE

Dieser oben genannte Bauplan der Blüte zieht sich durch die ganze Familie: von den basalsten Triben (z.B. *Fontanesia*) bis zu den abgeleiteten Oleeae. Somit kann die Familie selbst durch diesen Grundbauplan sehr gut definiert werden. Intrafamiliär wird es schwieriger, systematische Schlüsse zu ziehen. Basal trifft man sowohl auf Tetra- als auch auf Pleiomerie im Perianth. Je abgeleiteter die Triben, desto stabiler ist der Grundbauplan.

Nun darf man aber das pleiomere Perianth nicht als ursprüngliches primitives Merkmal ansehen. Durch die Ergebnisse dieser Studie wurde bewiesen, dass dem pleiomeren Perianth stets ein tetrameres zugrunde liegt und die Pleiomerie des Perianths somit als ein abgeleitetes Merkmal innerhalb der Familie gedeutet werden kann.

Hinsichtlich der Sympetalie in der Familie zeigt sich ein ähnliches Muster. An der Basis findet man eher früh sympetale Vertreter, aber auch solche, die keine Sympetalie aufweisen. Hingegen innerhalb der Oleinae sind spät sympetale Vertreter anzutreffen. Diese Ergebnisse widersprechen jenen von ERBAR

(1991), die die Oleaceae, nach der Analyse von nur zwei Arten (*Syringa vulgaris* und *Fraxinus ornus*) als rein früh sympetal charakterisierte.

GLIEDERUNG INNERHALB DER BASALEN LAMIALES

Die Oleaceae werden, basierend auf molekularsystematische Daten, gemeinsam mit den Carlemanniaceae nach den Plocospermataceae und vor den Tetrachondraceae und Calceolariaceae an die Basis der Lamiales gestellt (OXELMAN et al., 1999; BREMER et al., 2001; OLMSTEAD et al. 2001). Diese Einordnung wird auch durch die Morphologie weitestgehend bestätigt.

Die Oleaceae weisen viele Gemeinsamkeiten mit den Carlemanniaceae hinsichtlich der Zähligkeit der Blüte auf. Beide Familien sind durch ein tetrameres (teilweise pleiomeres) Perianth und ein dimeres Androeceum gekennzeichnet.

Auch die Calceolariaceae zeigen einen ähnlichen Blütenaufbau hinsichtlich ihrer Zähligkeit wie die Oleaceae. Der Kelch und die Krone sind tetrameren Ursprungs und das Androeceum ist durch Dimerie gekennzeichnet. Im adulten Zustand kommt es bei den Calceolarien zur Ausbildung einer Ober- und Unterlippe, die bei den Oleaceae nur sehr ansatzweise bei der Insertion der Petalen bei Ligustrum zu finden ist, in weiterer Entwicklung aber nicht vorhanden ist.

Die Tetrachondraceae sind durchwegs tetramer (inklusive Androeceum) und passen somit sehr gut in die Verwandtschaft der Oleaceae. Nur die Orientierung der Blüte ist eine andere. Die Blüte der Tetrachondraceae scheint um 90° gedreht zu sein im Bezug auf die Oleaceen-Blüte. Innerhalb der Oleaceae findet sich ein Hinweis auf eine solche Orientierung nur bei *Nyctanthes arbortristis*, dessen Kelch auch in diagonaler Position angelegt wird. Dieses homologe Merkmal lässt auf einen eventuellen gemeinsamen Vorfahren schließen und bestätigt somit die nahe Verwandtschaft der beiden Familien. Ein weiterer Trend ist in der Entwicklung der Stamina zu finden: Ungeachtet der Orientierung, auf Grund der Blütenentwicklung, kann man auf eine Erhöhung der Anzahl der Stamina von zwei auf vier annehmen. Dieser Trend ist sowohl innerhalb der Oleaceae erkennbar als auch innerhalb der basalen Lamiales.

Die Ordnung der Lamiales ist gekennzeichnet durch vorwiegend späte Sympetalie in der Blüte. Auch die den Oleaceae nahe stehenden Familien Gesneriaceae, Calceolariaceae und Tetrachondraceae weisen dieses Merkmal auf. Man könnte meinen, dass sich die späte Sympetalie innerhalb der Oleaceae entwickelt hat und in den weiteren Familien etablierte.

Auf Grund dieser gewonnenen Erkenntnisse scheint die Stellung an der Basis der Lamiales die richtige zu sein. Die Familie ist in ihren Merkmalen noch recht divers und weist auf einige Trends hin, die sich in weiterer Folge erst fixiert haben.

PART 1

POLYPREMUM PROCUMBENS L. (TETRACHONDRACEAE): FROM SEED TO FRUIT.

ABSTRACT

Polypremum procumbens is one of the 3 species of Tetrachondraceae, which family is referred to basal Lamiales by recent molecular studies. The plant is an annual to short-lived perennial herb, flowering already in the first year. The main axis comprises several nodes of decussate leaves and ends in a terminal flower. Side branches are dichasially branched, but the branches bear not only the prophylls, but there is an additional median leaf pair preceding the flower. The flowers are tetramerous (incl. androecium) and have a dimerous gynoecium. SEM-study of development shows a successive emergence of the floral organs. The sepal primordia emerge simultaneously and fuse basally. Later, the upper sepals embrace the lower ones, resulting in a descending aestivation. Also the petals fuse basally in a late stage (late sympetaly). The corolla mouth is closed by a ring of hairs, apparently supporting autogamy. The capsular fruit opens septicidally and then loculicidally. The merosity of the *Polypremum* flowers fits well into the alliance of Oleaceae, but the flower orientation is different, with the sepals emerging diagonally and the gynoecium appearing in a transversal position.

INTRODUCTION

In the family Tetrachondraceae there are two genera comprising three species: The genus *Tetrachondra* comprises two species, *T. patagonica* and *T. hamiltonii*. Their distribution is disjunct and separated by the Pacific: *T. patagonica* occurs in Patagonia, South America, and *T. hamiltonii* is restricted to New Zealand. Their origin is suggested to be in South America, and *T. hamiltonii* probably reached New Zealand due to long-distance dispersal. Anyhow, both species are found now in aquatic or semiaquatic habitats along lake or river margins (WAGSTAFF et al., 2000). The genus *Polypremum* consists of the sole species *Polypremum procumbens* L. Its distribution ranges from the eastern United States and Mexico over the West Indies to Central and South America. Its preferred habitats are open localities, where the plants grow on sandy soil or even on bare sand (ROGERS, 1986).

Formerly, the two genera proved difficult to assign, mainly because of their minute flowers and their peculiar morphology.

HAMILTON (1885) originally placed the two species of *Tetrachondra* in the genus *Tilliaea* (Crassulaceae). PETRIE (in OLIVER, 1892) established the genus *Tetrachondra* and included it in Boraginaceae. Later, *Tetrachondra* was placed in Scrophulariaceae (HALLIER, 1902; ENGLER & PRANTL, 1908), Lamiaceae (subfamily Tetrachondroideae, TAKHTAJAN, 1980) or in a family of its own, Tetrachondraceae (SKOTTSBERG, 1913). Recent molecular data based upon *rbc*L and *ndh*F sequences and phytochemical results suggest a position within basal Lamiales and indicate that *Polypremum* is the sister genus (OXELMAN et al., 1999; JENSEN, 2000; WAGSTAFF et al., 2000). Until these studies the genus *Tetrachondra* was treated as monotypic.

Polypremum underwent a similar odyssey in its classification. It has been (mis)placed in Rubiaceae (DE CANDOLLE, 1830; LINDLEY, 1836; BUREAU, 1856), Loganiaceae–Loganieae (former “Euloganieae”) (DE CANDOLLE, 1845; BENTHAM, 1857; SOLEREDER, 1895; HUTCHINSON, 1959), or in Loganiaceae–Buddleioideae (SOLEREDER, 1895) and Buddlejaceae (DOP, 1923; SCOGIN & ROMO-CONTRERAS,

1992). OXELMAN et al. (1999) and JENSEN (2000), using molecular and chemical characters, were the first to find a close relationship between *Polypremum* and *Tetrachondra*. The two genera are thus now combined in the family Tetrachondraceae. The family is placed in basal Lamiales, emerging after Plocospermataceae, Oleaceae and Carlemanniaceae, and before the recently established Calceolariaceae (OLMSTEAD et al., 2001) and before Gesneriaceae (OXELMAN et al., 1999; WAGSTAFF et al., 2000; BREMER et al., 2001).

Though the systematic position of the family seems clarified, its available morphology is still incompletely. Only HOLM (1924) presented a morphological study of *Polypremum*, which describes the habit, inflorescence and flower structure, and the anatomical structure of the vegetative organs in some detail. Furthermore, MOORE (1947, 1948) described the karyology and embryology of *Polypremum* for clarifying the disputed systematic position of the genus. The morphology and anatomy of *Tetrachondra patagonica* was described by SKOTTSBERG (1913).

During a field trip to Costa Rica, I was lucky to encounter a population of *Polypremum procumbens*. Back in Vienna, I cultivated and analysed the material. In this study, I can present a detailed morphological survey of *Polypremum*, focusing on the floral development. At first, the seed, seed germination, and seedling are described. Then I treat the habit and branching system, the flower development, pollination and fruit development.

The further aims of this study are (1) to compare the present results with those of past studies and those relating to *Tetrachondra*, and (2) to compare these results with data of families currently included in basal Lamiales.

MATERIALS & METHODS

Material of *Polypremum procumbens* L. was collected in the natural habitat, Playa Bejemar, Puntarenas, Costa Rica, in March 2004. Flowers and buds were fixed in 70% ethanol in the field. In the laboratory, the material was dissected in alcohol under a stereomicroscope, transferred into Formaldehyd-dimethyl-acetal (FDA) over night for dehydration, critical-point-dried in a Balzers Critical Point Dryer 030, using liquid CO_2, and mounted on stubs. After coating with gold-palladium in a Balzers Sputter Coater, the samples were viewed and photographed at 15kV in a Jeol T-300 scanning electron microscope.

For studying the habit, branching system, flower, pollination and fruit development, seeds were collected in the above locality and grown in a glasshouse at the Botanical Garden of Vienna. To determine if *Polypremum procumbens* is autogamous, some individuals were bagged and observed during several weeks. To study the germination and the development of the seedling, some seeds were sown and grown in petri dishes with filter paper and photographed with a Nikon D100 camera attached to a stereomicroscope (Olympus Europe SZH).

SEEDS

The seeds are small, about 250-300µm in diameter, and of a translucent yellowish-brown colour when mature. The shape is roughly isodiametric or irregularly polygonal. The distal end is flattened and wider than the proximal end. The seed coat surface is faintly reticulate-rugulose (Fig. 1a). In some seeds the remnants of the funicle are visible (Fig. 6l).

SEED GERMINATION AND SEEDLING

Germination is of the epigeal-phanerocotylar type. As shown in Fig. 1, root hairs grow out early from the base of the hypocotyl. During elongation of the hypocotyl, greening of the cotyledons within the testa takes place (Fig. 1c, d). At first, the cotyledons are tightly pressed together like praying hands (appressed vernation) in a nodding position. During early growth, the testa dries up and sometimes remains on one of the cotyledons before dropping. Then the cotyledons expand and develop into symmetrical, sessile, linear to narrowly lanceolate, green leafy organs (Fig. 1e). The twisting of the root in the seedlings of Fig. 1 is due to germination in flat petri dishes. During these early stages lateral roots do not develop.

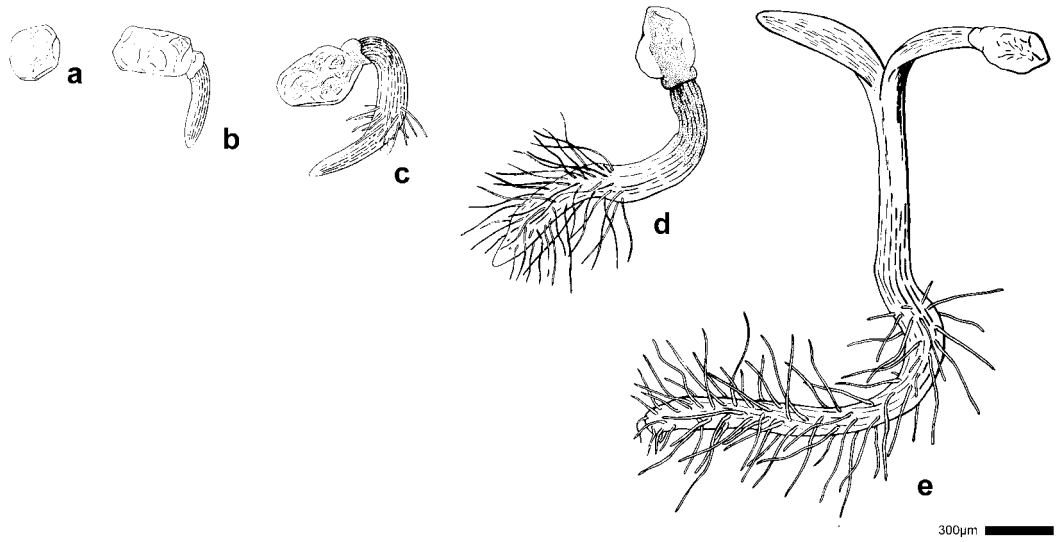

Fig. 1: *Polypremum procumbens*. Seed and seedlings in various stages. (c and d) Dotting indicates greening of the cotyledons. Scale bar: 300µm.

ROOT AND SHOOT SYSTEM

The young plant consists of a single ascending shoot axis and a well-developed primary root, from which successively lateral roots emerge endogenously (Fig. 3a, d). On average, at the 11th node (counted from the base, including the node of the cotyledons) the primary shoot axis produces a terminal flower. The basal internodes of the shoot axis are very short and terete; the upper ones are elongated and become progressively four-angled. The surface of the stem angles is more or less scabrid.

The leaves are opposite, sessile and of a uniform shape. Like the cotyledons, they are linear to narrowly lanceolate. The length is about 2 to 2,5cm, the width 3 to 4mm. The leaves are usually widest near or slightly above the middle. The opposed leaves of a pair are joined basally by a short membranaceous sheath. On the abaxial side the leaves are ciliolate to slightly scabrid along the margins and along the midrib. The lamina is covered with minute, sunken glandular hairs made up of a basal cell, a stalk cell, and a head usually comprising four cells (Fig. 8a).

The ramification of the main axis is somewhat variable. The development of the lateral shoots in the middle part of the main axis lags slightly behind the uppermost and the lower leaves. The two or sometimes three nodes above the cotyledons produce 2 axillary shoots each. These shoots occupy a decussate position, reflecting the position of the leaves. The following nodes, except the uppermost one, produce only one lateral shoot per node (in Fig. 3b and d noted as II, III, IV and V) in a definitely spiral arrangement. Each lateral shoot is also defined as a partial inflorescence of the whole branching system. The partial inflorescences (= lateral shoots, as shown in Fig. 3a') are cymosely branched. There is a clear gradient in the branching of the partial inflorescences. With increasing height, the number of nodes of the lateral shoots is reduced. The basal most lateral shoots comprise up to six nodes, and are slightly procumbent (Fig. 3b, d).

The lateral shoots of the main axis, except the uppermost ones, comprise several leaf pairs in decussate arrangement. These leaf pairs are referred here

to bracteoles. The term prophylls is not very appropriate in this case (by definition, prophylls are the first pair of leaves on a lateral shoot). After the last pair of bracteoles, the (terminal) flower follows. The internode between the two last bracteole pairs is very short, so that the flower is neatly embedded within these leaves. These four preceding bracteoles of the flower are of the same shape and size as the other bracteoles of the lateral shoot. The orientation of the (terminal) flowers of the lateral shoots depends on how many bracteole pairs have developed: if the number of bracteole pairs at the lateral shoot is even, then the two carpels of the flower appear in transversal position (the last bracteole pair is arranged in the median). But if the number is odd, the carpels occur in median orientation and the last bracteole pair is thus orientated in transversal position.

From the uppermost node of the main axis two lateral shoots emerge, so that a terminal dichasium is formed (denoted as I in Fig. 3b). The lateral shoots themselves represent somewhat irregular dichasia or transitions to cincinni ("dichasial-cincinnal" cymes, see TROLL, 1964; Fig. 3a – c). The orientation of the flowers within the dichasium is always in the way that the carpels of the flowers in first order are placed in transversal position pertaining to the main axis, the carpels of the flowers in second order in median position, those of flowers in third order in transversal position, and so on and so far (Fig. 2).

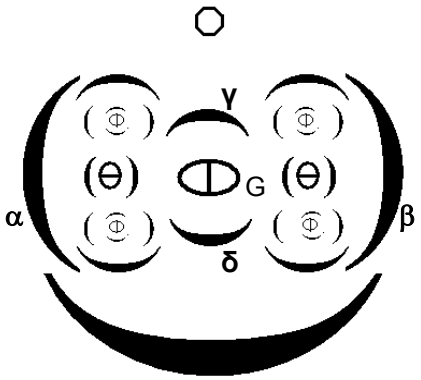

Fig. 2: *Polypremum procumbens*. Orientation of the carpels within the dichasium. α, β = lateral bracteole pair. γ, δ = median bracteole pair. G = gynoecium. Circle represents shoot axis.

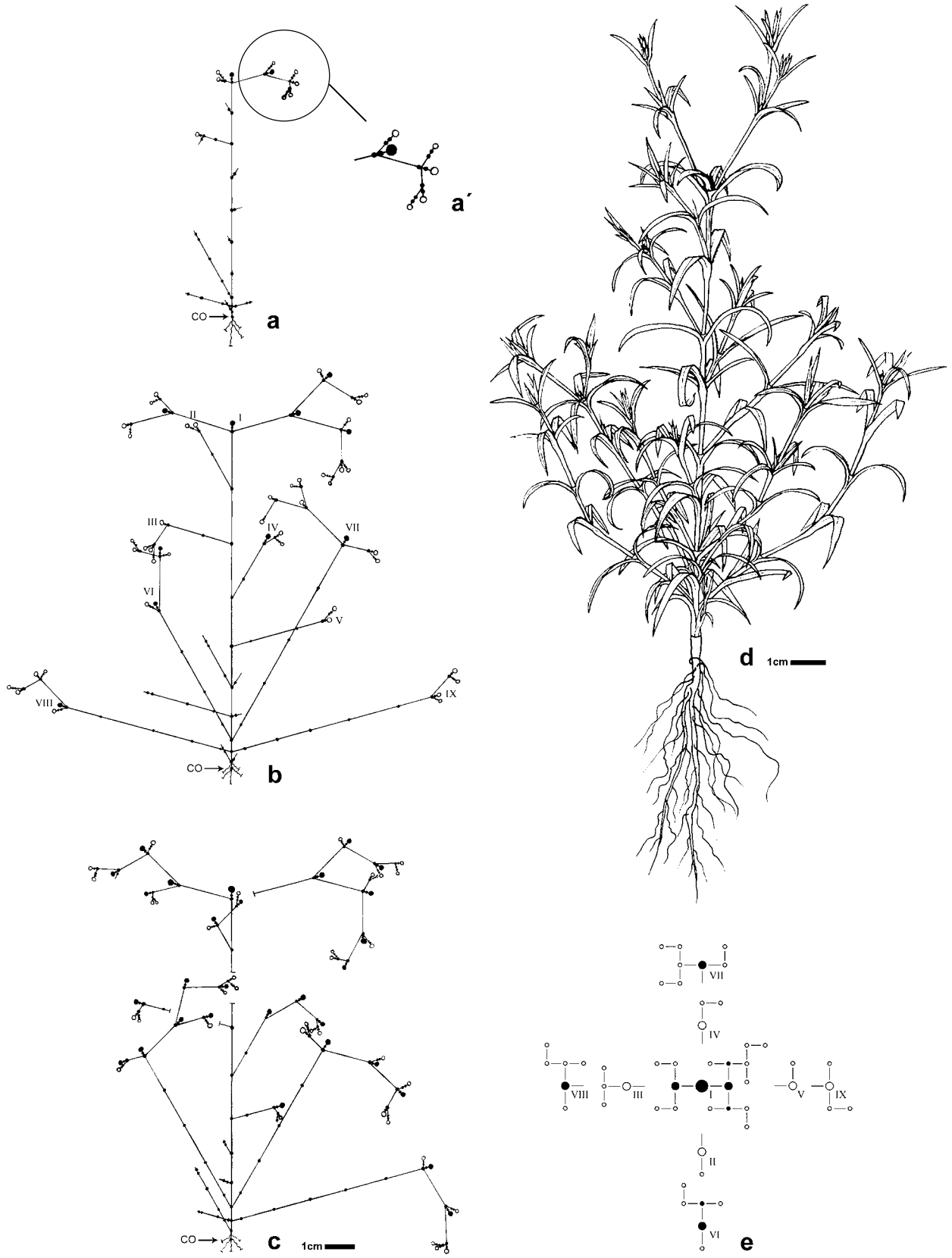

Fig. 3: *Polypremum procumbens*. (a – d) Diagrams of plants in various developmental stages. (a') Partial inflorescence. (d) Selected adult plant. (e) Branching pattern in upper view pertaining to b. (b and e) Schematic diagrams of the plant in d, I reflects the uppermost node, II – IX indicate well developed lateral shoots. Open circles: flowers, black circles: fruits, co = cotyledonary node. Scale bars: 1cm.

FLOWER ORGANOGRAPHY

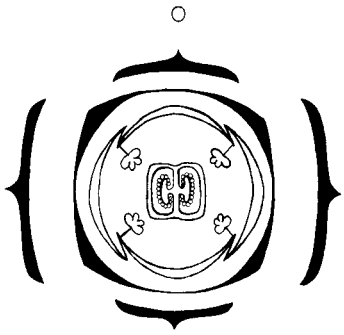

Fig. 4: Floral diagram. Subtending bracteoles and sepals are in black; petals are white. Circle represents shoot axis.

The minute flowers of *P. procumbens* are hermaphrodite. The tetramerous calyx is deeply four-parted, with the sepals connected at the base. The lanceolate calyx lobes are scabrous along their margins and along the midrib, and persist in the adult flower. The corolla is tetramerous, actinomorphic, subrotate to campanulate, and snowy white. The orbicular lobes are basally joined to form a short corolla. The corolla is bearded in the throat by the presence of a line of white hairs. The four stamens alternate with the corolla lobes and are attached to the middle of the corolla tube. The anthers are introrse and open by longitudinal slits. The gynoecium is bicarpellate and flask-shaped. The ovary is partly inferior with a terminal style terminating in a capitate stigma. The fruit is a laterally compressed capsule. Each locule has one peltate placenta, which is attached to the base of the septum. The capsule opens septicidally and loculicidally, and releases numerous small seeds.

FLORAL DEVELOPMENT

In plates 5 – 7 the flowers are oriented in the way that the adaxial side is on top and the abaxial side directs downwards (cf. Fig. 4).

