

Palynological contributions to the taxonomy of family Oleaceae, with special emphasis on genus *Forsythia* (tribe Forsytheae)

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ABSTRACT: Traditionally, the Oleaceae has been divided into subfamilies Oleoideae and Jasminoideae. In the present paper, the taxonomical results so far made on the family were reviewed on the basis of palynology. The subfamilial classification is not well supported palynologically, because both *Myxopyrum* of Jasminoideae and *Comoranthus* of Oleoideae having foveolate surface are well distinguished from the rest of the family having reticulate surface. The recent subfamily Nyctanthoideae (Takhtajan, 1977) including the monotypic *Nyctanthus*, was suggested to be included within the Jasminoideae although its closest relative on the palynological basis is different from that on the molecular basis. Tribal classification systems of the Jasminoideae are not well supported palynologically on the basis of surface character: presence or absence of bands on the mural ridge surface of the reticulum. On the basis of palynology, tribe Forsythiae including *Abeliophyllum*, *Fontanesia*, and *Forsythia* is monophyletic, and *Fontanesia* is well distinguished from the rest two. Korean species of *Forsythia* is divided into two: *Forsythia koreana* group and *F. ovata-nakai-saxatilis* group. Recent discovery of *F. saxatilis* at a locality of *F. ovata* raised a question if the distinction between the two species on the basis of hairiness would be right. In the recent molecular studies, *F. saxatilis* var. *lanceolata* seems to be identified as *F. saxatilis*. Molecular studies showed that *F. saxatilis* (seemingly var. *lanceolata* or var. *pilosa*) is close to *F. koreana*. The fact in which the molecular result showed a close relationship between *F. saxatilis* varieties and *F. koreana*, is controversial to the result by floral and vegetative morphology. An intensive taxonomic study of these taxa would be needed.

Keywords: Oleaceae, palynology, Forsythiae, *Forsythia*, *Myxopyrum*, *Comoranthus*

The Oleaceae (Hoffmansegg and Link, 1813-1820) consists of about 30 genera and 600 species. The family is characterized by woody habits with opposite or rarely alternate (*Jasminum* species) leaves; hypogynous, tetramerous, gamopetalous, sometimes apopetalous (*Fraxinus* spp.) or rarely apetalous (*Forestiera* and *Fraxinus* spp.) flowers with two or rarely four (*Hesperelaea* and *Tessarandra*) stamens on the floral tube; syncarpous ovary with two carpels; loculidical or septicial capsule, berry, drupe, schizocarp, or samara (Cronquist, 1981).

The family is considered monophyletic based on external morphology (Dahlgren, 1980; Green, 2004). However, the opinion of Hutchinson (1948) is different, as he mentioned "the family is an unnatural assemblage, and the dimerous androecium may have misled authorities into assuming a common origin for the taxa." He considered *Fraxinus* to be more closely allied to the Sapindaceae and *Ligustrum* to the Loganiaceae. Recently, a molecular systematics study based

on *RPS16* and *TRNL-F* genes using three species of the Verbenaceae as outgroups, supported the monophyly of the family (Wallander and Albert, 2000).

Possibly because of *Abeliophyllum*, a Korean endemic genus, and several endemic taxa of *Forsythia*, much attention to the family was paid by many Korean plant taxonomists including the present author (Lee and Park, 1982a, 1982b, 1984; Han, 1981). Since neither reviews nor critiques have been made on these studies, there seem to be problems in which many studies made some mistakes and confusions. An extensive palynological study made by Han (1981) was not published and its valuable contributions to the taxonomy of the Oleaceae have been neglected. In this paper, the taxonomic studies of the family with special emphasis on genus *Forsythia* (tribe Forsytheae) were reviewed, the palynological results will be used to evaluate the previous studies, and the issues awaiting solution were be discussed.