EARLY DEVELOPMENT AND CALYX FORMATION

Just before the emergence of the sepal primordia, the floral meristem is quadratic in outline. It is embedded between the two pairs of bracteoles and is about 50µm in diameter. At the edges of the floral meristem the primordia of the four sepals are the first to take shape (Fig. 5a). Already in this early stage and into following stages, a lateral compression of the developing flower can be observed (Fig. 5b). Between the sepal primordia meristematic bridges are formed. The basal margins of the primordia accrete and arise together, resulting in a

synsepalous calyx (Fig. 5b, c). The petal and the stamen primordia are initiated almost at the same time, sometimes the petals even lag behind (Fig. 5c). Until this stage the floral apex shows no trace of the gynoecium. The calyx lobes grow up and curve inwards to cover the inner floral organs (Fig. 5d – f). In the majority of cases, the two adaxial calyx lobes overlap the abaxial ones (descending aestivation). As organogenesis progresses, the calyx lobes reopen and get their adult structure, retaining their special overlapping position (Fig. 5g – j).

Corolla and Androecium

As mentioned above, the primordia of the corolla and the androecium are initiated nearly simultaneously (Fig. 6a), but the development of the petal primordia lags behind. The shape of the petal primordia is slightly angular, due to the restricted space inside the bud. Later on, the corolla lobes elongate and cover the stamen primordia. At the back of the stamens, interprimordial meristematic bulges are formed which connect the initially free petal primordia (late sympetaly) (Fig. 6c). While growing further up, the corolla lobes become rounded and the two transversal lobes begin to overlap the median ones, showing imbricate aestivation (Fig. 6e). In Fig. 6f a totally open flower is shown, presenting all the structures of an adult flower.

To demonstrate the development of the androecium, the calyx and corolla lobes have been removed in Fig. 6. In the stage of Fig. 6d, the previously globose stamens taper (Fig. 6g). The anthers become four-angled, then the differentiation of the four pollen sacs follows. The pollen sacs bulge out and the connectives differentiate (Fig. 6h, i). Mature stamens are shown in Fig. 6j and k. The anthers bend inwards over the stigma due to the curvature of the filament, dehiscing by longitudinal slits and shaking out the pollen grains onto the stigma.

Pollen

The pollen grains are around 10µm in diameter, elliptic in equatorial view and roundish in polar view, and tricolporate. The apertures are arranged equidistantly around the equator (zonotricolporate). The pollen surface is tectate-perforate (Fig. 6l).

GYNOECIUM AND FRUIT

By removing the stamens, the gynoecium becomes visible. The carpels begin to arise in the stage shown in Fig. 6d. The two carpel primordia of flowers within the dichasium are arranged in transversal position. They grow up by building a septum (Fig. 7a – c) and develop into a partly inferior gynoecium. On the surface the imprints of the stamens are visible. In the adult stage, but before pollination, the pistil is bottle-shaped. The stigma is papillose and shows a slight invagination in the median (Fig. 7d, e). After pollination, the papillae increase in size and pollen grains stick on their mucilaginous surface (Fig. 7f, g). After fertilization, the stigma papillae dry up and the ovary increases in size, showing a constriction in the median, at the position of the septum (Fig. 7h). Expansion of the ovary in transverse direction follows within the persistent calyx lobes. As shown in Fig. 7j, the mature capsule opens septicidally at first and then also loculicidally. In the ovary cavity the long, narrow and erect placenta is inserted near the base of the septum (Fig. 8f). Many seed funicles, forming cup-shaped cushions with a conspicuous abscission scar in the centre, cover the placental surface all over (Fig. 7k).

BREEDING SYSTEM

Some morphological structures point to autogamy: the ring of hairs bends over the throat and possibly prevents the entrance of insects (Fig. 8d, 9b). Also the anthers are arranged in a way that the pollen grains are shaken out onto the stigma of the same flower by slight vibration, caused by wind, passing animals, etc. (Fig. 6j, k). No special characters (i.e. nectaries, bright colours) are present for attracting pollinators. The flowers are minute and the corolla drops after one day. Under severe conditions (which may occur also in the glass house) the flowers sometimes do not open; nonetheless they develop fruits (partial cleistogamy).

In order to prove autogamy, the plants were bagged for several weeks to prevent contact with insects. Indeed, 100% of the flowers developed into fruits. Thus, it is clear, that *Polypremum procumbens* is self-fertile and autogamous.

EMBRYOLOGY, KARYOLOGY AND PHYTOCHEMISTRY

To complete the description of *Polypremum procumbens*, a short summary of the embryology and karyology by MOORE (1947, 1948) and the phytochemistry by (JENSEN, 2000) is given:

MOORE (1947, 1948) described, that the ovules are anatropous, tenuinucellate and unitegmic. The megaspore mother cell develops from a single hypodermal primary archesporial cell and divides, forming four megaspores in a linear tetrad. The chalazal megaspore develops into the embryo sac. The mature embryo sac is unusual in that its micropylar and antipodal ends extend to the surface of the ovule, forming non-aggressive haustoria. They do not invade the tissue of the parent sporophyte, even in advanced stages. Endosperm development is of the cellular type. With progressive endosperm growth, the cell walls adjacent to the endosperm thicken markedly and form a conspicuous wall enclosing the entire endosperm except the haustoria. After a considerable amount of endosperm has been formed, the zygote moves from the micropylar end of the embryo sac into the central region and divides. It is probable, that the movement of the zygote is effected by fluid pressure.

The proembryo consists of six cells. The micropylar cell elongates to some degree and serves as a suspensor. Further cell divisions lead to a spherical embryo. This remains connected with the suspensor which is composed of a single row of several cells.

MOORE (1947) also studied chromosomal features and found out, that *P. procumbens* contains a haploid chromosome number of n=11.

JENSEN (2000) identified as main components sorbitol and cornoside. Less abundant are salidroside and conandroside. No iridoids and verbascosides were found in the extract.

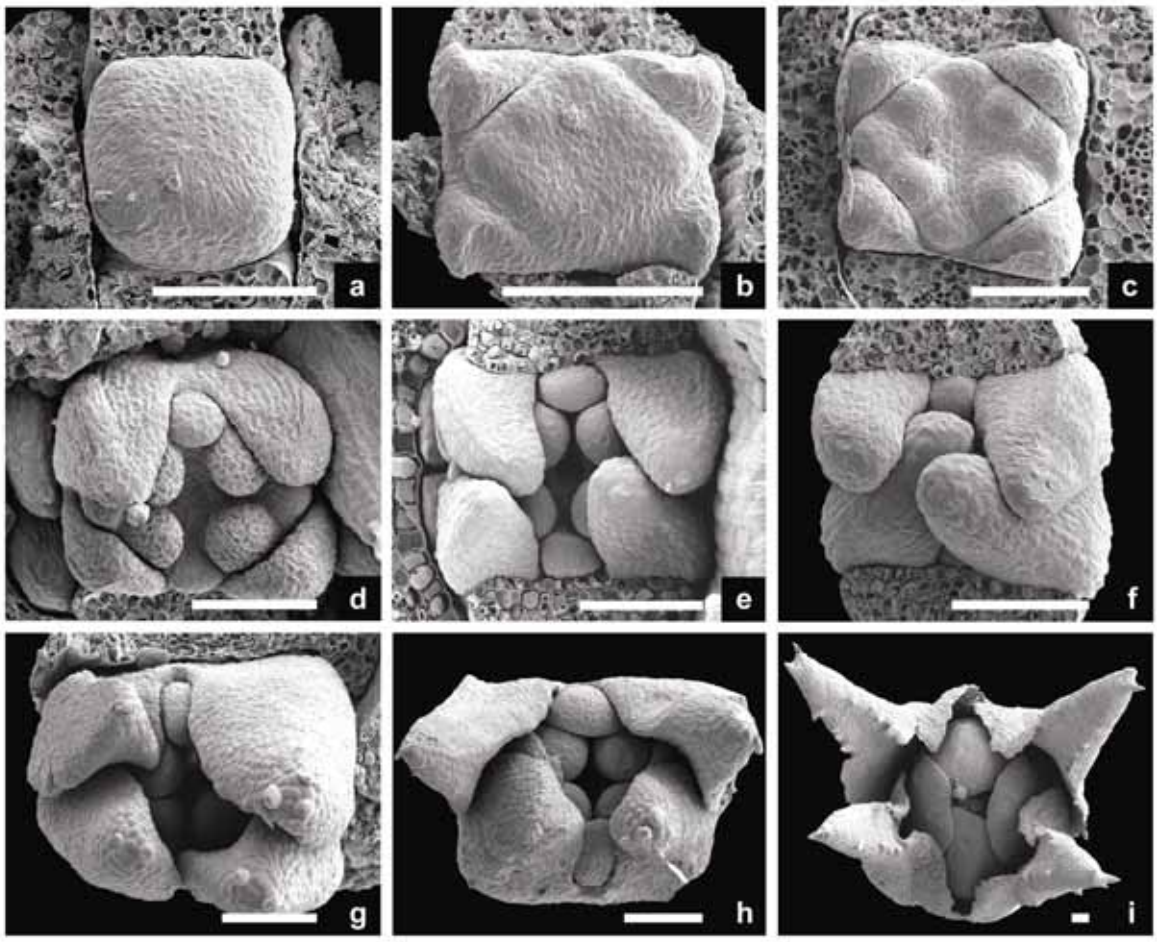

Fig. 5: *Polypremum procumbens*, floral development, ontogeny of the calyx. (a) Floral primordium embedded in the two pairs of bracteoles. (b) Initiation of the sepal primordia. (c) Formation of the petal and stamen primordia. (c – h) Further growth of the calyx lobes; note that the adaxial lobes overlap the abaxial ones. (i) Floral bud. Bracteoles removed in a – g. Scanning electron micrographs; scale bars: 100µm.

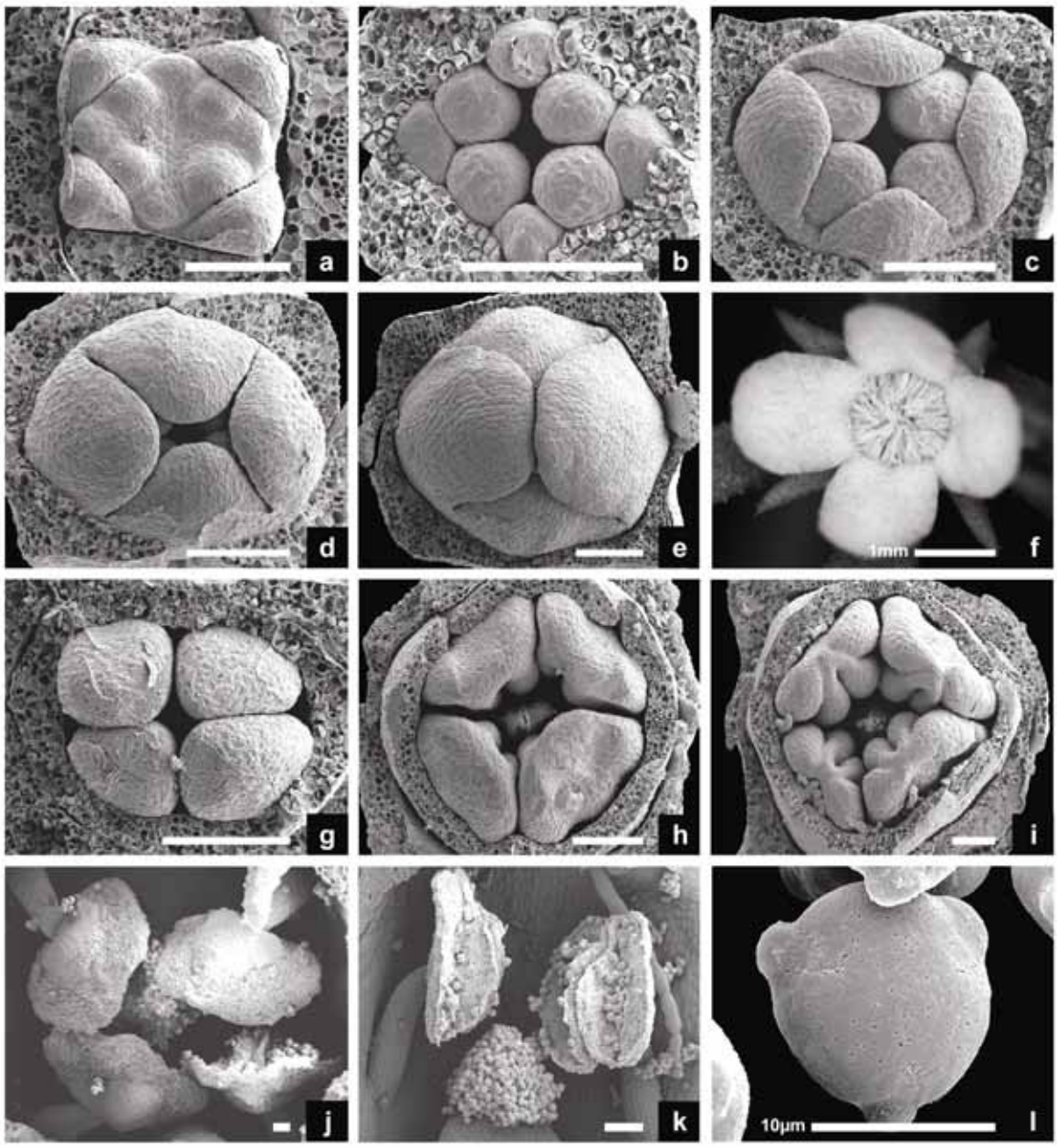

Fig. 6: *Polypremum procumbens*, floral development, ontogeny of the corolla and androecium. (a) Initiation of the petal and stamen primordia (bracteoles removed). (b and c) Growth of both organs (calyx removed). (d – f) Development of the corolla. (g – j) Development of the stamens (perianth removed). (k) Lateral view of a part of the androecium and the stigma; note the special position of the anthers. (l) Zonotricolporate pollen grain. Scanning electron micrographs, one photograph (f); scale bars: 100µm, 1mm (f), 10µm (l).

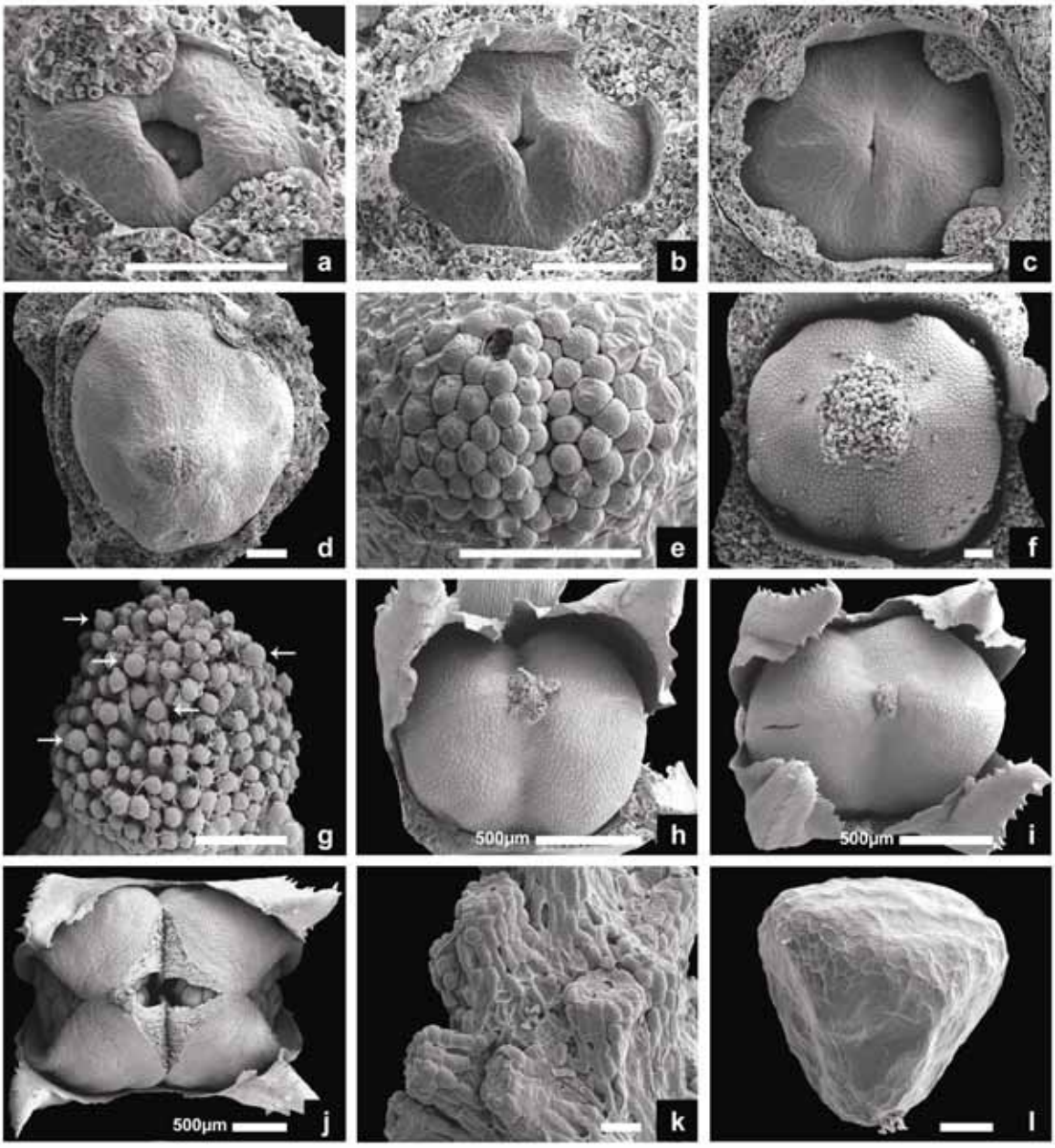

Fig. 7: *Polypremum procumbens*, floral development, ontogeny of the gynoecium and formation of the fruit. (a) Initiation of the carpel primordia. (b – d) Growth of the ovary. (e) Papillose surface of the stigma. (a – e) Development before pollination (perianth and androecium removed). (f) Pollen grains on the surface of the stigma and ovary (perianth and androecium removed). (g) Arrows point at singular pollen grains sticking on the papillose stigma. (h – j) Development of the capsule. (k) Surface of the placenta. (l) Seed. Scanning electron micrographs; scale bars: 100µm, 500µm (h – j).

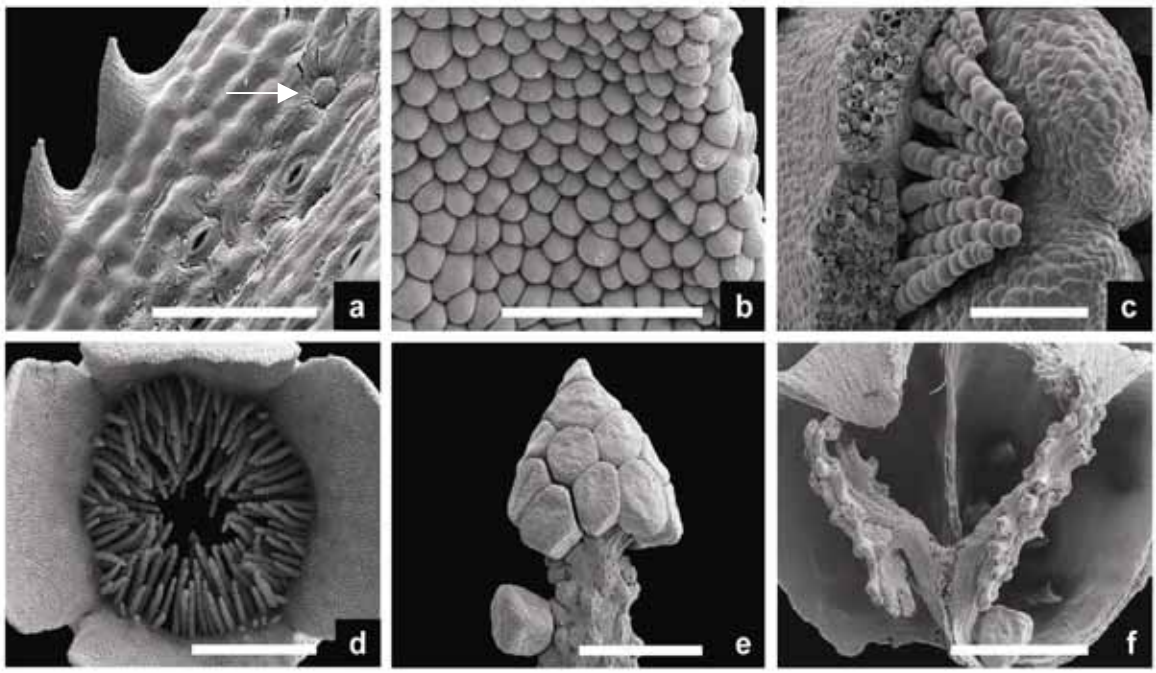

Fig. 8: *Polypremum procumbens,* morphological details. (a) Surface of a leaf, the arrow points at a glandular hair. (b) Structured surface of a petal lobe. (c and d) Hairs developed by the corolla. (e) Seeds on the placenta. (f) Position of the placenta. Scanning electron micrographs; scale bars: 100µm.

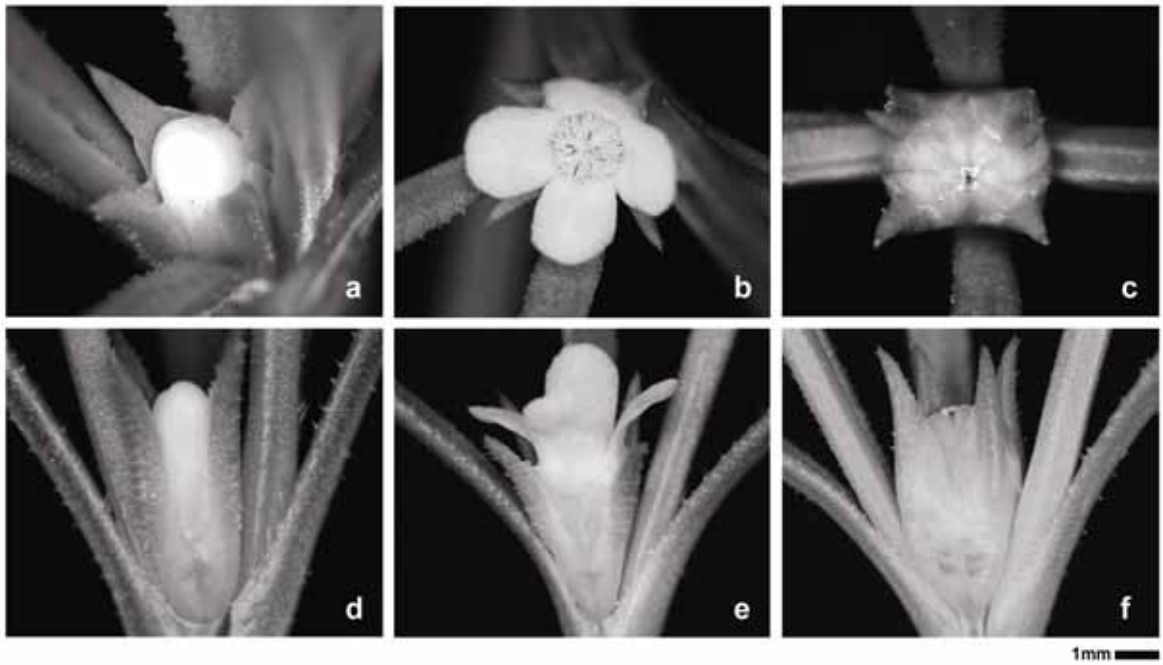

Fig. 9: *Polypremum procumbens*, a bud, open flower and fruit in upper view (a – c) and lateral view (d – f). Scale bar: 1mm.

DISCUSSION

MORPHOLOGY OF *POLYPREMUM*

HOLM (1924) was the only author, presenting a somewhat detailed study of the morphology and particularly anatomy of *Polypremum procumbens*. Several discrepancies of the results of this past and the current study exist. A short description of the whole family Tetrachondraceae was given recently by WAGSTAFF (2004). My results agree completely with this recent characterisation, and moreover, some gaps can be filled.

The description of the seeds is in agreement to the present study. But neither HOLM (1924) nor WAGSTAFF (2004) referred to the germination and the seedling structure. The present documentation of phanerocotylar germination is the first one.

Depending the vegetative structure and branching pattern, HOLM (1924) said that in the first season only a single stem is developed, which is mostly vegetative with few flowers appearing at the apex. In my material I discovered the converse: all the individuals bear numerous flowers. Already in these early stages the plant is well developed in its habit as shown in Fig. 3d. HOLM (1924) described that at the end of the season the flower-bearing stems die down to the ground, while some shoots, having developed from the axils of the basal leaves and from the axils of the cotyledons, overwinter. During the following seasons short basal shoots emerge, forming a large cushion from which many flower-bearing stems develop.

HOLM (1924) gave a rough description of the branching pattern of the lateral shoots. He referred to a regularly branched dichasium, but a better survey reveals that an irregular dichasium is more likely. The branching pattern of the main axis itself has not been done in detail in the past studies. Two axillary shoots are produced by the two or even three nodes above the cotyledons. Only one shoot each node is produced by the subsequent nodes in a spiral di-

rection, except the uppermost one, from which again two shoots emerge and from that point on the branching pattern is cymosely.

HOLM (1924) alluded also to the additional leaf pair preceding the flower. He only referred to Eichler, who explained the observed transverse position of the gynoecium of *Polypremum procumbens* as a consequence of the presence of these two pairs of "prophylla". Eichler attested that this transversal position of the gynoecium does not fit into the alliance with Loganiaceae (median gynoecium). But this additional pair of so called bracteoles is very important for the orientation of the terminal flower of the lateral shoots. Is the number of these leaf pairs even, than the carpels are oriented in transversal position. If the number is uneven, then they emerge in median position. Within the dichasia the branching pattern is as described in Fig. 2.

Regarding to the breeding system, only WAGSTAFF (2004) speculated that unspecialised pollinators for Tetrachondraceae visit the flowers.

Morphological structures (e.g. special position of the anthers, the ring of hairs, small flowers dropping after one day) and the absence of nectaries, scent, bright colours, conform with autogamy. The performed bagging experiments show, that all the flowers developed into fruits. Thus, autogamy is obligat.

POLYPREMUM COMPARED TO *TETRACHONDRA*

SIMILARITIES

Both, *Tetrachondra* and *Polypremum*, are characterised by many common traits: similar leaves (nearly the same form, amphistomatic, scabrid along the margins and the midrib, covered by glandular hairs, connected by a membranaceous sheath), the additional pair of bracteoles embedding the flower, the same chemical compounds, etc. (SKOTTSBERG, 1913; WAGSTAFF et al., 2000; JENSEN, 2000; WAGSTAFF, 2004).

Both genera share the same tetramerous floral ground plan. But the orientation of the flower is somewhat difficult to compare. SKOTTSBERG (1913) elaborated on the deeper morphology of *Tetrachondra patagonica*. He studied just material from the herbarium and had some difficulties to find the right floral ori-

entation. Thereby I think, that the orientation in both genera must be the same, that of *Polypremum*.

The breeding system of both genera appears also to be the same. Already SKOTTSBERG (1913) alluded to autogamy in *Tetrachondra patagonica* due to the specific position of the stamens, although the flower is lacking such a ring of hairs as it appears in *Polypremum*. Until now, no specialised pollinators were found (WAGSTAFF, 2004). These facts lead to the conclusion, that Tetrachondraceae are autogamous.

Also the embryology (MOORE, 1948; SKOTTSBERG, 1913) and the phytochemistry (JENSEN, 2000) is similar in *Tetrachondra* and *Polypremum*. Sorbitol, cornoside and caffeoyl phenylethanoid glycosides (CPGs) are present in both genera. This common appearance and the lack of iridoids suggests a close relationship between these two genera (JENSEN, 2000). Unfortunately, no chromosomal features of *Tetrachondra* are available.

DIFFERENCES

Differences between both genera are mainly due to their disjunct distribution and different habitats. *Tetrachondra* is adapted to semiaquatic places. Thus, forming mats of many plagiotropous sprouts. Whereas *Polypremum* prefers dry habitats, thereby developing orthotropous to procumbent sprouts. The flower of both genera is distinguished by the formation of hairs in the corolla of *Polypremum*, whereas in *Tetrachondra* no hairs are developed.

Very important are the differences in the gynoecium of both genera: *Tetrachondra* develops a superior ovary with a gynobasic style. The fruit type is composed by four one-seeded mericarps. In *Polypremum* a partly inferior ovary is developed with a terminal style resulting in the formation of a capsule with numerous small seeds.

INTERGENERIC RELATIONSHIPS

Morphological, phytochemical and molecular systematic data support the close relationship of the two genera. WAGSTAFF et al. (2000) stated, that *Polypremum* is distinguished from *Tetrachondra* by 24 molecular autapomorphies. That leads to the conclusion, that *Polypremum* is the more derived genus. But regarding to

the morphology, *Tetrachondra* is the one, who owns more derived morphological features. The fruit structure of *Tetrachondra* is a mericarp with only four seeds, which is the more derived fruit type than the numerous seeded capsule of *Polypremum*. It is not apparent, which events in the molecular structure lead to the "primitive" features in *Polypremum*.

SYSTEMATIC POSITION OF THE TETRACHONDRACEAE

According to molecular data, Tetrachondraceae emerge between Oleaceae and Calceolariaceae/Gesneriaceae in basal Lamiales (OXELMAN et al., 1999; JENSEN, 2000; WAGSTAFF et al., 2000).

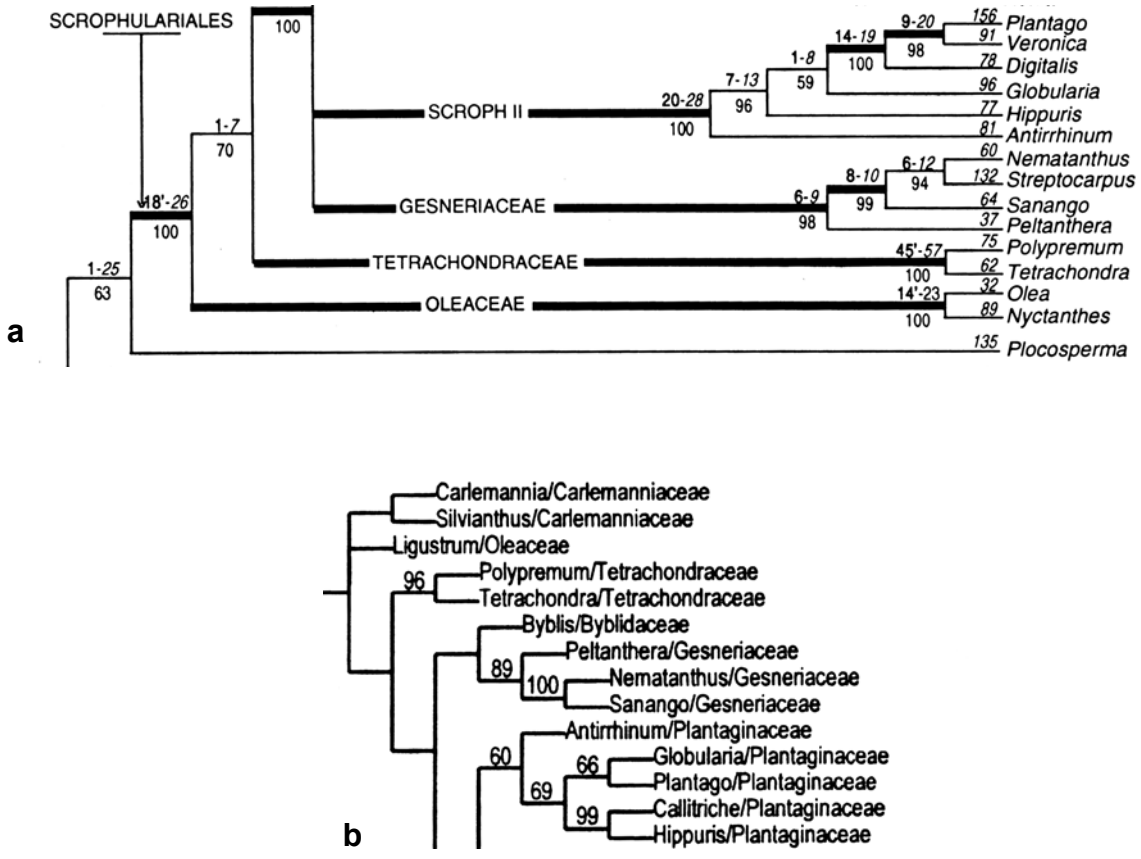

Fig. 10: Position of Tetrachondraceae in basal Lamiales based upon recent molecular studies by (a) OXELMAN et al. (1999) and (b) BREMER et al. (2001).

In Fig. 10 phylogenetic trees of recent studies are shown, focusing on the position of Tetrachondraceae and the allied families. According to OXELMAN et al. (1999), Plocospermataceae are sister to the rest of Lamiales. Tetrachondraceae are embedded between Oleaceae and the more derived Gesneriaceae (Fig. 10a). On the next step, Carlemanniaceae and Oleaceae form an unresolved polytomy, followed by Tetrachondraceae and then the rest of the order Lamiales (Fig. 10b).

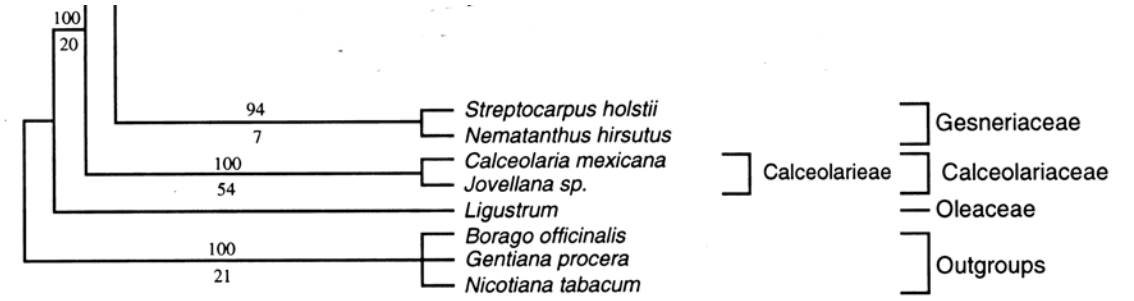

Fig. 11: Phylogenetic position of Calceolariaceae within basal Lamiales based on the study by OLMSTEAD et al. (2001).

According to OLMSTEAD et al. (2001), the position of Oleaceae is at the very base of Lamiales, followed by the newly established Calceolariaceae and Gesneriaceae (Fig. 11).

Thus, by summarising these phylogenetic analyses, one can say, that Tetrachondraceae emerge at a higher position as Oleaceae, but at a lower as Gesneriaceae, somewhere in the middle together with Calceolariaceae.

Regarding the merosity of the flower, Tetrachondraceae fit well into the alliance of Oleaceae, Carlemanniaceae and Calceolariaceae. These three families are characterised by tetramery, although in Carlemanniaceae pentamery, in Oleaceae penta- and pleiomery occurs regularly and in Calceolariaceae next to truly tetramerous flowers, a trimerous genus appears.

But the orientation of the calyx of *Polypremum*, which is initiated in diagonal position, is somewhat different as in all the representatives of Oleaceae in-

vestigated in this study (orthogonal positioned calyx) with the sole exception of *Nyctanthes arbor-tristis* L and of Calceolariaceae investigated in a previous study (MAYR & WEBER, 2005). In *Nyctanthes* the tetramerous calyx is initiated the same way as in *Polypremum*, namely simultaneously in diagonal position. Thus, a closer connection between the two families can be drawn. It is likely, that this similar morphological trait (diagonal orientation of the calyx) is originally developed within Oleaceae and carried on to the more derived Tetrachondraceae.

In general, Oleaceae and Carlemanniaceae as well as Calceolariaceae are characterised by the development of two stamens, only some more derived taxa within Oleaceae in the tribe Oleineae form four stamens in orthogonal position. *Polypremum* itself always develops four stamens in diagonal position. This tetramery of the androecium can be seen throughout the whole order of Lamiales in various families (e.g. Buddlejaceae, Gesneriaceae, Globulariaceae, Myoporaceae, Nesogenaceae, Plantaginaceae, Verbenaceae; KUBITZKI & KADEREIT, 2004). Disregarding the orientation of the androecium, the formation of the four stamens in Tetrachondraceae can be seen as a trend, which indicates the increase from two to four stamens from the most basal families Carlemanniaceae, Oleaceae and Calceolariaceae to the more derived ones within the order. This disagrees with ENDRESS (1999), who studied different morphological lineages within the order, focusing on evolutionary trends, indicating a reduction of the androecium from four to two stamens, which is due to the reduction or loss of the upper or of the lower pair.

With the most basal family, Plocospermataceae, and the more derived family, Gesneriaceae, Tetrachondraceae do not have much in common concerning floral morphology. The bisexual flowers of Plocospermataceae are penta- to hexamerous, and from Gesneriaceae onwards, pentamery has established.

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PART 2

FLORAL ONTOGENY IN OLEACEAE

ABSTRACT

Recent molecular studies on the systematics and phylogeny of Oleaceae are complemented here by the study of floral ontogeny. Covering all five tribes, fifteen selected species were studied, from flower initiation to anthesis by means of SEM.

With few exceptions, the family is characterised by a characteristic pattern of floral development. The tetramerous calyx is initiated in orthogonal position, with the primordia emerging simultaneously on the floral apex. The corolla emerges partly as a continuous mound from which four petal lobes emerge in diagonal position (early sympetaly). Partly the petal primordia emerge separately, fusing later to a corolla tube (late sympetaly). The primordia of the two stamens arise in transversal position. The gynoecium is bicarpellate throughout the family, the two carpel primordia emerge in median position.

Deviant are the genera *Nyctanthes*, *Menodora* and *Jasminum*, with the calyx composed of more than four sepals. Regarding the corolla, four genera (*Nyctanthes*, *Menodora*, *Jasminum* and *Schrebera*) are characterised by pleiomery. There is evidence that perianth pleiomery is a derived feature within the family. Four stamens occur in a number of species of Oleeae–Oleinae or as a teratology within the tribe Oleeae. Whether they represent an ancestral condition or a secondary acquisition is uncertain.

Intrafamiliar relationships as well as the affiliation of Oleaceae to basal Lamiales are discussed.

INTRODUCTION

Oleaceae is a family comprising currently 25 genera (inclusively the extinct genus *Hesperalaea* from Mexico) and approximately 200 species. The distribution ranges from the Old World to the New World, from temperate to subtropical and even tropical regions, the Antarctic being the only continent without any representatives of Oleaceae. Due to the cultivation as ornamentals (privet, jasmine, lilac) or crops (olive), some of the species are naturalized and are pretty common in some regions.

Traditionally, Oleaceae have been classified in the orders Scrophulariales (CRONQUIST, 1981), Oleales (TAKHTAJAN, 1986) or Gentianales (as "Contortae", HUBER, 1991). Nowadays they are assigned to Lamiales, occupying a rather basal position, preceded by Plocospermataceae and Carlemanniaceae, and followed by Tetrachondraceae, Calceolariaceae and Gesneriaceae (WAGSTAFF & OLMSTEAD, 1997; OXELMAN et al., 1999; BREMER et al., 2001; OLMSTEAD et al., 2001).

Within the family a considerable morphological variation can be observed. The most common growth pattern are trees, shrubs and woody climbers, herbaceous representatives are rare (e.g. *Menodora*, *Dimetra*). The plants are characterised by opposite leaves and by flowers with a tetramerous perianth. The tetramery of the calyx and the corolla is disturbed in several genera, e.g. *Jasminum*, *Nyctanthes*, *Schrebera,* where a pleiomery occurs. Also flowers without a perianth occur in some genera (e.g. *Fraxinus*). One of the more consistent characteristics of the family are the two stamens per flower. However, four stamens are developed naturally only in species of the subtribe Oleinae. As a teratology four-staminate flowers can occur in several species of the tribe Oleeae (e.g. *Fraxinus*).

The flowers of Oleaceae are hermaphrodite, but unisexual flowers occur within some genera, i.e. *Fraxinus* (SCHULZ, 1892). Heterostyly is a phenomenon

which is observed in several species of *Forsythia*, *Nyctanthes*, *Schrebera* and *Jasminum*.

Despite the strong morphological differences within the family, recent molecular data confirmed the monophyly of the family and contributed essentially to the intrafamiliar classification of the family (WALLANDER & ALBERT, 2000).

The subject of this study is the floral ontogeny, to which little attention has been paid in former studies. The main problem to be solved is whether the oleaceous flower has a truly tetramerous perianth or is made up of successive whorls of tow (like the dimerous androecium and the gynoecium), as proposed by TORGÅRD (1924) and WEBER (1928). The second open problem is whether the characteristic diandry is an ancestral condition or derived from tetrandry.

In the present study, I attempted floral developmental analyses (1) to determine the constitutive floral developmental pattern, regarding merosity and sympetaly, by the use of the scanning electron microscope (SEM), (2) to support or disprove recent systematic relationships within the family and (3) to discuss the relationships of Oleaceae with the related families of basal Lamiales.

MATERIALS & METHODS

The most recent classification of Oleaceae was worked out by WALLANDER & ALBERT (2000). With regard to that classification, I attempted to investigate at least one representative of each tribe. The following species were studied:

Tribe	Subtribe	Species
Myxopyreae		*Nyctanthes arbor-tristis* L.
Fontanesieae		*Fontanesia fortunei* CARRIÈRE
Forsythieae		*Forsythia europaea* L.
Jasmineae		*Jasminum fruticans* L.
		Jasminum nudiflorum LINDL.
Oleeae	Ligustrinae	*Syringa villosa* VAHL
		Syringa josikaea JACQ. F.
		Syringa laciniata MILL.
		Ligustrum ibota SIEB.
		Ligustrum japonicum subsp. *rotundifolium* THUNB.
		Ligustrum ovalifolium NAKAI
Oleeae	Fraxininae	*Fraxinus excelsior* L.
Oleeae	Oleinae	*Chionanthus virginicus* L.
		Olea europea L.
		Phillyrea vilmoriana BOISS. & BAL.

Most of the fresh material was collected by myself in the Botanical Garden of the University of Vienna (HBV) and fixed in 70% ethanol. Fixed material of *Olea europaea* was obtained from the BG Kiel, Germany. The samples were dissected under a stereomicroscope. Then the material was dehydrated in Formaldehyd-dimethyl-acetal (FDA) for 24hrs, critical-point-dried in a Balzers Critical Point Dryer 030, mounted on stubs and sputtered with gold (Balzers Sputter Coater). The preparations were viewed and photographed in a Scanning Electron Microscope Jeol T-300 at 15kV at the Institute of Botany, Vienna.

Based on the classification of WALLANDER & ALBERT (2000) as shown in Fig. 18, I want to describe the selected species of the tribes, starting with the most basal ones.

FONTANESIEAE – *Fontanesia fortunei* CARRIÈRE

On the floral apex regularly four sepal primordia are initiated simultaneously, two in transversal and two in median position. In the very early stages no connection of the sepal primordia can be observed (Fig. 1b, c). Later they get interconnected just at their basis, due to interprimordial growth (Fig. 1f, i). The calyx lobes grow up and show an open aestivation (Fig. 1c, d and e). In the adult flower, the calyx lobes are free, patent and small in comparison to the petals (Fig. 1l).

Shortly after the initiation of the calyx primordia, in alternate position to the sepals, four apart petal primordia emerge simultaneously from the convex floral apex (Fig. 1b, c). They do not become connected by meristematic bridges, but behind the stamens the petals touch, or even overlap each other, whereas in the transversal they don't touch at all (Fig. 1f, i, k). No interprimordial growth occurs, no sympetaly is observable, thus, the petals remain free and grow up to elongated, rounded corolla lobes, showing a right-hand contorted aestivation in the bud stage (Fig. 1g, l).

Shortly after differentiation of the petal primordia, two stamen primordia are formed in transversal position on the floral apex (Fig. 1d). While growing up, they bend slightly inwards (Fig. 1f), but soon become separated (Fig. 1h). In Fig. 1k a slight connation to the basis of the corolla can be seen. Later on, the nearly mature stamens increase in length and stretch across the corolla lobes. The filaments remain short (Fig. 1j). At last, in the adult flower, the filaments grow up, so that the stamens hang out of the corolla.

After removing the calyx lobes, corolla and androecium, the gynoecial primordia become visible (Fig. 1i). They are located in median position in the

flower centre. Interprimordial growth results in a syncarpous, bilocular, superior gynoecium. The bottle-shaped ovary passes into a very short style and terminates in a prominent, deeply bilobed stigma (Fig. 1k, l).

TERATOLOGIES

A few buds with a fifth sepal primordium at the abaxial side of the floral meristem were observed. In such buds a fifth petal lobe occurs consistently (Fig. 15a). Rarely, flowers with three stamens were observed.

FORSYTHIAEA – *Forsythia europaea* DEGEN & BALDACCI

Although exploring several dozen of buds, I have not found any young stages. I just can give a brief information on the organisation of the adult flower:

The four calyx lobes seems to be free, but are connected at their bases to form a small calyx tube. The calyx lobes are oriented in orthogonal position. In alternate position to the sepals the prominent petals emerge, which are interconnected to a tube of 1/4 of the length of the corolla. The stamens are oriented in transversal position and are inserted in the corolla tube at their very basis. The carpels develop in the median to a bottle-shaped gynoecium with a bilobed stigma.

TERATOLOGIES

No teratologies were observed in the material. So it seems, that the floral development of *Forsythia* exhibits a very regular pattern. This leads to the conclusion that the floral development of *Forsythia* does not much differ from that of *Fontanesia*. Both emerge on branches at the basis of the family tree.