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Taxonomic problems on the subfamilial classification

The classical taxonomy of Oleaceae divided the family into subfamilies Jasminoideae and Oleoideae (Bentham, 1876). The system was supported on the basis of the number and attachment of ovules and the presence of constriction at the apex of the fruit (Knoblauch, 1895), and on the basis of chromosome number, i.e., the Jasminoideae $n = 11-14$ and the Oleoideae $n = 22-23$ (Taylor, 1945). The subfamilial system has been followed by many taxonomists (Johnson, 1957; Engler, 1964; Lawrence, 1970). As *Nyctanthes* of the family Nyctanthaceae or the Verbenaceae was transferred to the Oleaceae, the third subfamily Nyctanthoideae was added (Takhtajan, 1997). However, Wallander and Albert (2000), based on the chloroplast DNA sequences, did not support this treatment but included *Nyctanthes* within tribe Myxopyreae of subfam. Jasminoideae. They did not assign the tribes of the subfamily Jasminoideae because it is paraphyletic in their phylogenetic tree. It is thought that on the basis of their phylogenetic tree, there would be no problem to accept the subfamily Jasminoideae even though the tribes of the Jasminoideae are paraphyletic. It is because of the matter of philosophical issue of taxonomy, as asserted in a conservatism concept of taxonomy in which not only monophyletic but also paraphyletic group should be accepted as a taxonomic group (Cronquist, 1987; Alexander, 2011). The infrafamilial systems by several authors are summarized in Wallander and Albert (2000) and Han (2001).

Disregarding the issue whether we accept the paraphyletic group or not, the molecular systematics study of the Oleaceae (Wallander and Albert, 2000) well supports the previous treatments and the subfamilial classification except the Nyctanthoideae of Takhtajan (1997) because *Nyctanthes* is nested with *Dimetra* within the tribe Myxopyreae of the subfamily Jasminoideae. According to the molecular study, the Jasminoideae is a heterogeneous group contrast to the homogeneous Oleoideae, and the latter was regarded to be originated from the former as suggested by an allopolyploidy (Taylor, 1945), and a serological data (Piechura and Fairbrothers, 1983).

Contributions of pollen morphology to the subfamilial classification

A pollen morphology of the Oleaceae (Han, 2001; Han et al., 2002) was observed under the direction of the present author. The pollen morphology of the family showed that the aperture type is tricolpate, tricolporate or tricolporoidate, and the surface is generally reticulate to micro-reticulate or

foveolate. Foveolate aperture type is not known within the family (Erdtman, 1971; Kiew, 1984; Nilsson, 1988), but it was due to limited sampling of genera. The palynological results dealing with 52 species of 24 genera (Han, 2001) did not support both subfamilial and tribal systems and several specific points are discussed as follows.

The pollen morphology revealed that *Myxopyrum* of the Jasminoideae and *Comoranthus* of the Oleoideae (Taylor, 1945; Wallander and Albert, 2000) having foveolate surface are closely related to each other and distinguished from the rest of genera having reticulate to micro-reticulate surface. A dispute might be possible, if this character is not important enough to distinguish the infrafamilial taxa. On the basis of the present author's short insight, however, it is suggested that this character can be applied to evaluate the subfamilial classification of the family. Is this pollen character really strong enough to raise such a suggestion? It may not be so, if this character is variable within the family. But having the foveolate surface is very rare within the family in which the reticulate surface is most common. The foveolate surface is more primitive than the reticulate surface (Walker, 1974; Walker and Doyle, 1975; Ji, 1989), and this character would be expected to give an important base to understand the phylogeny among the tribes and genera within the family as well as to evaluate the subfamilial classification. Regardless of the above corollary, isn't it enough to raise the same suggestion only from the fact in which both *Myxopyrum* and *Comoranthus* belonging to the Jasminoideae in Johnson (1957) but to the different subfamilies (Taylor, 1945; Wallander and Albert, 2000)? On this regards, the treatment of the Oleaceae without dividing subfamilies but with dividing tribes by Fernald (1950) and Green (2004) would be understood.