MYXOPYREAE – *Nyctanthes arbor-tristis* L.

I studied the development of the terminal flower of the inflorescences, which are described as trichasial cymes. The terminal flower is embedded between a pair of small prophylls (Fig. 2a, b). This leaf pair does not develop much further, it stays inconspicuous and becomes covered with numerous hairs. In the axes of the following leaf pair in median position, young floral meristems can be ob-

served (Fig. 2a, b). These lateral flowers are missing prophylls. The orientation of the floral apex in the following description is in the way that the prophylls are directed in transversal position.

The four sepal primordia emerge at the same time in diagonal position at the floral apex (Fig. 2a). This is a very unusual orientation of calyx lobes within the Oleaceae. Due to meristematic bridges the primordia are connected with each other very early to form a common mound (synsepaly). Remarkably, the two upper and the two lower lobes move together. This results in a space in transverse position, opposed to the prophylls (Fig. 2b). The calyx grows up as a ring with four lobes, but during development, two more lobes arise from the free space of the meristem of the calyx tube (Fig. 2d). The lobes bend inwards and with the help of the hairs on their margins, the lobes interlock. The original tetramery of the calyx persists by reduction of the size of the lobes which are developed later on (Fig. 2). In the adult flower, the calyx persists as a slightly lobed tube, while the corolla with the inserted stamens drops.

For observing the development of the corolla and the androecium, the calyx was removed (Fig. 2c, e, h). In Fig. 2c, the uniform ring primordium is formed, thus indicating an early sympetaly and the two stamen primordia are scarcely visible. The stamen primordia are placed in transverse position. In the early stages of development of the corolla the number of lobes arising on the primordia rim is hardly identifiable. Later on, usually six lobes are differentiated. But the amount of lobes can vary between five up to eight. Soon the lobes show a contort aestivation, regularly right-handed (Fig. 2h, i). As the corolla tube grows upward, the developing stamens are carried up along with it, resulting in a well developed stamen-corolla tube. In Fig. 2j introrse anthers are shown, each differentiated into four pollen sacs. A short filament is formed.

In Fig. 2k and l, the calyx, corolla and stamens have been removed. The two gynoecial primordia are located on the flanks of the concave floral apex at the base of the young corolla tube, alternate to the stamens in median position (Fig. 2k). As they grow upward, they become interconnected by interprimordial growth. Further growth produces a bottle-shaped syncarpous gynoecium. The ovary, a very short style and a slightly two-lobed stigma can be observed (Fig. 2l), which becomes prominently two-lobed in the adult flower.

TERATOLOGIES

The examined flowers did not show much teratologies. In my material I found just a few buds with 3 developed stamens. In these flowers, the other organs showed the normal developmental pattern (Fig. 15b, c).

JASMINEAE – *Jasminum fruticans* L.

The floral meristem is embedded in-between two prophylls (Fig. 3a). At the edges of the floral meristem the primordia of the sepals are the first to take shape (Fig. 3b). Generally, five sepal primordia can be seen (Fig. 3b, c). Immediately after inception of the sepal primordial, interprimordial growth occurs, thus initiating the calyx tube in a very early stage of development. The calyx lobes grow up and bend inwards. On their tips hairs emerge (Fig. 3f). In the adult flower the calyx tube remains short (about 1/3rd of the length of the corolla) and the calyx lobes grow out to narrow, elongated and acuminate organs (Fig. 3k).

After removing the sepal primordia, the rest of the floral meristem becomes visible. Five petal primordia are formed simultaneously, in alternate position to the sepals as a uniform primordia rim, occupied with the developing lobes (Fig. 3d). Within the young bud, the floral organs are tightly packed together (Fig. 3e). The corolla lobes increase and on their tips hairs develop at the edges. The aestivation of the corolla lobes is quincuncial-imbricate (Fig. 3g). After the development of the corolla lobes, the elongation of the stamen-corolla tube starts. In the adult flower the lobes spread and become patent. The corolla lobes measure 1/3rd the length of the whole corolla.

Nearly simultaneously with the differentiation of the petal primordia, two androecial primordia emerge in transversal position (Fig. 3d). As the calyx and the corolla grow upwards, the developing introrse stamens are carried up along with the petals, forming a prominent stamen-corolla-tube in the adult flower. In *J. fruticans* heterostyly occurs.

Two carpel primordia get initiated in alternation to the stamens. After fusion, a globose ovary is formed which passes into an elongated four-angled style bearing a two-lobed stigma at the top (Fig. 3i, j, l).

TERATOLOGIES

The floral structure of *Jasminum fruticans* shows much variation. I observed the insertion of four sepal primordia as well as the regularly five ones, but rarely also the development of six primordia occurs. In case of tetramerous calyx I found both a diagonal as well as an orthogonal position of the primordia (Fig. 15d, e). Also the differentiation of six and seven petal primordia occurred very often (Fig. 15f). Regarding to the androecium, in above-average many flowers three stamens were found.

JASMINEAE – *Jasminum nudiflorum* LINDL.

The floral development of *Jasminum nudiflorum* is very similar to that of *Jasminum fruticans*. However, the number of differentiated floral organs is very regular.

Regularly, six sepal primordia are formed at the floral apex, which is embedded between a pair of prophylls (Fig. 4a). The insertion of the primordia seems to be quite similar to that of *Nyctanthes arbor-tristis*. Four sepal primordia, apparently in diagonal position, are developed at first, whereas the two remaining primordia emerge later in the median on the meristem. It appears as if two calyx whorls would emerge (Fig. 4b). After early interprimordial growth a calyx tube is developed. This remains short as in *J. fruticans*. The calyx lobes are also elongated (2/3rd of the calyx length) and patent, but not as narrow as in *J. fruticans*.

After inception of the sepal primordia, a girdling corolla primordium is initiated (Fig. 4c). On its rim, later on, six corolla lobes arise. The lobes grow up and an ostensive differentiation into two whorls can be observed (Fig. 4d, e). Four outer lobes of the corolla form the “outer whorl”, while the “inner whorl” consists of the two inner lobes in median position. The same way as in *J. fruticans* a stamen-corolla tube is developed. In the adult flower the lobes are 1/3rd the length of the corolla and slightly acuminate.

The stamens and carpels emerge in the same way as in *J. fruticans*. Two stamen primordia are differentiated in transversal position (Fig. 4b, c). The filaments get connected with the corolla tube later on. This species of *Jasminum*

shows also heterostyly. I observed the morph, in which the stamens are inserted in the middle of the length of the stamen-corolla tube. Two carpel primordia are formed in alternate position to the stamen primordia (Fig. 4f). In the adult flower, the gynoecium is differentiated in a round, somewhat flattened ovary, a very long style with an indistinct bilobed stigma.

TERATOLOGIES

No anomalous flowers were found.

OLEEAE – LIGUSTRINAE – *Syringa josikaea* JACQ. F.

At first the sepal primordia are formed as a mound (Fig. 5a, c). Continuous growth occurs and later on four calyx lobes emerge out of this rim (Fig. 5c – e). The lobes bend hyponastically, whereby the median ones are more prominent than the transverse ones (Fig. 5b, e). In a later stage the calyx tube increases and hairs emerge from the surface (Fig. 5g, i). In the adult flower, only tiny calyx lobes are noticeable.

The four petal primordia are initiated separately on the floral apex in diagonal position, no well developed corolla ring primordium, thus, no early sympetaly can be observed (Fig. 5d). Remarkable is, that the two upper and the two lower primordia touch each other, even fuse in the median, whereas behind the stamens no interconnection is observed (Fig. 5f). The corolla lobes become developed more and more, show a valvate aestivation, and also in later stages of development this non-fusion of the corolla lobes in the transverse can be seen (Fig. 5k). This space may be the result of the inception of the androecial primordia. At the base, under these lobes, a circular meristem is developed, which grows up to the stamen-corolla tube, which is prominent in the adult flower. The acuminate corolla lobes become patent after opening and are in length 1/3rd of the corolla.

Shortly after the inception of the petal primordia, two androecial primordia are formed in transversal position (Fig. 5d, f). Further growth can be observed (Fig. 5k) and when the corolla tube arises, the stamens are carried up with it. A stamen-corolla tube emerges. The stamens are inserted at the corolla tube at

the base of the insertion of the corolla lobes. Only a very short filament can be identified.

In alternate position to the stamen primordia two carpel primordia emerge out of the remaining floral meristem, resulting in a syncarpous gynoecium (Fig. 5l), which is composed of a globose ovary, a longish style and a distinctive bilobed stigma.

TERATOLOGIES

In the material aberrations in the calyx, corolla and androecium have been found. Buds with three sepals and/or five to six petals and/or three stamens are documented in Fig. 15g, h.

OLEEAE – LIGUSTRINAE – *Syringa laciniata* MILL.

From the inception, the sepal primordia are interconnected in a mound (Fig. 6a – c). The tetramery of the calyx is scarcely visible in this very early stage of development. Later on, a calyx tube and somewhat irregular, but always four, calyx lobes are differentiated from this ring and grow up. The aestivation of the lobes is valvate. In the adult flower a short prominent calyx tube with small calyx lobes can be observed.

The primordia of the corolla are formed together in a mound (Fig. 6b). Four lobes in diagonal position emerge on this primordial ring. Remarkable is also the early interconnection of the petal lobes in the median, whereas in the transverse they stay just a bit longer separate (Fig. 6d, cf. *Syringa josikaea*). The corolla lobes bend inwards and in this stage no differences in sympetaly are observable (Fig. 6f). The lobes grow up together with the corolla tube, showing a valvate aestivation (Fig. 6f). Finally, in the adult flower, the acuminate corolla lobes open and become patent.

Nearly simultaneous with the inception of the petal primordia, the two stamen primordia emerge in transverse position (Fig. 6d). As the corolla tube grows upward, the developing stamens are carried half way up. This results in the differentiation of a stamen-corolla-tube.

The two gynoecial primordia are situated in the median (Fig. 6i). In the adult flower they build up a bottle-shaped, syncarpous gynoecium, forming a globose ovary, an elongate style and a prominent, two-cleft stigma.

TERATOLOGIES

No anomalous flowers were found.

OLEEAE – LIGUSTRINAE – *Syringa villosa* VAHL

At first, on the edge of the floral meristem, the formation of a rim can be observed (Fig. 7b). This mound approaches like a tetragonal girdling primordium (Fig. 7c). According to the other representatives of *Syringa*, it is supposed that the four straight lines of the rim correspond to the four sepal primordia. During further upgrowth, a short calyx tube with four more ore less distinct lobes is formed (Fig. 7f, g).

In Fig. 7c four petal primordia alternating with the calyx lobes take shape. They are inserted as a broad tetragonal corolla ring primordium (Fig. 7d; early sympetaly). The formation of the primordia rim is somewhat irregular, because in the median (behind the developing stamens) the primordia fuse not as early as in the transverse (cf. *Syringa josikaea* and *S. laciniata*). Out of this rim four corolla lobes are formed. Also in this developmental stage the phenomenon of the free space in the whirl of the corolla in the transverse can be observed (Fig. 7e). The floral organs increase and the corolla lobes show a valvate aestivation (Fig. 7h). Due to the early sympetaly, a short corolla tube is developed out of this rim. Thus, the adult flower shows a long corolla tube (2/3rd of the length of the corolla) with four acuminate patent corolla lobes.

Two stamen primordia emerge in transverse position on of the floral apex shortly after initiation of the petal primordia (Fig. 7e). The developing stamens are carried along with the corolla, resulting in a stamen-corolla-tube. The stamens are inserted at the base of the insertion of the corolla lobes. A very short filament can be recognised.

The two gynoecial primordia are placed alternately to the androecial ones, forming a syncarpous gynoecium (Fig. 7i). This consists of a globose ovary, an elongate style and a prominent bilobed stigma.

TERATOLOGIES

In the fixed material I observed 3-merous flowers with three sepals, three petals and three stamens. Also a normally developed flower with three stamens occurred (Fig. 15i).

OLEEAE – LIGUSTRINAE – ***Ligustrum japonicum*** ssp. ***rotundifolium*** THUNB.

From the floral apex, which is embedded between two prophylls, regularly four sepal primordia are formed at the same time in orthogonal position (Fig. 8a, b). Shortly after the inception of the sepal primordia, interprimordial growth occurs, which results in the development of a calyx tube. The calyx grows up, the lobes bend inwards to protect the inner floral organs. Aestivation is valvate (Fig. 8e). In the adult flower, the calyx tube does not appear very prominent, measuring ca. 1/4th of the length of the corolla tube. No lobes on the tube are observable.

While the calyx differentiates, the four petal primordia emerge in diagonal position as a primordia rim (early sympetaly). The two upper and the two lower lobes are touching each other in the median and fusing, nearly forming an upper and a lower lip, while in the transverse a free space remains between the primordia (Fig. 8d; cf. *Syringa*). The aestivation is valvate (Fig. 8f). During further development, also the lobes behind the stamens get interconnected at their bases due to the emergence of meristematic bridges. This results in a uniform corolla tube. In the adult flower, a long prominent stamen-corolla tube is formed (2/3rd of the length of the corolla). The corolla lobes open at first transversally, while in the median the corolla lobes remain in contact (Fig. 8h, i). Later on, all lobes become patent.

Very soon after the formation of the petal primordia, the stamen primordia emerge in transversal position (Fig. 8d). They develop into normal stamens, typical of Oleaceae. The stamens are inserted into the corolla, resulting in a

stamen-corolla tube. They are attached with a short filament exactly at the basis of the insertion of the corolla lobes and break through the corolla (Fig. 8i).

At last, in the median of the floral apex two gynoecial primordia emerge (Fig. 8j). They fuse due to interprimordial growth and increase. A globose ovary is formed, which passes into a stepped and elongated style. At the apex a slightly two-cleft prominent stigma can be observed (Fig. 8k, l).

TERATOLOGIES

Buds with five sepal primordia occurred occasionally in my material. No other anomalies were found.

OLEEAE – LIGUSTRINAE – *Ligustrum ibota* SIEBOLD

At the periphery of the floral meristem, the four sepal primordia are initiated at about the same time in orthogonal position (Fig. 9a). Very early a calyx tube is formed due to interprimordial growth. The calyx lobes bend inwards, closing the bud entirely, and the calyx tube grows up (Fig. 9b, d). A lot of hairs emerge on the surface of the calyx. In later stages of development, the lobes cease their growth, so that the calyx seems to consist of the tube only. The calyx tube opens and the corolla grows up (Fig. 9g, k).

After removing the calyx, the development of the corolla can be observed: Very early a not very regular developed primordia rim is formed from the meristem, indicating early sympetaly in this species (Fig. 9c). Four petal lobes arise on this rim in alternate position to the sepal primordia (Fig. 9e). In *L. ibota* the same phenomenon occurs as described previously for the species of *Syringa* and *Ligustrum*. Behind the stamens, in transversal position, the petal lobes do not get connected, whereas in the median, they move towards each other. While further growth, the petal lobes bend inwards and show a valvate aestivation (Fig. 9f). The previously mentioned primordia rim develops into a prominent stamen-corolla tube. In the adult flower, the four lobes at the top of the corolla tube become patent and measure about 1/3rd the length of the corolla.

In Fig. 9e one can see the insertion of the two stamen primordia in transversal position. They increase and differentiate into stamens of the normal form

of Oleaceae (Fig. 9, e, h, j). In *L. ibota*, the filament is also fused with the corolla tube, forming a distinct stamen-corolla tube. The stamens are inserted in the corolla tube shortly under the basis of the corolla lobes.

In succession, the gynoecial primordia are formed in alternate position to the stamens. After interprimordial growth the carpels grow up and differentiate into a flask-shaped gynoecium, with an ovary, an elongated style and a spheroidal, slightly two-lobed stigma (Fig. 9i, l).

TERATOLOGIES

In the material occasionally buds with five sepal lobes occurred (Fig. 15j). I have also seen one bud with three developed stamens (Fig. 15k).

OLEEAE – LIGUSTRINAE – *Ligustrum ovalifolium* NAKAI

After the inception of the two bracteoles (Fig. 10a), the four sepal primordia are simultaneously initiated orthogonally on the floral apex. Very soon they become interconnected at their bases by interprimordial growth, building up a calyx tube. The calyx lobes bend inwards and the calyx tube grows up. As in *L. ibota*, the calyx lobes become reduced in their length and the calyx tube increases. Later on, the corolla grows through the open calyx tube (Fig. 10b, c, e, h).

As shown in Fig. 10d, the four petal primordia are formed simultaneously on the floral meristem alternating to the sepal primordia as an uniform corolla ring primordium (Fig. 10d, f). In this species, the fusion of the primordia lobes in the median happens also before the fusion in the transverse. Thus, the gap between the upper and lower lobes is also well observable (Fig. 10f; cf. *Syringa* and *Ligustrum* spp.). Later on, the corolla lobes grow up, showing a valvate aestivation (Fig. 10h). A very prominent stamen-corolla tube is built up by the elongation of the incepted primordia rim.

Immediately after the inception of the petal primordia, the stamen primordia emerge (Fig. 10d). They show the same development as those of *L. ibota*/*L. japonicum*. The filaments are fused with the corolla to a stamen-corolla tube in the adult flower.

The two carpel primordia are located in median position and grow up in the same way as in *L. ibota*/*L. japonicum*, forming a globose ovary, which passes into an elongated style and ends up in a prominent, slightly bilobed stigma.

TERATOLOGIES

No abnormalities were found in the material.

OLEEAE – FRAXININAE – *Fraxinus excelsior* L.

Fraxinus excelsior is described in the literature as a dioecious, androdioecious, gynodioecious or polygamous tree with hermaphrodite and/or unisexual flowers. Thus, the developmental pattern of the flowers is quite weird, even in one inflorescence. *F. excelsior* belongs to the section *Fraxinaster* and the flowers are organised as specified below:

From the floral apex normally no sepals and petals emerge. The first organs, which come in sight are the two androecial primordia in transversal position (Fig. 13a). They develop to two free stamens. From the remaining meristem, two carpel primordia alternating with the stamens arise, developing into a syncarpous, bottle-shaped gynoecium (Fig. 13b, c). The flattened ovary passes into a short style and ends in a two-lobed stigma.

TERATOLOGIES

Nearly more “abnormal” developed flowers than “normal” ones were observed in my material. In several buds a perianth seemed to be developed, but it was not possible to determine the disposed primordia. Normally two stamens are developed, but also three or four occur very often. In the gynoecium I have found only the one teratologic form with three developed carpels (Fig. 16a – f).

OLEEAE – OLEINAE – *Chionanthus virginicus* L.

At the hemispherical floral meristem, the four sepal primordia are initiated separately at about the same time in orthogonal position (Fig. 11a). Immediately after inception of the primordia, interprimordial growth occurs, thus initiating the calyx tube in a very early stage of development. At first, the calyx lobes grow

up, before the further development of the calyx tube starts. In the adult flower, the calyx lobes are just connected at their bases to form a short tube. The lobes themselves are lanceolate and narrowly elongated and are about 2/3rd of the length of the calyx.

Regrettably, an intermediate stage, showing the inception of the petal and androecial primordia, was not found in the material available. So, it is not possible to describe the developmental chronology of these floral organs.

The petal primordia are formed separately and in alternate position to the sepal primordia on the convex floral apex. In this very early stage of development, they are not connected to a meristematic rim, and no early sympetaly occurs (Fig. 11b). After further growth, the corolla lobes develop into long and narrow lobes, which hang out from the flower. The initially free petals are connected due to the formation of meristematic bridges on the abaxial side of the stamen primordia (late sympetaly). In the median no fusion of the petals occurs (Fig. 11f).

Two stamen primordia emerge in transversal position and look very prominent in this very early stage (Fig. 11b). The position of the androecial primordia is almost within the corolla whorl, so that the petal primordia move away from each other in transversal direction (Fig. 11c, d). In the adult flower, the stamens are just connected at their bases with the short two-parted corolla tube. The filament formed is very short.

In Fig. 11f two carpel primordia, located commonly in the median, can be observed. They increase into a syncarpous gynoecium, which is differentiated in a globose ovary, a short style (as long as the ovary) and a slightly bilobed stigma (not as distinctive as in *Ligustrum* or *Syringa*).

TERATOLOGIES

One bud with three stamens was found in the material (Fig. 15l).

OLEEAE – OLEINAE – *Olea europaea* L.

The flowers are andromonoecious. The adult hermaphrodite flowers consist of a small calyx (with a short tube and short calyx lobes), four petals, which are con-

nected to a corolla tube supporting four round lobes, two stamens (inserted in the corolla tube) with large anthers, and a pistil composed of a bilobulate stigma, a short style and a bilocular ovary with four ovules. Staminate flowers result from pistil abortion at varying stages of gynoecium differentiation.

Unfortunately, in this developmental series the youngest stages are lacking.

Noticeable is the common four-merous calyx basally joined into a calyx tube, with hairs at the margins of the lobes. The surface is covered with peltate hairs (Fig. 11a).

For observing the development of the corolla, the calyx was removed. Alternating to the sepal lobes, four petal lobes are formed. They are also arranged in this special way that in the transverse between the petal primordia (behind the stamens) a free space occurs, whereas in the median they are close together (Fig. 11b). Further upgrowth occurs and the two adjoined petal primordia interlock. The aestivation is valvate (Fig. 11c).

Two stamen primordia are formed simultaneously in transversal position (Fig. 11d). Each of them forms an introrse anther (Fig. 11e). Shortly after stamen inception, two carpel primordia emerge in the median (Fig. 11f). They develop into a syncarpous gynoecium. After CUEVAS & POLITO (2004), pistil abortion occurs in staminate flowers, which takes place four weeks before bloom. By this time stamen development is well advanced. A non-functional, rudimentary pistil can be seen in the mature flower.

TERATOLOGIES

In the examined material no teratologic flowers were found.

OLEEAE – OLEINAE – *Phillyrea vilmoraniana* BIOSS. & BAL.

At the edges of the floral apex, four petal primordia emerge in orthogonal position. Very early, meristematic bridges between the primordia are formed, resulting in building up a calyx rim (Fig. 12a – c). On the calyx rim, four sepal lobes get shaped. Due to the pressure within the floral buds, deformations and a tem-

poral unequal differentiation of the primordia can occur (Fig. 12b). In the adult flower a short calyx tube is developed, which bears prominent calyx lobes.

At about the same time, the petal and stamen primordia become initiated separately. The petal primordia are located in diagonal position. Interprimordial growth occurs in a very early stage of development, but nevertheless indicating late sympetaly, resulting in a very short corolla tube (measuring the length of the calyx) in the adult flower. Fig. 12c shows, that the corolla lobes come apart in the transverse, giving space to the developing stamens, but they do not interconnect in the median. The aestivation of the older corolla lobes is a contort one (Fig. 12d).

The androecial primordia are formed in the transverse and grow up to introrse stamens (Fig. 12e). The filaments are connected to the short corolla tube in the adult flower, resulting in a stamen-corolla tube.

Two gynoecial primordia emerge in median position and after interprimordial growth, they increase into a syncarpous gynoecium (Fig. 12f). An ovary passes into a short style with a slightly two-parted stigma.

TERATOLOGIES

No teratologies were found in the material examined.

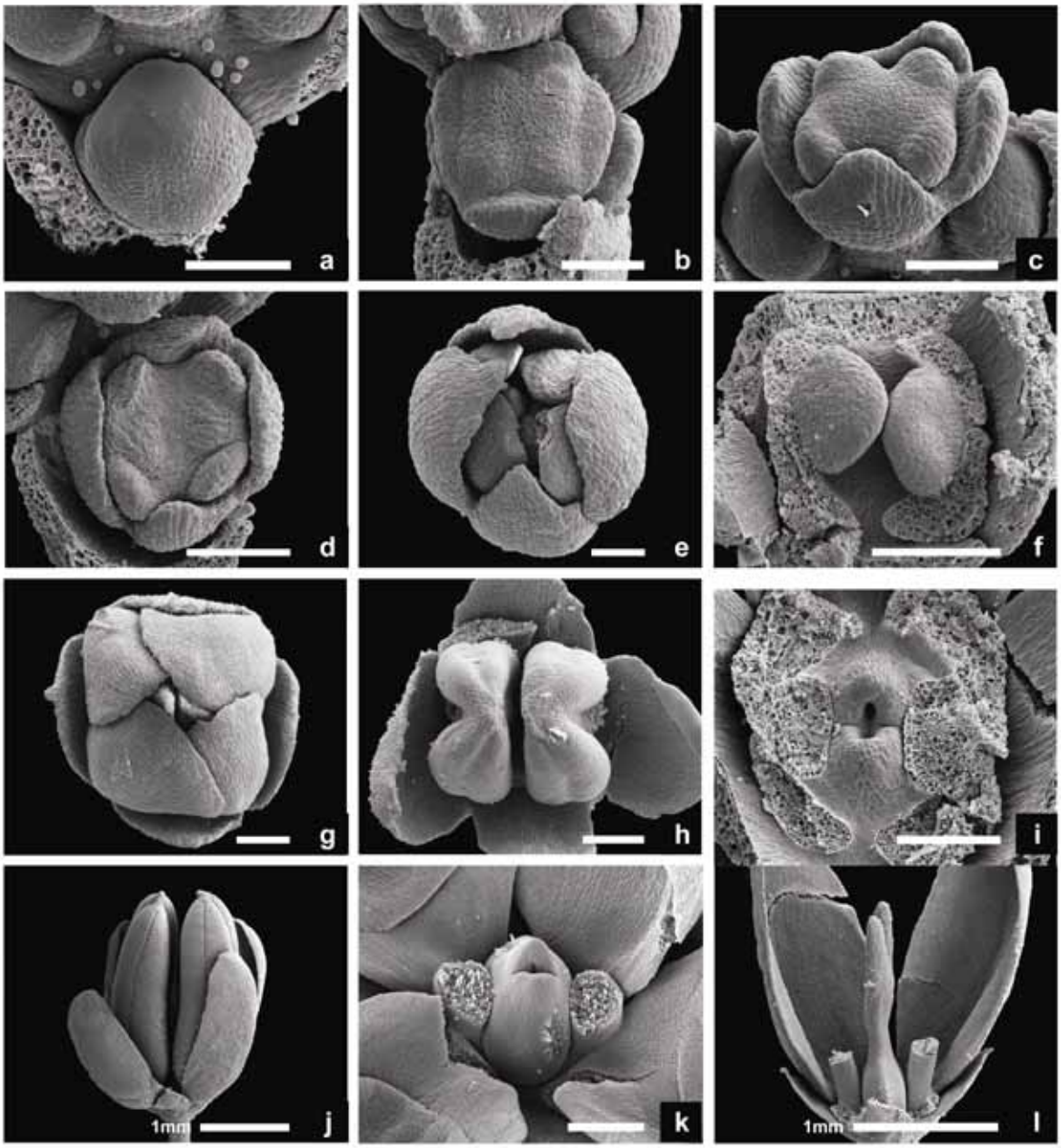

Fig. 1: *Fontanesia fortunei*, floral development. (a – c) Early formation of the sepals and petals; no early sympetaly takes place. (d) Initiation of the stamens. (e) Flower bud. (f) Stamens (perianth removed). (g) Contort aestivation of the corolla. (h) Older stage of stamen development (corolla removed). (i) Initiation of the carpels. (j) Flower in lateral view; note the elongated anthers. (k and l) Development of the gynoecium (stamens removed). Scanning electron micrographs; scale bars: 100µm, 1mm (l).

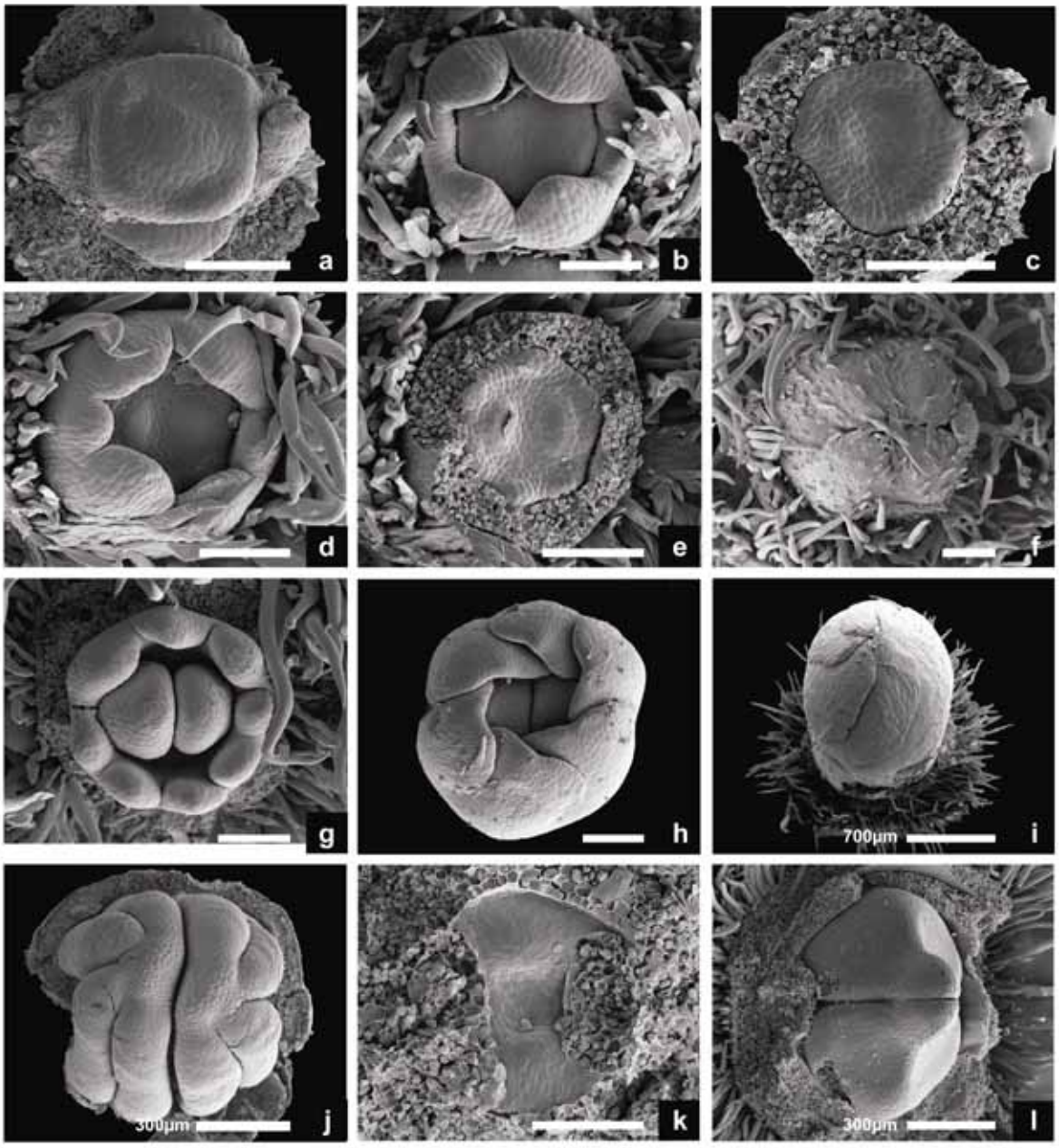

Fig. 2: *Nyctanthes arbor-tristis,* floral development. (a and d) Formation and growth of the four sepal primordia in diagonal position; note the bracteoles in the transverse. (c) Initiation of the corolla mound. (d and e) Initiation of the stamens in transversal position. (f) Flower bud. (g – i) Growth of the corolla; note the contort aestivation. (j) Developed stamens (perianth removed). (k and l) Formation of the gynoecium (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm, 700µm (i), 300µm (j, l).

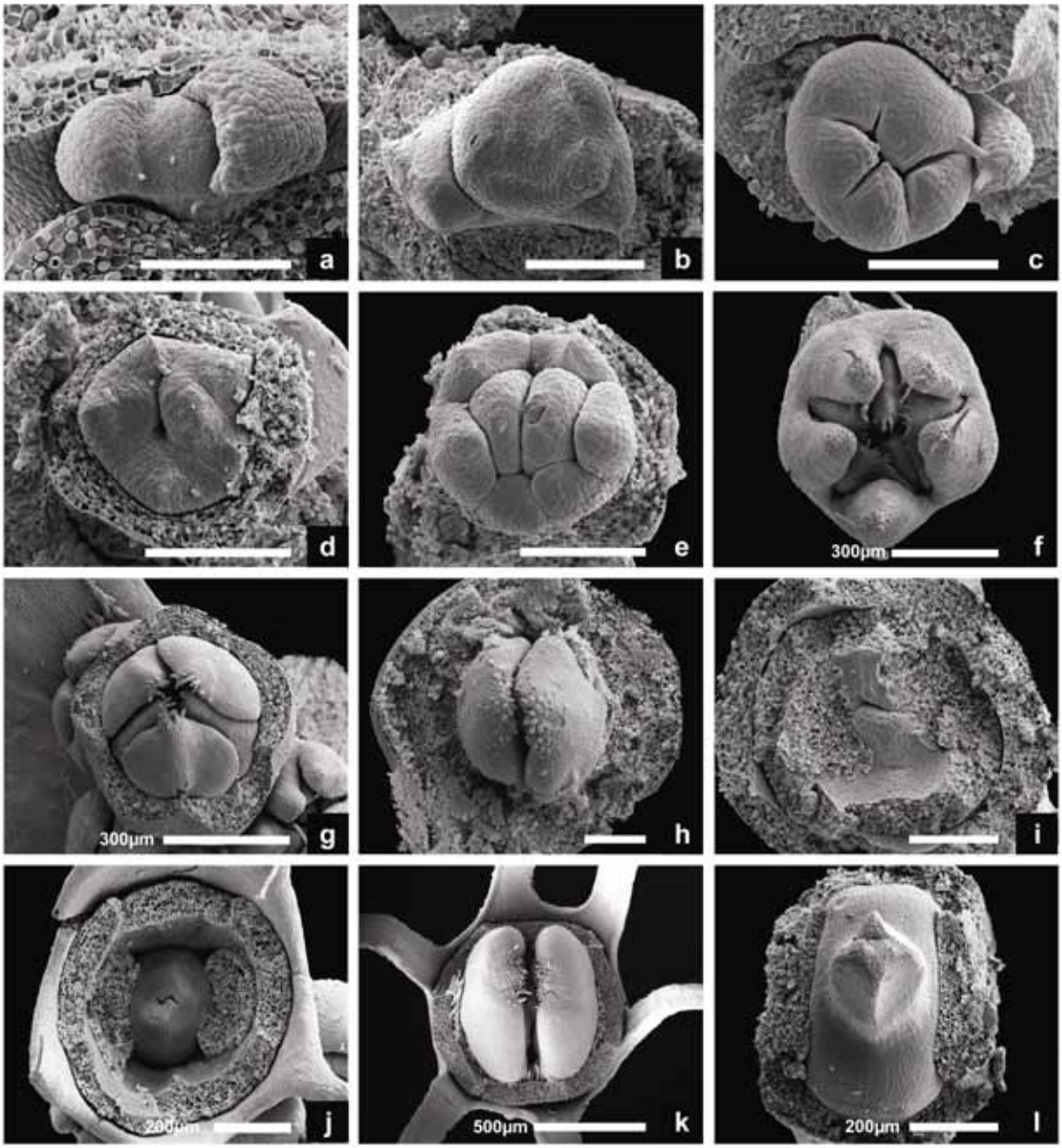

Fig. 3: *Jasminum fruticans*, floral development. (a) Floral primordia embedded between a pair of prophylls. (b and c) Formation of the pentamerous calyx. (d and e) Initiation and growth of the pentamerous corolla (calyx removed). (f) Floral bud. (g) Quincuncial-imbricate aestivation of the corolla. (h) Stamens. (I and j) Initiation and development of the gynoecium (perianth and stamens removed). (k) Further developed stamens. (l) Further developed gynoecium. Scanning electron micrographs; scale bars: 100µm, 200µm (l), 300µm (f, g), 500µm (k).

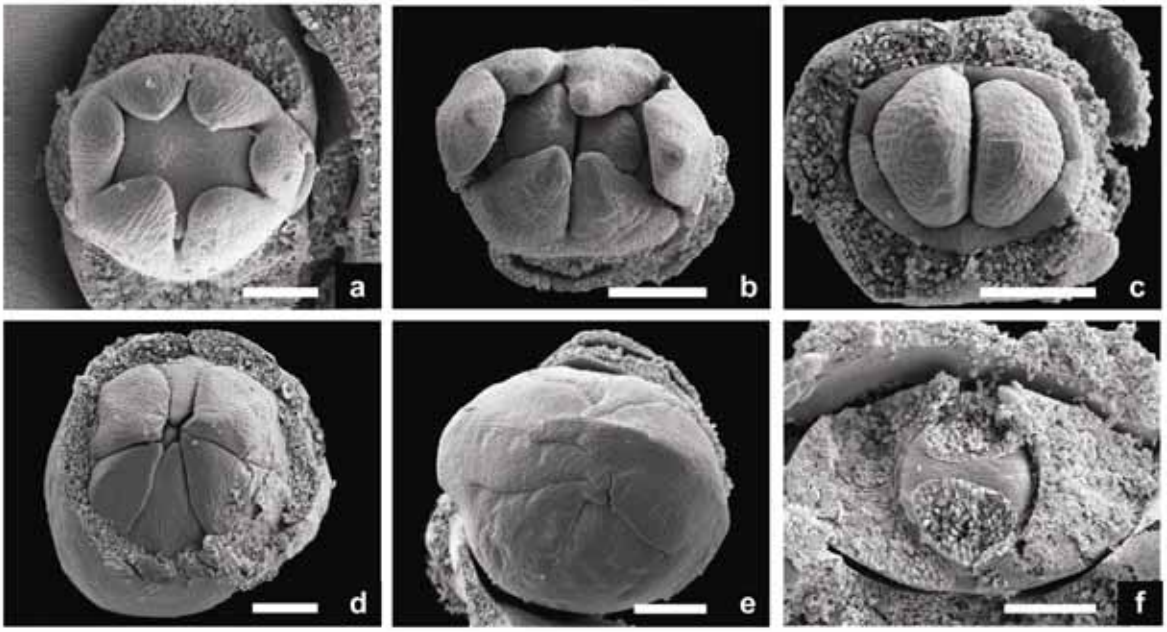

Fig. 4: *Jasminum nudiflorum*, floral development. (a and b) Formation and growth of the sepals and orientation of the stamens. (c – e) Development of the petals (calyx removed), early sympetaly takes place. (f) Initiation of the carpels (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm.

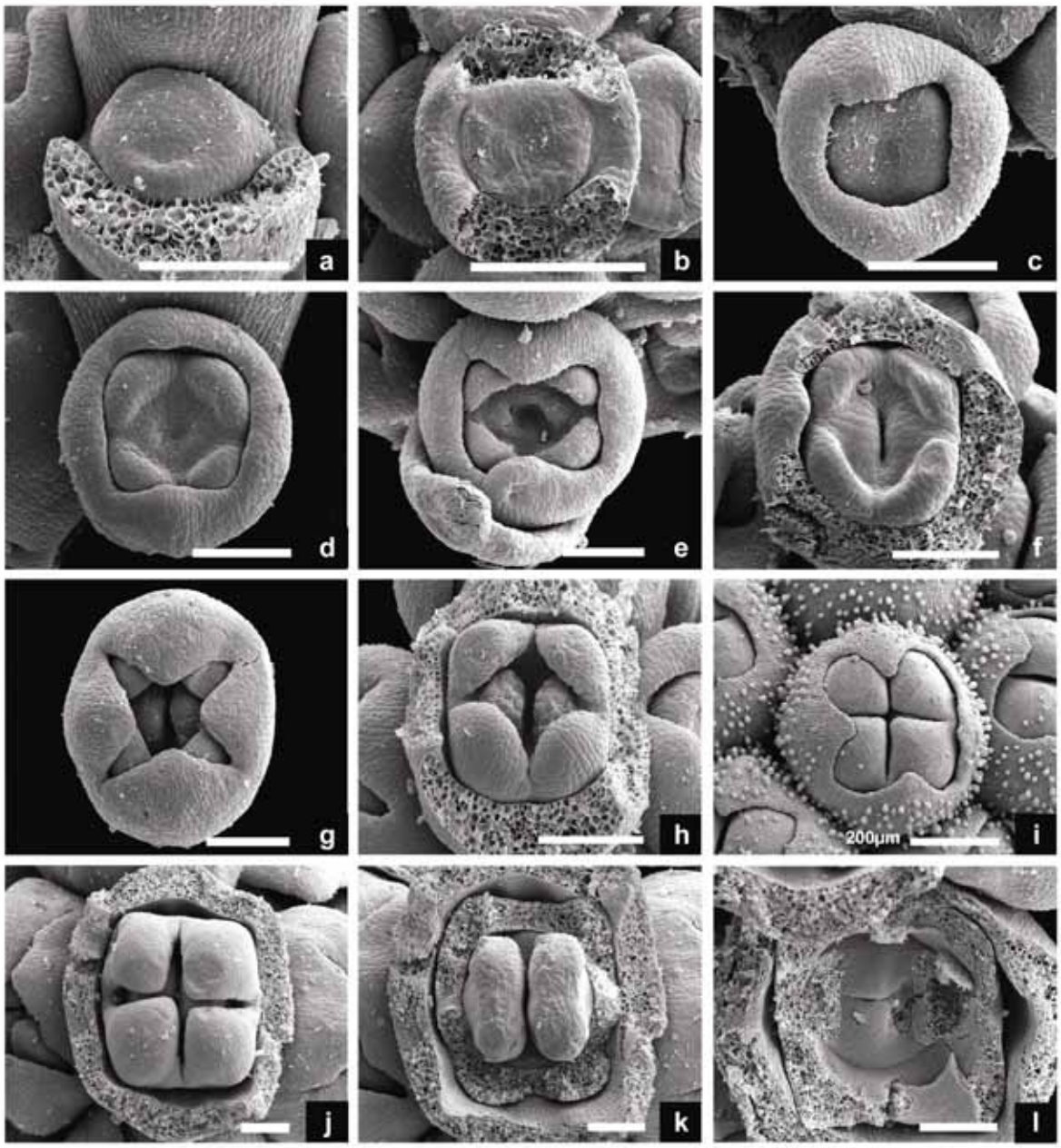

Fig. 5: *Syringa josikaea*, floral development. (a – c) Formation of the calyx mound (calyx removed in b). (d) Initiation of the petals as well as the stamens. (e and f) Growth und fusion of the petals and development of the stamens, no early sympetaly is supported by these pictures. (g) Flower bud. (h – j) Further development of the corolla. (i) Emergence of trichomes on the outer surface of the calyx. (k) Stamens (perianth removed). (l) Formation of the carpels (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm; 200µm (i).

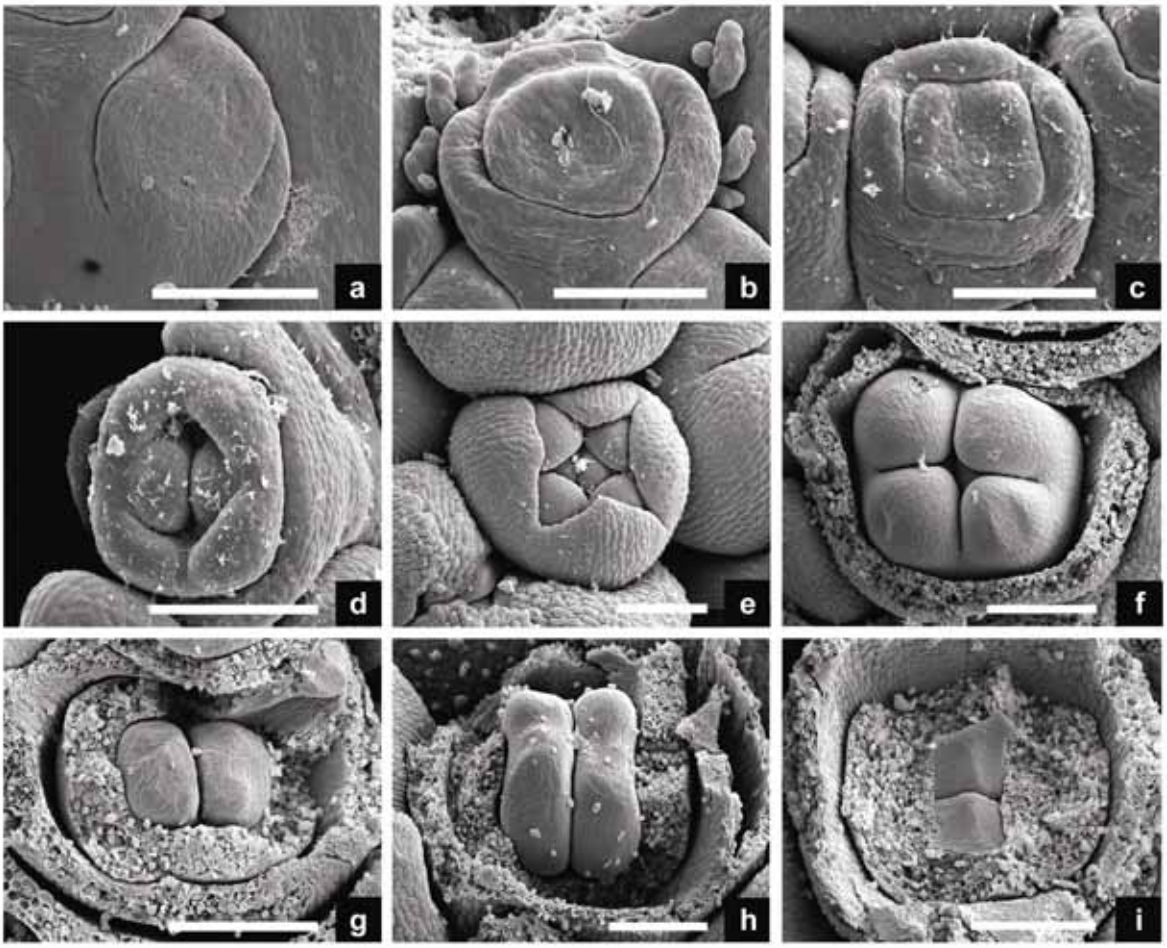

Fig. 6: *Syringa laciniata*, floral development. (a – c) Formation of the calyx and the corolla as a mound. (d – e) Further development of the petals with valvate aestivation and formation of the stamens. (g and h) The development of the stamens (perianth removed). (i) Formation of the carpels (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm.