How about the position of *Nyctanthes* of the third subfamily Nyctanthoideae (Takhtajan, 1997)? The molecular result (Wallander and Albert, 2000) revealed that *Nyctanthes* is nested with *Myxopyrum* and *Dimetra* within the Myxopyreae. The pollen morphology of *Nyctanthes* is the closest to that of *Schrebera* within Schrebereae of the subfamily Jasminoideae (Johnson, 1957; Engler, 1964; Takhtajan, 1997). This relationship was not supported by Wallander and Albert (2000) in which *Schrebera* is included subtribe Schrebereae of tribe Oleae. Since the tectum of reticula in both *Nyctanthes* and *Schrebera* is quite thick and large, the two genera are well distinguished from the rest genera without such a surface. In the sense in which *Nyctanthes* and *Schrebera* show the close affinity palynologically, the treatment of *Nyctanthes* as a member of Myxopyreae including *Myxopyrum* with the foveolate pollen surface, seems to be also problematic.

Taxonomic problems on the tribal classification

The subfamilial and tribal classification systems by several authors are not congruent to each other as well as to the molecular data (Wallander and Albert, 2000). Pollen morphology raises another question about this matter on the basis of mural ridge character of the pollen surface reticula (Han, 2001; Han et al., 2002). It was found that there are two kinds of mural ornament among the species with reticulate pollen surface: one psilate and another banded at the top of the ridges of reticular muri. Such a distinction has never been recorded within the family. There are some incongruities between the mural ornament and the subfamilial as well as tribal systems.

Let's compare the pollen morphological data with the system of Wallander and Victor (2000): Psilate mural surface are found in most tribes of subfamily Jasminoideae such as Jasmineae (*Jasminum* and *Menodora*), Forsythieae (*Forsythia* and *Abeliophyllum*), Schrebereae (*Schrebera*), and Myxophyleae (*Nyctanthes*). However, tribes Ligustrinae (*Syringa* and *Ligustrum*), Fraxineae (*Fraxinus*), and some Oleaceae genera of the subfamily Oleoideae (*Picconia*, *Henianthus*, *Forestiera*, and *Priohymnanthus*) are also psilate, whereas the banded surface found in the rest of tribe Oleaceae of the subfamily Oleoideae (*Notelaea*, *Olea*, *Hesperelaea*, *Phillyrea*, *Noronhia*, *Osmanthus*, *Chionanthus* and *Nestegis*) and the tribe Fontanesieae (*Fontanesia*) of the Jasminoideae. Thus, the palynological results does not support the subfamilial system and suggests especially a revision of the tribe Oleoideae in which both psilate and banded muri coexists.

Before proceeding to the next discussion, there is one more thing to mention. *Jasminum* and *Menodora* belong to the tribe Jasmineae. Pollen morphology of both genera suggests two points. First, the pollen morphology is not enough to distinguish the two genera and supports the position of *Menodora* nested among *Jasminum* species of the molecular phylogenetic tree (Wallander and Albert, 2000) as well as the identity of gene relocation pattern within chloroplast genomes by multiple, overlapping inversions (Lee et al., 2007). Thus, a suggestion to merge the two genera would be possible. Second, their lumen surface and winding pattern of muri are more similar to those of *Abeliophyllum* and *Forsythia* than to those of *Ligustrum* and *Syringa*, and support the classical subfamilial separation if above mentioned problems are disregarded.

Circumscription and origin of the tribe Forsythieae

Let's focus on the tribe Forsythieae which include *Forsythia*

and *Abeliophyllum*. The monotypic position of *Abeliophyllum* separated from *Forsythia* (Nakai, 1920) is evident and doubtless (Kim and Kim, 2004). In the 20th century taxonomy, *Fontanesia* was treated as its own tribe Fontanesieae being separated from Forsythieae (Johnson, 1957), whereas *Fontanesia* and *Abeliophyllum* were treated as the tribe Fontanesieae being separated from the Forsythieae including *Forsythia* only (Taylor, 1945). The pollen morphology (Han, 2001) and molecular results (Wallander and Albert, 2000) well support the close relationship between *Forsythia* and *Abeliophyllum* (Johnson, 1957).