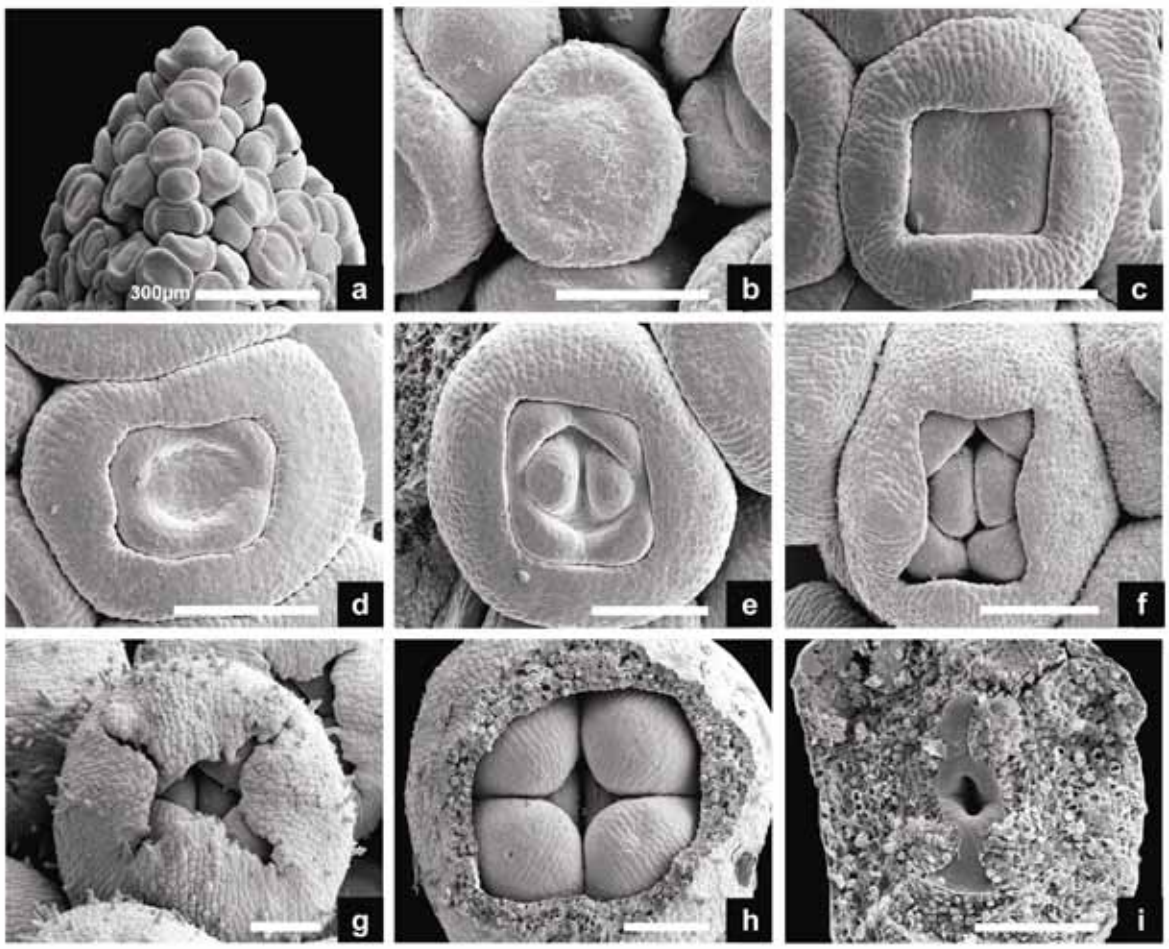

Fig. 7: *Syringa villosa*, floral development. (a) Lateral view of the apex of an inflorescence. (b) Initiation of the calyx as a mound. (c and d) Development of the petals with demonstrating early sympetaly. (e) Formation of the stamens. (g) Flower bud. (h) Aestivation of the corolla. (i) Initiation of the carpels is shown (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm, 300µm (a).

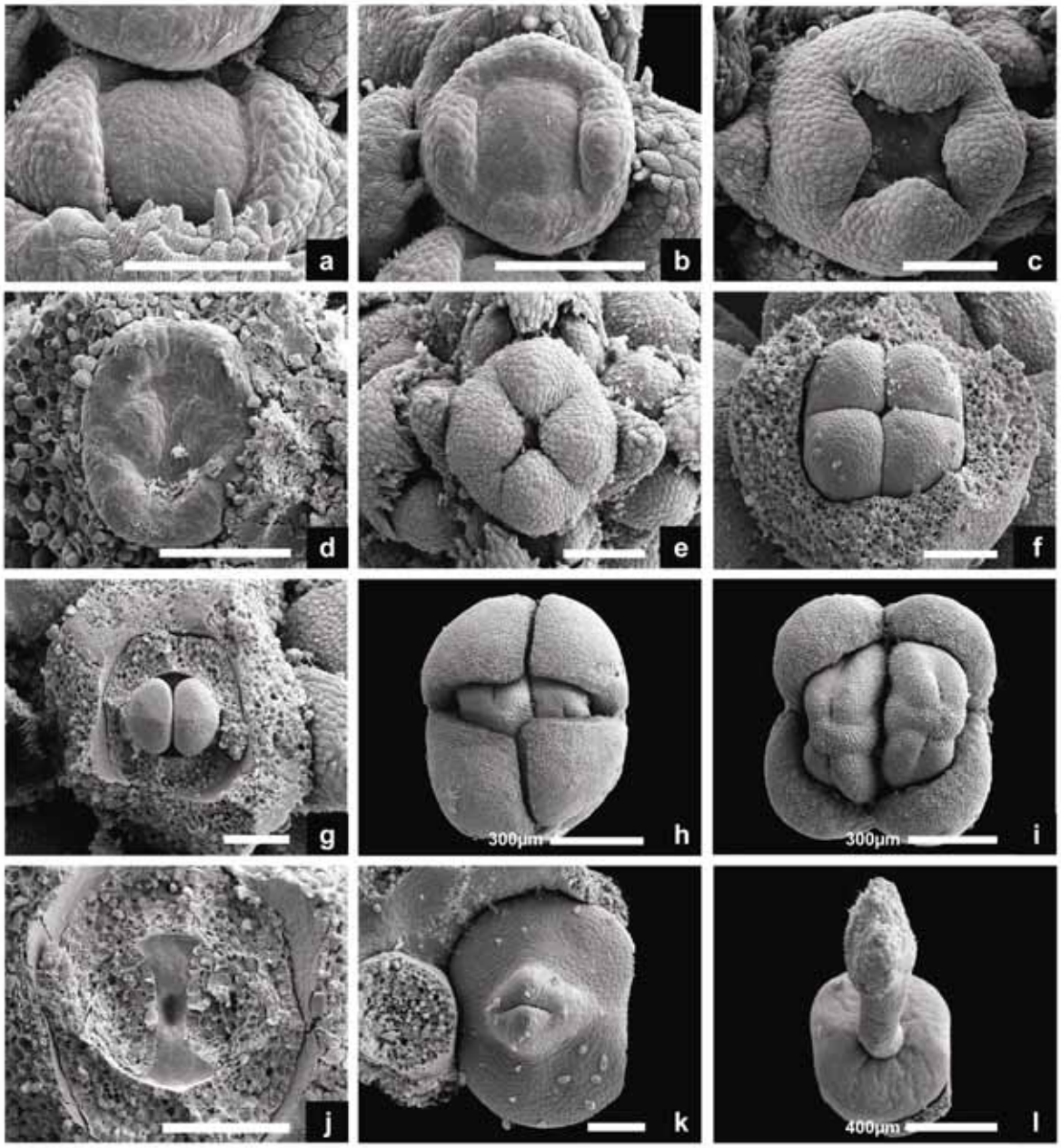

Fig. 8: *Ligustrum japonicum* ssp. *rotundifolium*, floral development. (a) Floral primordium with the two prophylls. (b and d) Formation of the calyx. (d) Initiation of the petal and stamen primordia, note the apparent formation of an “upper” and “lower lip”. (e) Calyx lobes. (f) Valvate aestivation of the corolla (calyx removed). (g – i) Development of the stamens. (j – l) Formation of the gynoecium is shown (removed perianth and androecium). Scanning electron micrographs; scale bars: 100µm, 300µm (h, i), 400µm (l).

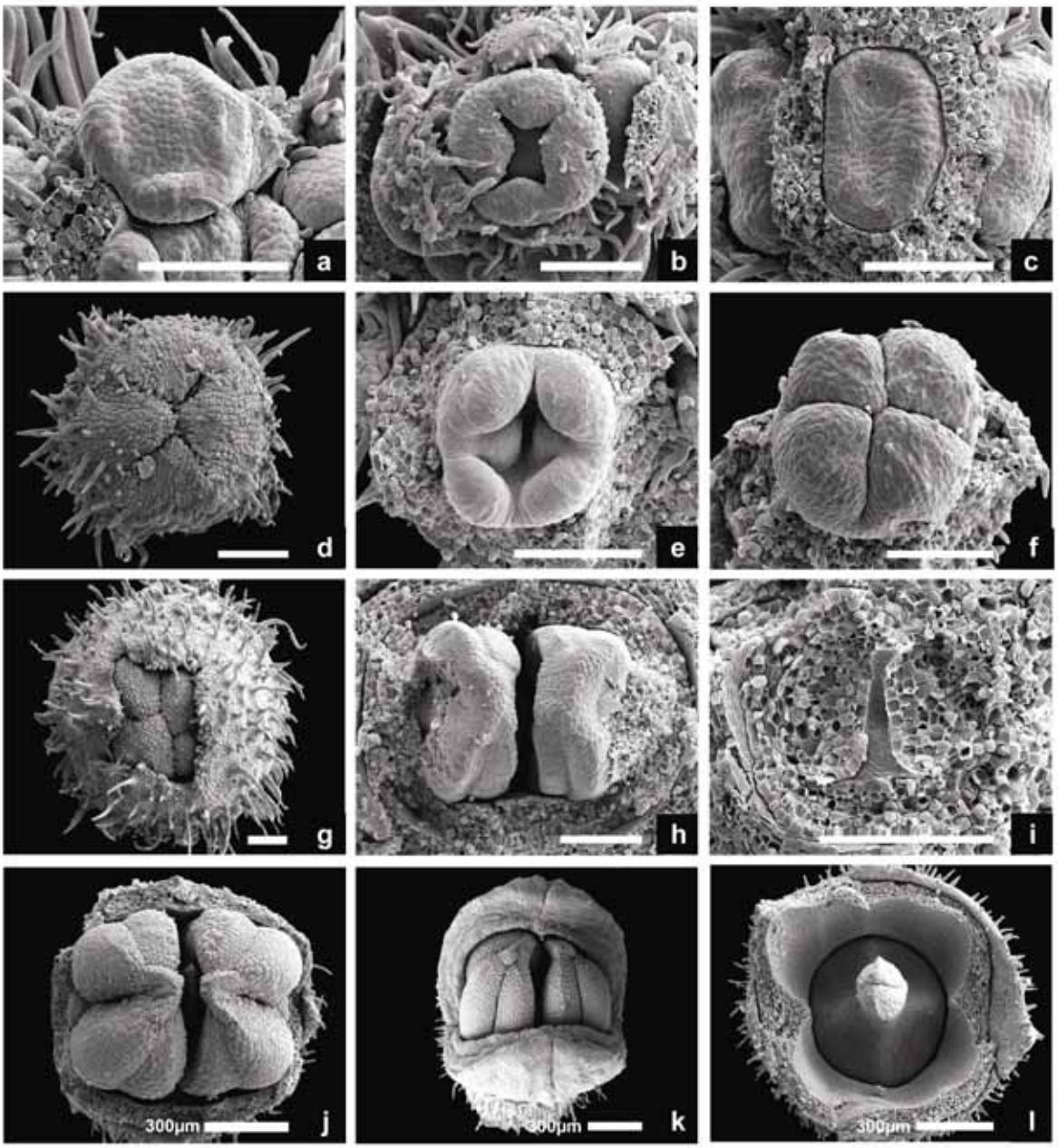

Fig. 9: *Ligustrum ibota*, floral development. (a and b) Formation of the sepals in orthogonal position. (c) Initiation of the corolla mound. (d) A young floral bud with closed calyx lobes. (e – g) Development of the corolla, note the apparently two lipped corolla and the initiation of the stamens in e. (g) Floral bud. (h, j and k) Developmental series of the stamens. (i and l) Formation of the gynoecium. Scanning electron micrographs; scale bars: 100µm, 300µm (j – l).

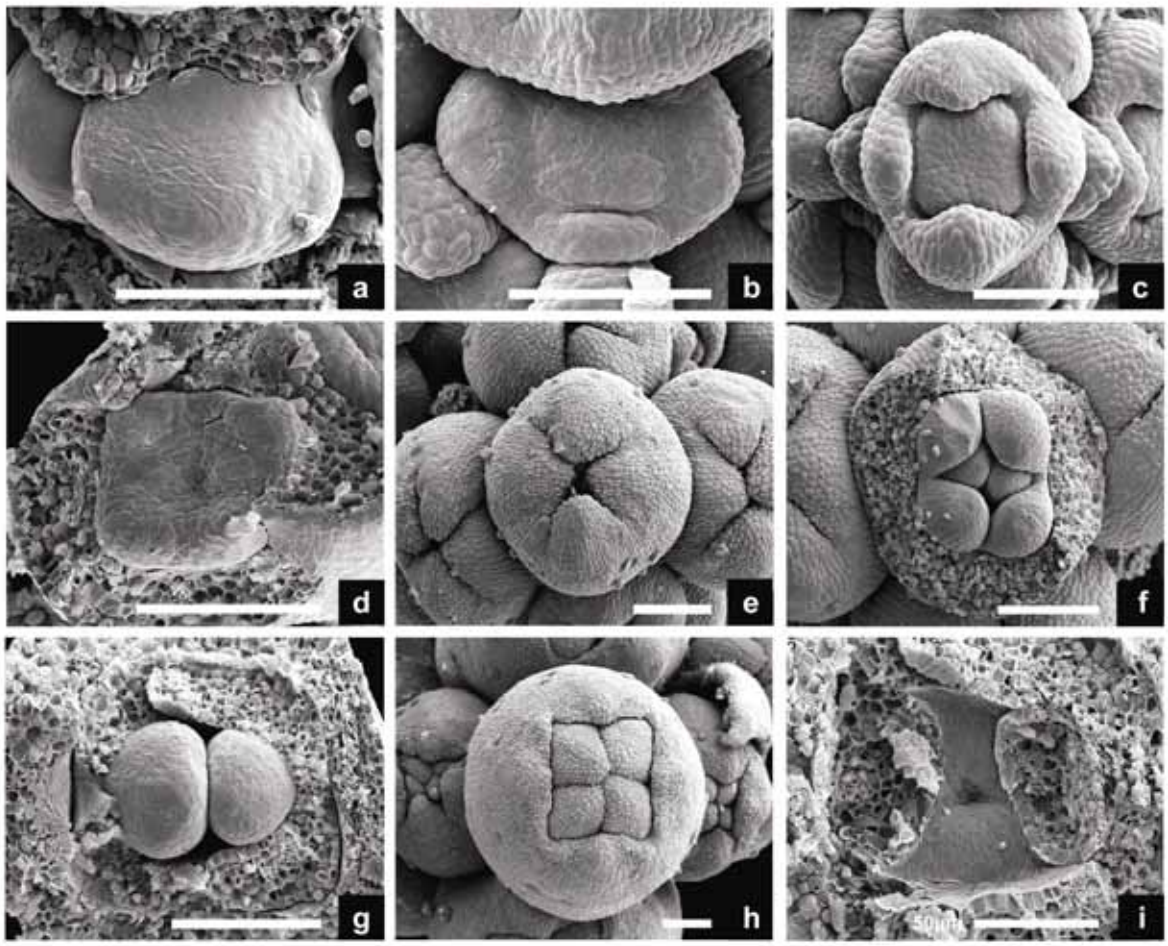

Fig. 10: *Ligustrum ovalifolium*, floral development. (a – c) Development of the calyx. (d) Initiation of the petals as a mound and the formation of the stamens (sepals removed). (f and g) Growth of the stamens. (h) Floral bud. (i) Initiation of the gynoecium. Scanning electron micrographs; scale bars: 100µm, 50µm (i).

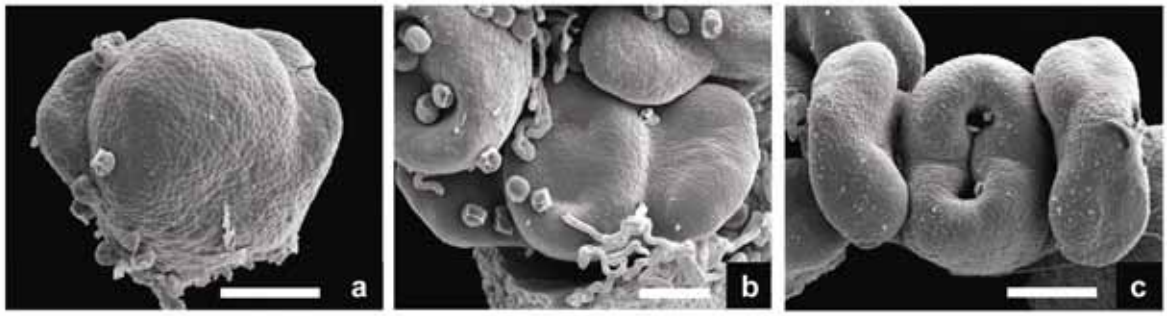

Fig. 11: *Fraxinus excelsior*, floral development. No perianth is developed. (a) Initiation of the stamens. (b and c) Further androecial development and formation of the carpels. Scanning electron micrographs; scale bars: 100µm.

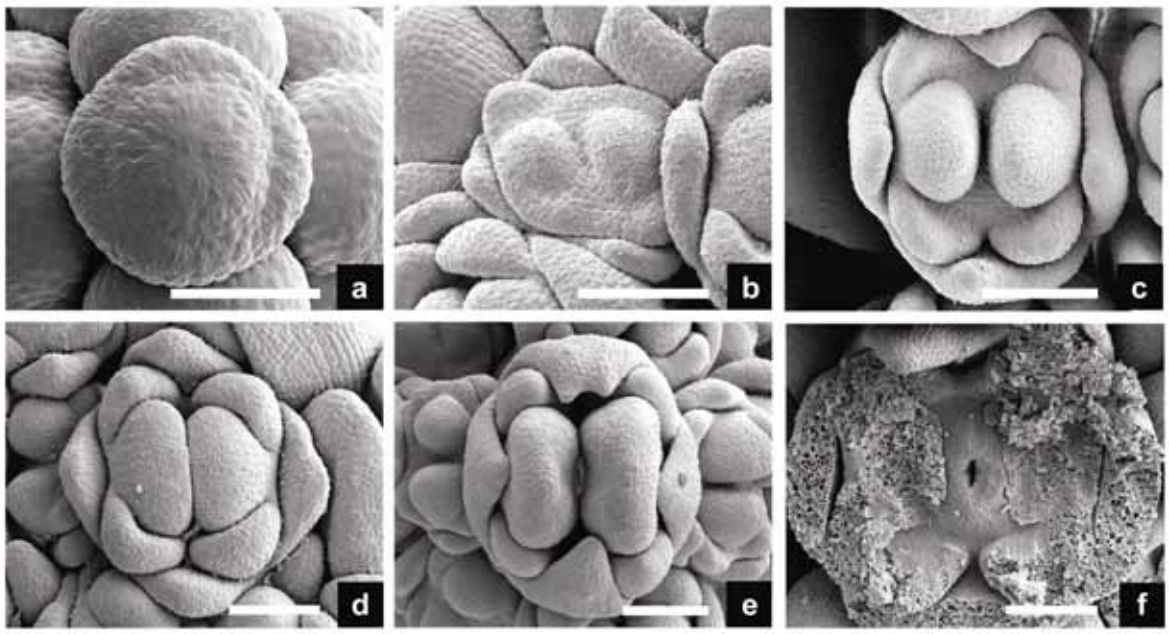

Fig. 12: *Chionanthus virginicus*, floral development. (a) Floral primordium with developing sepals. (b) Initiation of the petals as well as the stamens. (c – e) Formation of all the perianth and the androecium. (f) Development of the gynoecium. Scanning electron micrographs; scale bars: 100µm.

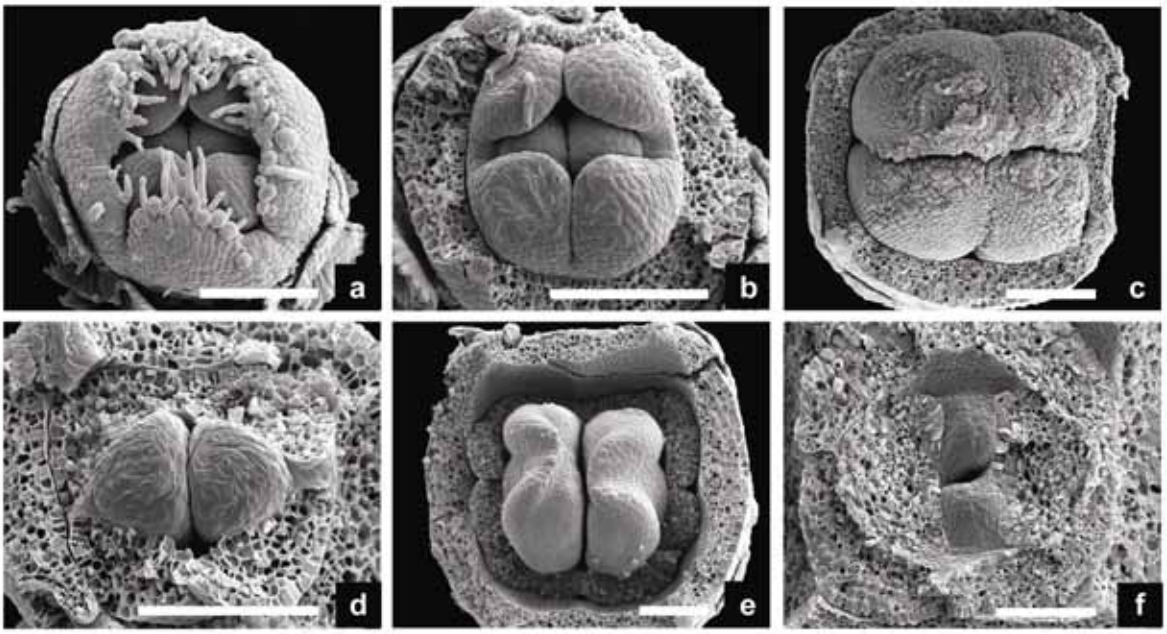

Fig. 13: *Olea europaea*, floral development. (a) Developed calyx. (b and c) Formation of the apparently two lipped corolla (calyx removed). (d and e) Development of the stamens (perianth removed). (f) Initiation of the carpels (perianth and stamens removed). Scanning electron micrographs; scale bars: 100µm.

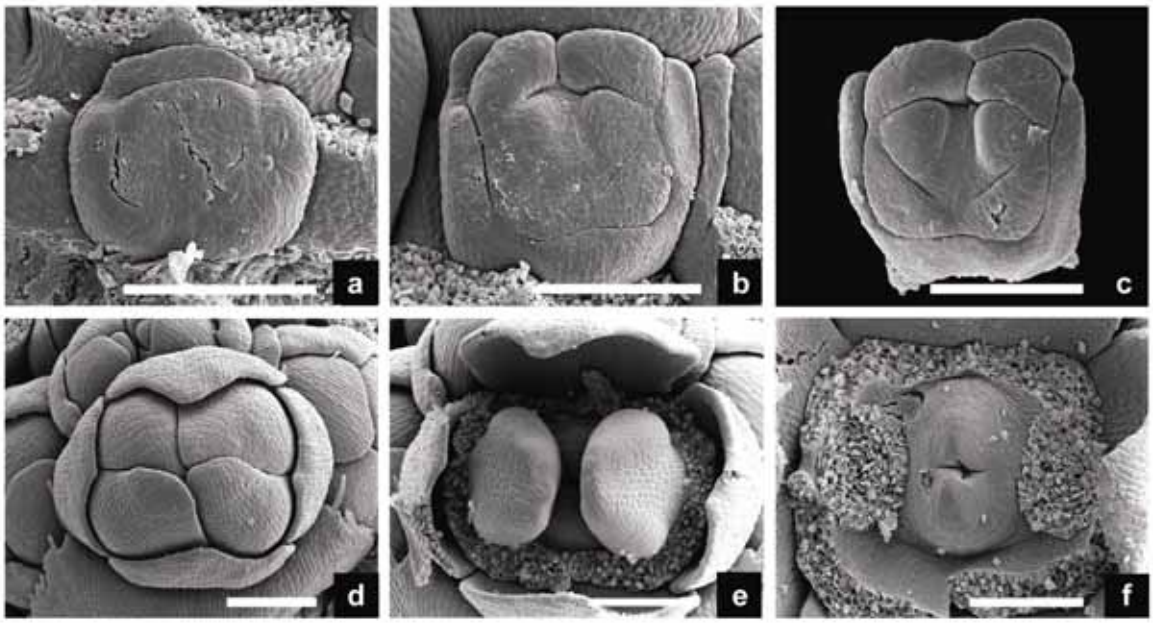

Fig. 14: *Phillyrea vilmoraniana*, floral development. (a) Floral apex with the adaxial sepals initiating first. (b and c) Formation of the petals, again the adaxial ones develop at first, and the initiation of the stamens. (d) Floral bud. (e) Developing stamens (corolla removed). (f) Carpels (corolla and androecium removed). Scanning electron micrographs; scale bars: 100µm.

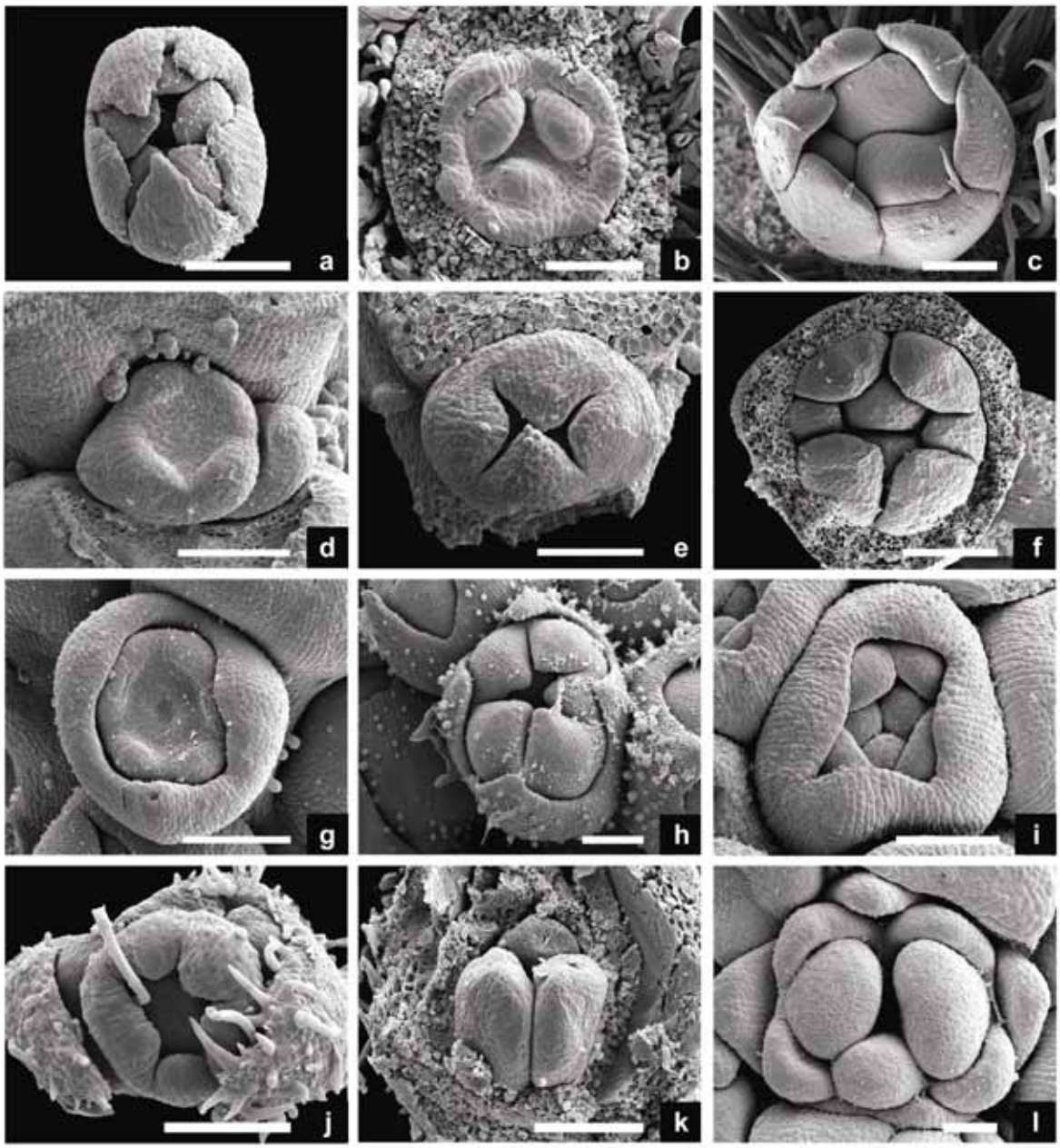

Fig. 15: Teratologies. (a) *Fontanesia fortunei*, pentamerous perianth. (b and c) *Nyctanthes arbor-tristis*, formation of three stamens (calyx removed). (d and e) *Jasminum fruticans*, formation of four sepals in diagonal position (d) and in orthogonal position (e). (f) *Jasminum fruticans*, six developed petals (calyx removed). (g and h) *Syringa josikaea*, three sepal lobes are developed in g, five petal lobes are shown in h. (i) *Syringa villosa*, three stamens are formed. (j and k) *Ligustrum ibota*, formation of five petal lobes (j) and 3 stamens (k, perianth removed). (l) *Chionanthus virginicus*, formation of three stamens. Scanning electron micrographs; scale bars: 100µm.

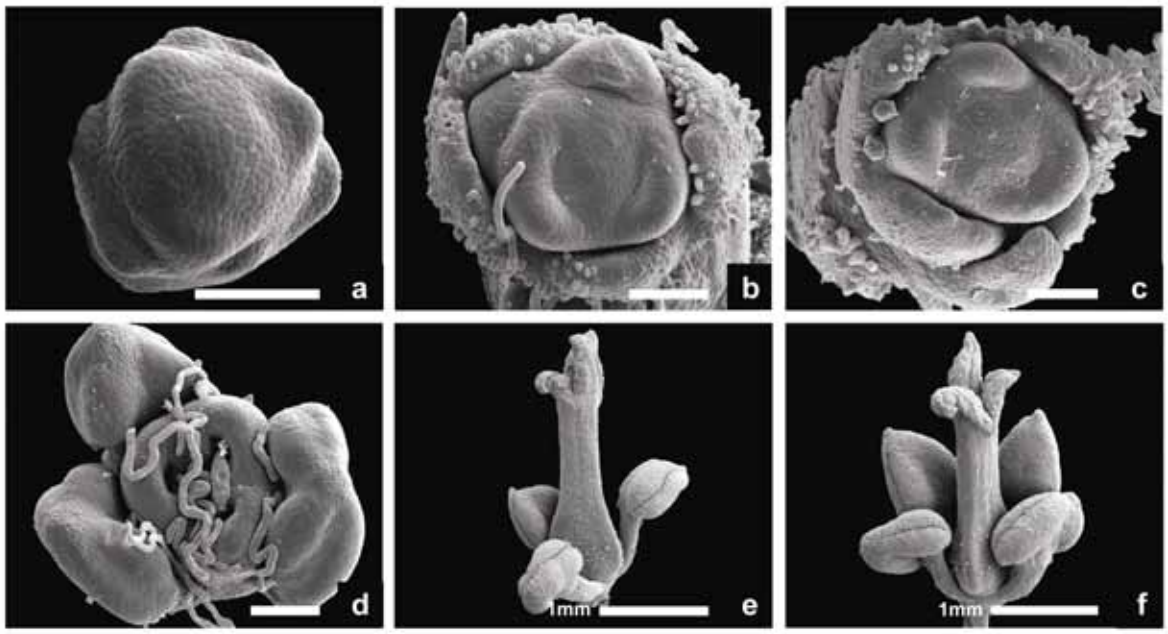

Fig. 16: Teratologies. *Fraxinus excelsior*. (a) Initiation of primordia of an indefinite origin. (b and c) Development of a not clearly defined perianth. (d and e) Trimerous androecium and gynoecium. (f) Combination of a tetramerous androecium and a trimerous gynoecium. Scanning electron micrographs; scale bars: 100µm, 1mm (e, f).

ANALYSIS OF THE OLEACEOUS FLOWER

Several authors already studied the considerable diversity of the floral pattern of Oleaceae and tried to find a common floral ground plan:

(1) EICHLER (1875) characterised the calyx as dimerous and dicyclic (composed of two dimerous whorls). The monocyclic corolla was said to be tetramerous and in diagonal position to the axis. The stamens and carpels were said to represent dimerous whorls. He mentioned that *Tessarandra* has a tetramerous androecium, but did not go into details of the merosity problem. He described the flower of *Jasminum* separately. With the perianth being 5 – 10merous and the calyx being apparently monocyclic, but in some species two whorls would be visible.

Eichler also discussed the problematic floral orientation within the inflorescence. If prophylls are present, then the carpels are aggregated in the median, if prophylls are absent, the whole flower is rotated and the carpels are oriented in transversal position.

(2) TORGÅRD (1924) described the floral ground plan according to merosity (except *Jasminum*) as follows: S_{2+2}, C_2, A_2, G_2. Thus, only *Fraxinus dipetala* conforms to this ground plan. The tetramerous corolla of all the other representatives of the Oleaceae is due to the epipetalous split of the primary petals. He stated that the corolla of *Jasminum* was dicyclic and originally dimerous.

Torgård gave a short description of the orientation of the flower on short shoots, which is due to the number of the bracteoles. If the number of bracteoles is uneven, the last leaf pair on the short shoot, which is embedding the flower, is oriented in transversal position and thus, the carpels are placed in the median. Concerning the orientation of the flower within an inflorescence, his results conform with those of EICHLER (1875).

(3) WEBER (1928) concluded that the ground plan comprises a calyx, corolla, androecium and gynoecium, which are all dimerous and dicyclically arranged, with continuous decussation. The two whorls of each organ are about

to converge, forming apparently one whorl in the adult flower. He stated that in *Jasminum* the original two whorls of petals still can be seen and that in all the other genera of the Oleaceae one of the two whorls is absent. The abort of some whorls is compensated because of the split of the remaining sepals/petals into multiple lobes. He revealed that the tetramerous androecium of *Tessaranda* is due to presence of all two dimerous whorls and in all the other genera one androecial whorl is lacking.

Weber mentioned also the variable orientation of a flower on a short shoot and agreed with EICHLER (1875). The different orientation is not the result of an abort of two stamens or carpels in a originally tetramerous androecium or gynoecium, but the different aggregation of the fertile organs is due to the different orientation of the whole flower.

(4) A recent description of the Oleaceae was given by GREEN (2004). He described the calyx as well as the corolla as generally four-lobed, up to 15-lobed in case of the calyx and up to 12-lobed in case of the corolla. The corolla is usually sympetalous and rarely absent. The androecium is dimerous, but tetramery occurs scarcely. If the flower is sympetalous, a stamen-corolla tube is formed. He stated that the bicarpellate gynoecium forms a syncarpous, superior ovary with an terminal style and a two-parted stigma. The ovary contains two ovules per loculus on axile placentae, but sometimes also one to four or numerous ovules occur. The fruit is a capsule, or a one-seeded berry, or a drupe, or a samara.

In the present study, by surveying the floral development from insertion to anthesis, the following general pattern of the floral ground plan becomes apparent:

CALYX – the four sepal primordia are initiated simultaneously in orthogonal position.

COROLLA – four petal primordia are developed simultaneously in diagonal position.

ANDROECIUM – the two stamen primordia are initiated simultaneously in transversal position.

GYNOECIUM – two carpel primordia are initiated simultaneously in median position.

Within this regularity, some exceptions occur. In the species examined, only in *Nyctanthes* and *Jasminum* a pleiomerous calyx (5 – 8lobed) as well as a pleiomerous corolla (5 – 8lobed) were found. In the literature, additionally, *Menodora* is known for its same floral ground plan as in *Jasminum* and *Schrebera* for its pleiomerous corolla, but has a tetramerous calyx. Also representatives without a calyx and/or corolla occur (e.g. *Fraxinus excelsior*).

ONE OR TWO WHORLS?

The results of the present study make a dicyclic arrangement of the calyx, corolla, androecium and gynoecium unlikely. The simultaneous formation of the calyx on the floral apex, explicitly show a monocyclic calyx. Although the genus *Jasminum* was always treated as a good example for a dicyclic calyx (EICHLER, 1875; TORGÅRD, 1924; WEBER, 1928), no evidence for dicycly is found in the floral ontogeny. The sepal primordia are inserted concurrently within the same whorl on the floral apex. In later stages the specific contort aestivation of the calyx lobes may give a reason to the assumption of dicycly. Regarding the corolla, the clearly simultaneous initiation of the petal primordia of all species observed give evidence to a monocyclic corolla. Also in the other pleiomerous genus *Nyctanthes*, no proof for dicycly of the calyx, corolla, androecium and gynoecium is found in the floral ontogeny.

DIMERY OR TETRAMERY?

If there is no evidence for dicycly, why should there be one for dimery? Ontogenetically, a clear monozyclic calyx is formed consisting of generally four orthogonal sepals (cf. *Fontanesia*, *Syringa*, *Ligustrum*, *Chionanthus*, *Olea*, *Phillyrea*). Even in the controversial genus *Jasminum* teratological buds with a tetramerous calyx were found (Fig. 15d, e). Generally, in *J. fruticans* a pentamerous calyx occurs. If a monocyclic tetramerous calyx is presumed, than I can interpret this pleiomery as a consequence of split of one of the initially four sepals. In *J. nudiflorum* regularly a hexamerous calyx is formed. The explanation here is a bit more difficult. It seems, that the development of the calyx in *J. nudiflorum* is very similar to that in *Nyctanthes arbor-tristis*. At first, four sepals originate diagonally and later on, in the same whorl, two additional sepal lobes

emerge in the median, resulting in a hexamerous calyx. Although in *Nyctanthes arbor-tristis* more than four calyx lobes are built up in the adult flower, the primarily inserted sepals are clearly only four. Therefore, nothing argues against the assumption of a consistently tetramerous calyx.

Already EICHLER (1875) stated a tetramerous monocyclic corolla. The results of the current study totally agree with his results. The four petal primordia in most species observed (except the pleiomerous *Nyctanthes*, *Jasminum*, *Menodora* and *Schrebera*) are initiated simultaneously in one clear whorl. No evidence for dimery in the corolla is found.

Next to the dimeric androecium of the Oleaceae (EICHLER, 1875; TORGÅRD, 1924; WEBER, 1928; GREEN, 2004; present study), a few genera/species are known, where a tetramerous androecium occurs: four stamens are characteristic to *Hesperalaea palmeri* (KNOBLAUCH, 1895), *Chionanthus fluminensis* (formerly *Tessarandra fluminensis;* EICHLER, 1875), *Chionanthus quadristaminea* (WEBER, 1928) and to the two species of *Priogymnanthus* (GREEN, 2004; WALLANDER, personal comm.). As a teratology, four stamens are found in several species of the genera *Fraxinus* (Fig. 16), *Chionanthus*, *Forestiera*, *Olea*, *Nestegis*, *Notelea* and *Osmanthus* (BENTHAM, 1876; GREEN, 2004; WALLANDER, personal comm.). Despite the fact, that several teratologies were found, no staminodes occurred in the material observed.

ORIENTATION OF THE FLOWER

In the tetramerous Oleaceae-flower, which is described as the “normal case”, the calyx appears in orthogonal position, the corolla in diagonal position. The androecium is oriented in transversal aggregation and the gynoecium in median position. This emplacement depends (a) on the number of the bracteoles on a short shoot and (b) on the presence or absence of the prophylls in the inflorescences/dichasia, which is described well in EICHLER (1875), TORGÅRD (1924) and WEBER (1928). If the number of the bracteoles is uneven/if the prophylls are present, then the carpels are oriented in the median (the prevalent case) and vice versa (the less frequent case).

Just one species is out of place: *Nyctanthes arbor-tristis*. The study of the floral development indicates that the sepal primordia are not initiated in or-

thogonal position, but in diagonal position. Later in development, generally two additional lobes emerge in transversal position within the whorl of the calyx. A 6 – 8lobed synsepalous calyx becomes developed.

SYMPETALY

Two forms of sympetaly have to be distinguished: early sympetaly (the petals are connected already at their initiation) and late sympetaly (the petals are initiated separately and become connected later on by the formation of interprimordial meristematic bridges). Transitions between early and late sympetaly are known (ERBAR, 1991, 1996).

Within Oleaceae early and late sympetaly occur equally. *Fontanesia fortunei*, a very basal genus of Oleaceae, shows no sympetaly (Fig. 1c), only a very slight connection at the very base of the petal lobes behind the stamens occurs frequently, which indicates a transition to late sympetaly (Fig. 1f). In the tribe Myxopyreae, *Nyctanthes arbor-tristis* shows early sympetaly (Fig. 2e). Also in the genera *Jasminum*, *Syringa* and *Ligustrum* early sympetaly is very common, although in *S. josikea* no early sympetaly is noticeable (Fig. 5d), whereas in *S. laciniata* (Fig. 6c, d) and *S. villosa* (Fig. 7d) a uniform ring primordium is differentiated very clearly. All the representatives of the subtribe Oleinae observed are characterised by late sympetaly (i.e., *Chionanthus*, *Olea*? and *Phillyrea*). In *Olea europaea* the most young stages are lacking, so I just can assume the late fusion of the petal primordia to a corolla tube. *Chionanthus virginicus* (Fig. 12b, c) and *Phillyrea vilmoraniana* (Fig. 12b, c) do not show any formation of a primordia ring in early floral development, thus, indicating late sympetaly.

INTRAFAMILIAR CLASSIFICATION

The relationships within the family based upon sequence data were recently studied by WALLANDER & ALBERT (2000) (Fig. 17 and 18).

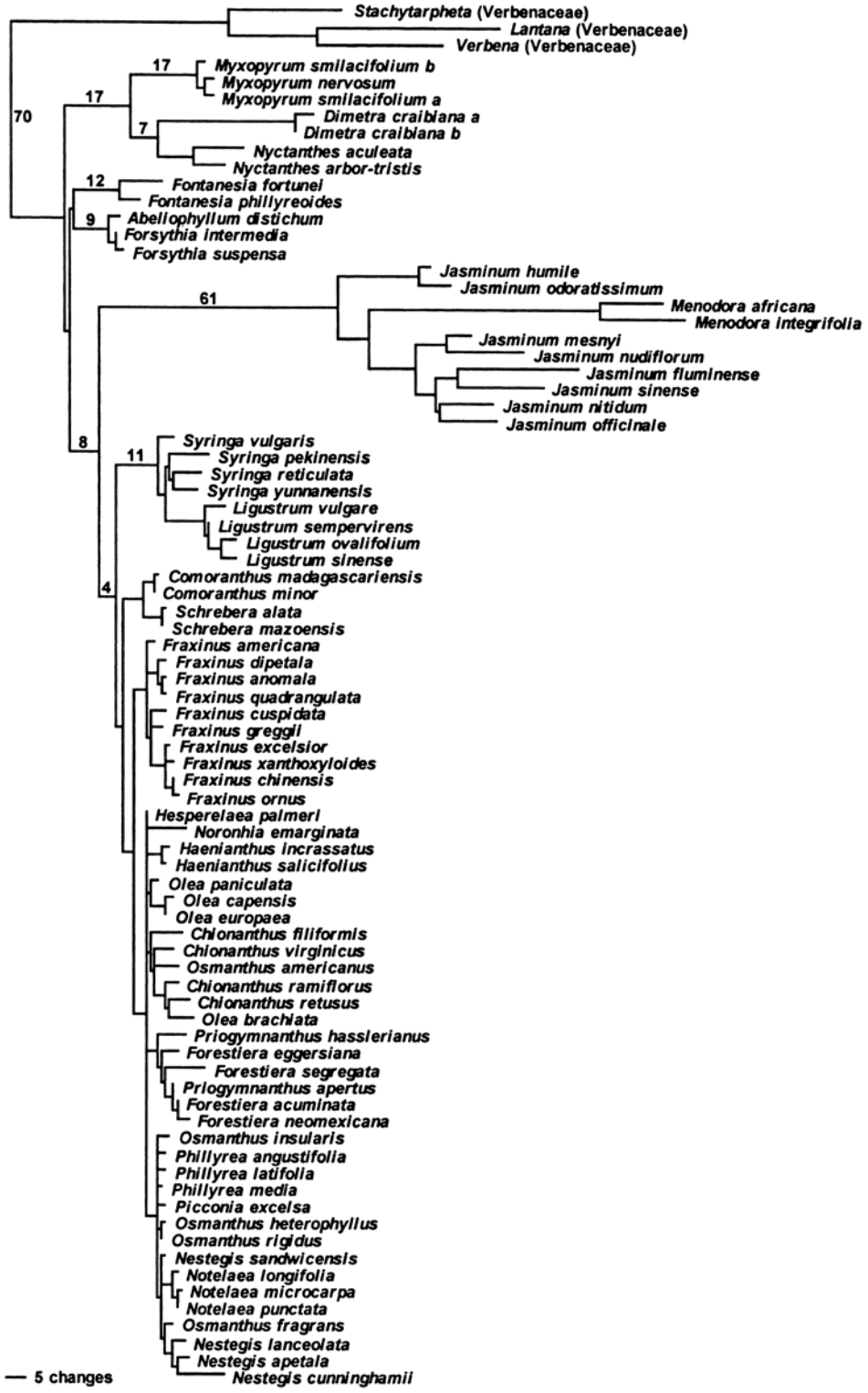

Fig. 17: Phylogram of Oleaceae by WALLANER & ALBERT (2000). Numbers indicate numbers of changes.

This phylogenetic analysis is completed by several preceding studies concerning karyology (TAYLOR, 1945), fruit structure (ROHWER, 1993), wood anatomy (BAAS, 1988), chemotaxonomical features (JENSEN, 1992). One aim of the current study is to parallel this phylogenetic tree with the dataset of flower morphology.

Throughout the family, from the most basal tribes to the most derived ones, in all tribes and even in all subtribes, this distinct pattern of floral development and the ground plan of the adult flower occurs as described above. Some exceptions in this floral development can be find in the most basally placed tribes, but the more derived the genera are, the more stable they are in their floral morphology (Fig. 18).

TRIBE FONTANESIEAE

Fontanesieae is closely related to the tribe Forsythieae at the very base of Oleaceae (WALLANDER & ALBERT, 2000). *Fontanesia fortunei* itself shows the typical tetramerous floral pattern described above. Noteworthy, this species does develop neither a calyx- nor a corolla tube, which otherwise is a very common character in the more derived Oleaceae. In fact, *F. fortunei* represents a species, which tends to be anemophilous. This is supported by the formation of elongated filaments, so that the stamens hang out of the flower.

TRIBE FORSYTHIEAE

Regarding to EICHLER (1875), the floral diagrams of *Forsythia* and *Abeliophyllum* are very similar and resemble that of *Fontanesia*. Thus, I can assume, that the floral development of both tribes, Fontanesieae and Forsythieae is similar. This is in support of a close relationship (Fig. 17).

TRIBE MYXOPYREAE

In the phylogram of WALLANDER & ALBERT (2000) Myxopyreae emerge at the very base of the family. This tribe is characterised by a high difference of several features (chromosome number, fruit type; Fig. 18).

Regarding to the floral ground plan, the genera *Myxopyrum* and *Dimetra* show a regular pattern concerning tetramery as described above. Only *Nyctanthes* is different. In the past, many studies dealt with the systematic position of *Nyctanthes* within Oleaceae, using different methods. Most of them support the affiliation of this genus to Oleaceae (BIGAZZI, 1989; KSHETRAPAL & TIAGI, 1970; KURIACHEN & DAVE, 1989; MOHAN & INAMDAR, 1983; ROHWER, 1994). Referring to the floral ontogeny *N. arbor-tristis*, shows a completely different floral development than any other genus/species investigated. The insertion of the primarily four sepals is not in orthogonal position, but in the diagonal one. This is unique within the family. In further development the formation of secondary sepal lobes within the same whorl occurs.

Due to the fact, that *Nyctanthes* is embedded in *Dimetra* and *Myxopyrum* and the insertion of primarily four sepal primordia, one can say that the pleiomerous floral ground plan of *Nyctanthes* has been derived from the originally tetramerous oleaceous flowers. Thus, the flowers of *Nyctanthes* can not be determined as primitive, but as derived.

TRIBE JASMINEAE

This tribe differs from the related tribes by long branch lengths in the phylogram (Fig. 17), indicating many differences in the genome. This can be seen also in the morphology. Regarding to the formation of the calyx, generally five sepals are initiated in *Jasminum fruticans* instead of four. Anyway, the fifth calyx lobe always looks a bit “vestigial”. Thus, one can assume a primarily four-merous calyx. Starting from a monocyclic calyx, the formation of the fifth sepal could be due to the split of one of the initially four sepal primordia. In a few buds of *J. fruticans* I found four sepals (Fig. 15d, e), consequently supporting the theory of an originally four-merous, monocyclic calyx. Hence, pentamery is found also in the corolla of *J. fruticans* alternating with the sepals. Then again, in *Jasminum nudiflorum* the perianth is consistently hexamerous. Thus, the floral development of the genus *Jasminum* differs in its merosity from all the other members of Oleaceae. In the formation of the calyx and corolla, it only can be compared with *Nyctanthes*. This concludes the derived floral pattern of *Jasminum*.

TRIBE OLEEAE

This tribe consists of 4 subtribes, which are quite similar in their floral developmental pattern.

The two genera of subtribe Ligustrinae, *Syringa* and *Ligustrum*, are characterised by the typical floral scheme as described above (four orthogonal sepals, four diagonal petals, two transversal stamens and two median carpels). Additionally, in both genera a calyx tube is developed with reduced calyx lobes. Furthermore, a very frequent feature is the formation of the distinct stamen-corolla tube. Due to the very similar ontogeny of the flower, a very close systematic relationship of the two genera can be assumed. This is supported by a recent study concerning the paraphyly of *Syringa* (LI et al., 2002). The genus *Ligustrum* form a well-supported clade and is nested within the paraphyletic *Syringa*.

WEBER (1928) produced a floral diagram of *Schrebera*, subtribe Schreberinae, which differs from the four-merous pattern described above. The calyx is generally four-merous, the corolla consists of eight petals. Whereas the second genus of this subtribe, *Comoranthus*, pursues the four-merous scheme (GREEN, 2004).

The subtribe Fraxininae is composed of the single and (concerning the floral ground plan) very diverse genus *Fraxinus*. In *F. excelsior* no perianth is formed. In the very frequent normal case, two stamens in the transverse and two carpels in the median become initiated. Teratologies in the androecium (three and four stamens are observable) and in the gynoecium (three carpels occurs, never four) are very common (Fig. 16). Next to the different amount of fertile floral organs as teratologies, also the formation of sterile floral organs occurs very frequently. The determination of these teratologies is difficult, but I assume, that these are residuals of the primal perianth. Within the genus *Fraxinus*, a perianth is well developed in the section *Bumelioides* (with the well known species *F. dipetala* and *F. ornus*). The former is permanently dimeric and monocyclic, whereas the latter forms a tetramerous calyx as well as a tetramerous corolla, which fits well into the tetramerous scheme.

All representatives of the subtribe Oleinae examined (*Chionanthus virginicus*, *Olea europea* and *Phillyrea vilmoraniana*) show the same tetramerous flo-

ral developmental pattern. According to WEBER (1928) and EICHLER (1875) also the floral diagrams of the remaining members of this subtribe do not show any serious deviations. It must be pointed out that only in *Forestiera* the calyx and the corolla are absent and in the genus *Priogymnanthus* generally only the calyx is lacking (GREEN, 2004). In other respects, this subtribe is the best supported one in all the past and recent studies (ROHWER, 1993; TAYLOR, 1945; WALLANDER & ALBERT, 2000). A particularity within this clade is the formation of four stamens, in *Hesperalaea palmeri* (KNOBLAUCH, 1895), *Chionanthus fluminensis* (=*Tessarandra fluminensis*) (EICHLER, 1875), *Chionanthus* q*uadristaminea* (WEBER, 1928) and in the two species of *Priogymnanthus* (WALLANDER, personal comm.; GREEN, 2004), and in a teratological way in several species of the genera *Chionanthus*, *Nestegis*, *Notolea*, *Olea* and *Osmanthus* (BENTHAM, 1876; WALLANDER, personal comm.; GREEN, 2004). The occasional formation of four-staminate flowers only in the more derived tribe Oleeae, especially in the subtribe Oleinae, leads to the conclusion, that the bi-staminate flowers are the original ones and the flowers with four stamens developed are the more derived ones.

SYMPETALY

In previous studies the systematic value of sympetaly was pointed out by ERBAR (1991, 1996). ERBAR (1991) described the oleaceous flowers as early sympetalous. Only two representatives of the family were examined in her study, *Syringa vulgaris* and *Fraxinus ornus*, whereas *F. ornus* does not show any sympetalous traits. From this results she concluded the whole family to be early sympetalous.

Consequently, the whole family is a very diverse family concerning sympetaly. The basally branched tribes of Oleaceae show mainly early sympetaly (*N. arbor-tristis*), even no sympetaly (*Fontanesia fortunei* with transitions to late sympetaly) occurs. The more derived tribes Jasminae and Ligustrinae are characterised by early sympetaly. The observed species in the tribe Oleinae all show late sympetaly. A trend from early sympetaly among the basal tribes to late sympetaly in the more derived tribes can be found.

Noteworthy is, that late sympetaly as a character is very common within the rest of the order Lamiales and that this characteristic trait is found in families like Bignoniaceae, Buddlejaceae, Globulariaceae, Pedaliaceae, Plantaginaceae, Scrophulariaceae, Verbenaceae (ERBAR, 1991), and also in the very closely related families Gesneriaceae, Calceolariaceae and Tetrachondraceae. One can say, that late sympetaly has been achieved within Oleaceae and that this characteristic trait was preserved in all advanced families.

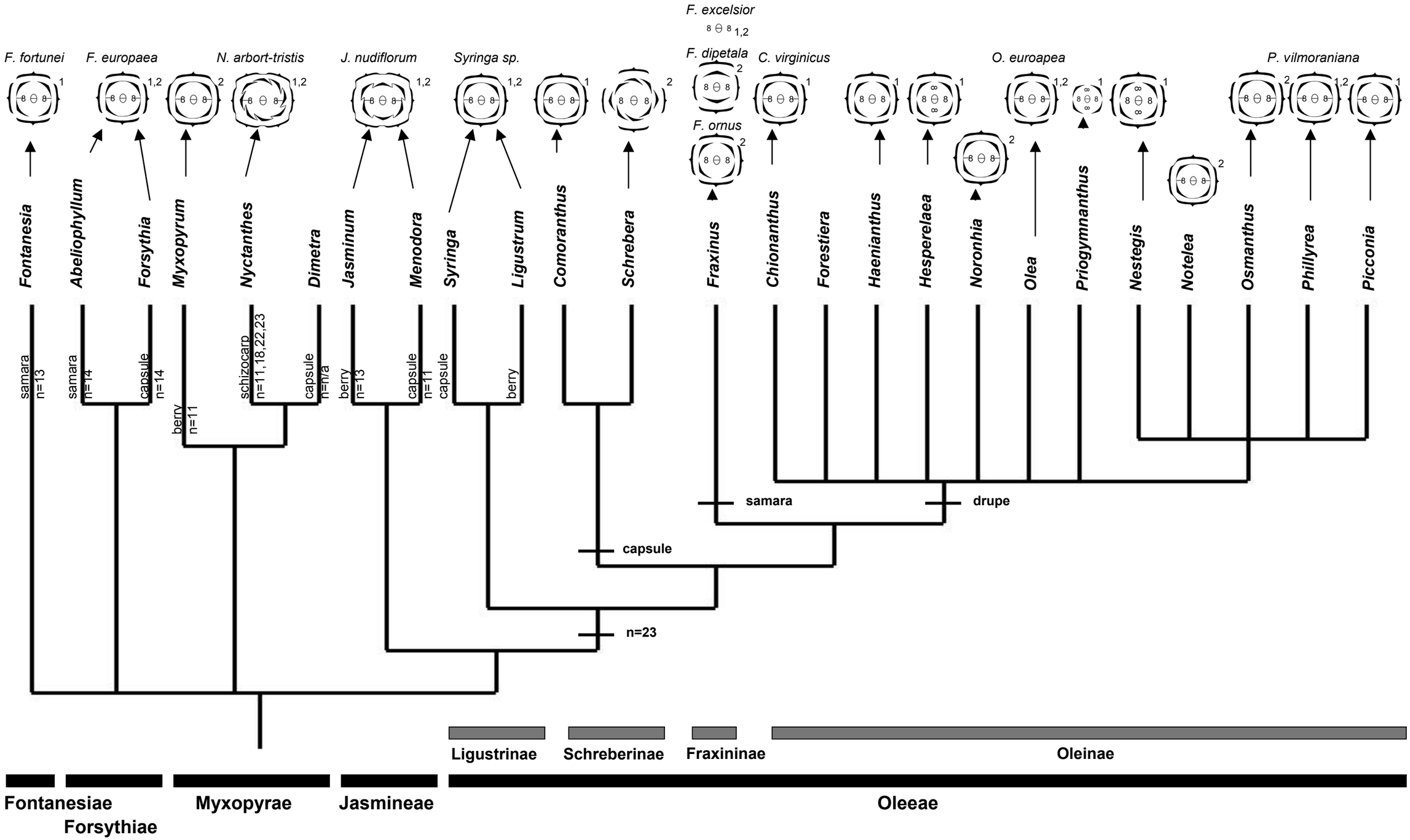

Fig. 18: Phylogenetic tree based upon the recent molecular phylogeny of Oleaceae by WALLANDER & ALBERT (2000). The floral diagrams indicate the continuous tetramerosity of the perianth within the Oleaceae. The numbers after each diagram stand for the author: (1) diagrams created by myself, partly with the material available, partly with data from the literature (GREEN, 2004), (2) diagrams after WEBER (1928), modified in diagrams labelled with 1, 2. Fruit characters (ROHWER, 1993; GREEN, 2004) and karyology (TAYLOR, 1945) are included to replenish this phylogeny.

OLEACEAE AND THE FAMILIES OF BASAL LAMIALES

If we take a look beyond Oleaceae, the next relatives are Plocospermataceae, Carlemanniaceae, Tetrachondraceae, Calceolariaceae and Gesneriaceae as shown in Fig. 19 (OXELMAN et al., 1999; BREMER et al., 2001; OLMSTEAD et al., 2001).

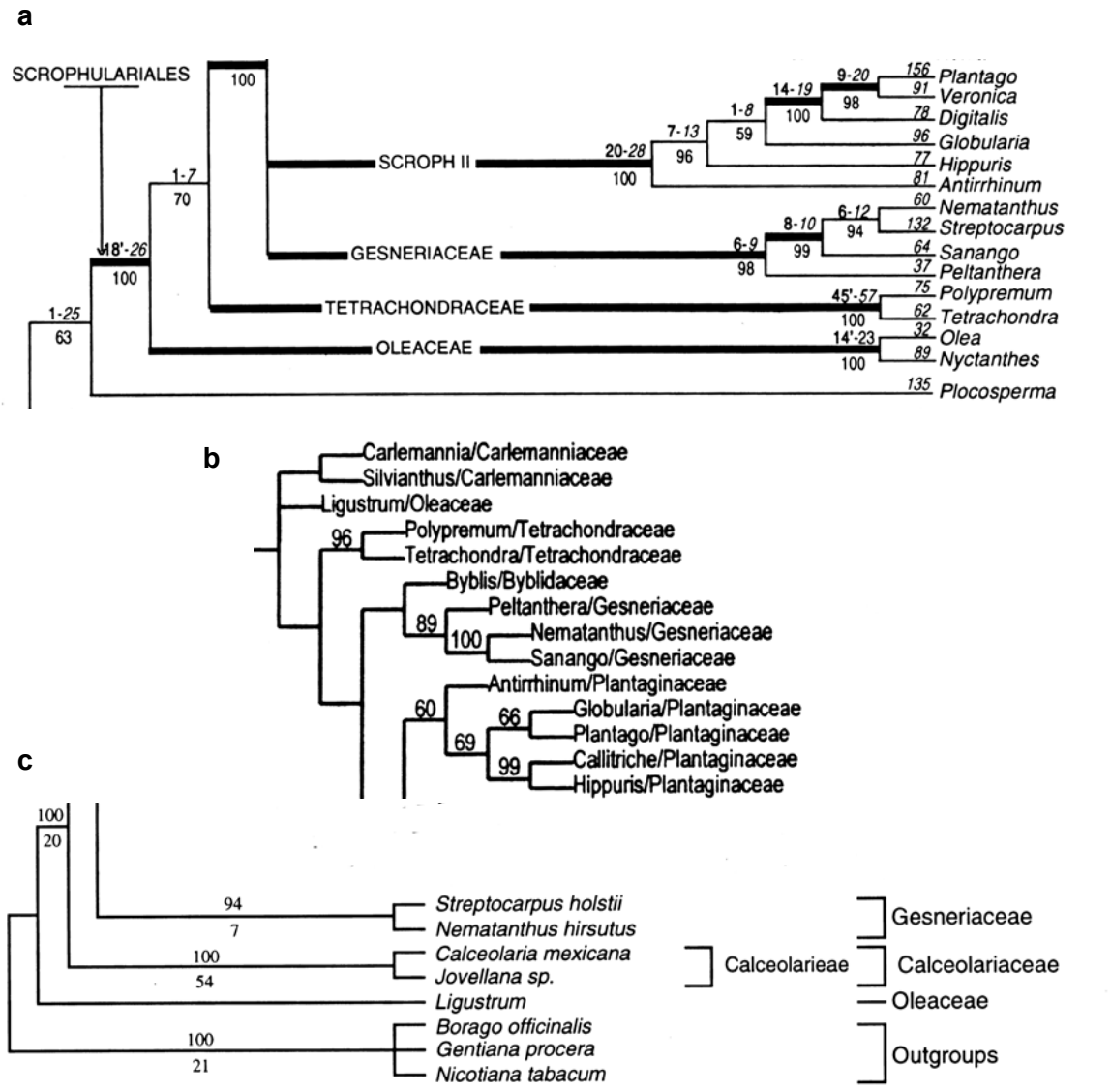

Fig. 19: Relationships in basal Lamiales based upon recent molecular studies by (a) OXELMAN et al. (1999), (b) BREMER et al. (2001) and (c) OLMSTEAD et al. (2001).

PLOCOSPERMATACEAE

The most basal family within Lamiales is the monotypic family Plocospermataceae. It is the sister to the remainder of the order (OXELMAN et al., 1999). Formerly, *Plocosperma* was affiliated to Loganiaceae (BENTHAM, 1876; LEEUWENBERG, 1967) and Apocynaceae (CRONQUIST, 1981). *Plocosperma* includes woody shrubs to trees with bisexual flowers. The floral pattern is described as pentamerous (incl. androecium; STRUWE & JENSEN, 2004) and the fruit is a one-seeded thin, linear capsule. The morphological traits correspond rather to the more derived families in the Lamiales (e.g. Gesneriaceae) than to Oleaceae and Tetrachondraceae.

CARLEMANNIACEAE

Both families, Carlemanniaceae and Oleaceae, emerge as an unresolved polytomy in the phylogram of BREMER et al. (2001) (Fig. 19b). Both share similar morphological characteristics, especially in the flower. Carlemanniaceae are described in the literature as tetra- or pentamerous. One special trait they do have in common, namely the two stamens, inserted in the corolla tube (THIV, 2004). But within Oleaceae, in the subtribe Oleinae also four stamens are formed naturally or as a teratology. Within this family a trend in evolutionary development can be observed: increase from two to four stamens from the most basal tribes to the more derived ones. If this trend is allocated not only to Oleaceae but to the whole order, one can say, that the tetramerous androecium in the more derived families has its origin in the dimerous androecium of the most basal families (Oleaceae, Carlemanniaceae and Calceolariaceae).

TETRACHONDRACEAE

Previous studies (OXELMAN et al., 1999; JENSEN, 2000; WAGSTAFF et al., 2000; BREMER et al., 2001) have verified the close relationship of Tetrachondraceae with Oleaceae (Fig. 19a – c). Regarding the merosity of the flower, Tetrachondraceae fit well into the alliance of Oleaceae. However, the floral orientation is different. The diagonal positioned calyx of *Polypremum* is different to all representatives of Oleaceae investigated, with the sole exception of *Nyctanthes ar-*

bor-tristis. In *Nyctanthes* the tetramerous calyx is initiated the same way as in *Polypremum*, namely simultaneously in diagonal position. It is likely, that this morphological trait (diagonal orientation of the calyx) is originally developed within Oleaceae and carried on to the more derived Tetrachondraceae.

Oleaceae are characterised by the development of two stamens, only some more derived taxa within the tribe of Oleeae form four stamens in orthogonal position. *Polypremum* itself always develops four stamens in diagonal position. This tetramery of the androecium can be seen throughout the whole order of Lamiales in various families (e.g. Buddlejaceae, Gesneriaceae, Globulariaceae, Myoporaceae, Nesogenaceae, Plantaginaceae, Verbenaceae; KUBITZKI & KADEREIT, 2004). Disregarding the orientation of the androecium, the formation of the four stamens in Tetrachondraceae can be seen as a trend, which indicates the increase from two to four stamens from the most basal families Carlemanniaceae, Oleaceae and Calceolariaceae to the more derived ones within the order.

CALCEOLARIACEAE

The family Calceolariaceae was established by OLMSTEAD et al. (2001) and emerges now after Oleaceae within basal Lamiales (Fig. 19c). Calceolariaceae are also characterised by a tetramerous perianth and this family fits thus very well into basal Lamiales (MAYR & WEBER, 2005). Regarding the floral ontogeny and ignoring the floral symmetry in the adult flower (zygomorphic), the insertion of the floral organs is very similar to that of Oleaceae. Only the corolla is two-lipped and it is very plausible, that it is derived from a truly tetramerous one. Also in the subtribe Ligustrinae an apparent two-lipped corolla in very early developmental stages can be seen (Fig. 8d and 9e). Thus, the comparison of the developmental pattern of both, Oleaceae and Calceolariaceae, supports previous studies regarding to the affiliation of both families. The formation of two stamens in transversal position as well indicates a close relationship of both families.

GESNERIACEAE

From Gesneriaceae onwards, pentamery has established, which is very common within the derived families of the order Lamiales. Thus, a comparison with Oleaceae is not necessary.

CONCLUSION

The present study reveals, that Oleaceae fits best with Tetrachondraceae regarding the floral morphology and ontogeny. This morphological similarity conforms to present molecular studies clarifying the affiliation of Oleaceae to basal Lamiales (WAGSTAFF & OLMSTEAD, 1997; OXELMAN et al., 1999; BREMER et al., 2001; OLMSTEAD et al., 2001). Nevertheless, discrepancies in the fruit structure of both families occur.

The family of Oleaceae is in its morphological characteristics very diverse yet. Although, trends in evolutionary development can be observed, which already have been established in higher Lamiales.

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