Palynologically, the Korean endemic genus *Abeliophyllum* would be thought to be originated from the common ancestor with *Forsythia* (Han, 2001). Furthermore, pollen morphology implies that *Forsythia* might have been derived from *Abeliophyllum* or its ancestor because pollen surface pattern of *Forsythia* shows frequently very small reticula inserted among large reticula. This hypothesis is supported by the molecular results as well (Wallander and Albert, 2000; Tae et al., 2005).

On this regards, the former hypothesis in which *Abeliophyllum* would have been derived from *Fontanesia* (Lee and Park, 1982a) is wrong. This hypothesis was made based on a cladistic study of exomorphology of the Korean Oleaceae showing that the samara of *Abeliophyllum* is more similar to the shortly winged flat fruit of *Fontanesia* than to the capsule of *Forsythia*, and this fruit shape was implied *Fontanesia* to be intermediate between *Forsythia* and *Abeliophyllum*. A previous pollen study (Lee and Park, 1982b) also made the same hypothesis based on the aperture morphology showing a pore type of *Fontanesia* (tricolporoidate) intermediate between *Forsythia* (tricolpate) and *Abeliophyllum* (tricolporate). The intermediate position of *Fontanesia* between *Forsythia* and *Abeliophyllum* was proven to be erroneous on the basis of later pollen study (Han, 2001) and molecular study (Wallander and Albert, 2000) of the Oleaceae. Needless to say, it was evident that the scanning electron microscopic observation is more accurate than the light microscope observation of the surface character.

The aperture type evolution has been regarded important in constructing main phylogenetic lines in many families such as Acanthaceae (Scotland, 1992), Boraginaceae (Liu et al., 2008), Leguminosae (Graham et al., 1980), Proteaceae (Feuer, 1990), Scrophulariaceae (Argue, 1980), etc. However, this may not be true in the Oleaceae as well as many other families such as Campanulaceae (Lee et al., 1988), Compositae (Perveen, 1999), Euphorbiaceae (Park and Lee, 1988), Lauraceae (Van der Merwe et al., 1990), Liliaceae (Kosenko, 1999), Polygonaceae (Hong et al., 1987), Ranunculaceae (Lee and Blackmore, 1992),

etc. In the family the aperture evolution from trocolpodoidate to tricolporate types appear in various lineages (e.g., *Menodora*, *Abeliophyllum*, *Ligustrum*, *Hesperelaea*, *Osmanthus*, and *Picconia*) and do not match with the tribal systems. Such an apertural evolution seems to be convergently arisen.

On the other hand, Tae et al. (2005) reported that *Fontanesia* and *Jasminum* as an outgroup, come at the base of *Forsythia* and *Abeliophyllum*. They might have thought that all three genera of *Fontanesia*, *Forsythia*, and *Abeliophyllum* belong to the tribe Forsythieae and interpreted that the tribe is monophyletic, even though there has been no such treatment (*Fontanesia* has never been included in the Forsythieae). Of course, their interpretation on the monophyly is taxonomically possible. But pollen morphology shows that *Fontanesia* having small reticula and banded ridge of the muri, is quite different from both *Forsythia* and *Abeliophyllum* having large reticula and smooth ridge of the muri (Han, 2001). It would be natural that the two tribes Fontanesieae and Forsythieae are sister group derived from a common ancestor as suggested from Wallander and Albert (2000).

Relationships among *Forsythia* taxa and misidentification problems

Forsythia belonging to the tribe Forsythieae consists of about 10 species. Species are distributed mainly in the east Asian temperate region. In Korea there were four endemic species reported. *F. koreana* is distributed throughout the peninsula. *F. ovata* was reported from Mt. Soraksan, Kangwondo and later the present author found at several other localities (Dukhangsan and Taebaeksan) in Kangwondo. *F. nakaii* was reported from Mt. Changsoosan, Hwanghaedo; few individuals were planted but disappeared in Hongneung Arboretum; many individuals were widely planted importing back from the United States. *F. saxatilis* was reported from Mt. Bukhansan, Kyoungkido, but was never found anymore. During the present author sought this species, two varieties of *F. saxatilis* were found: var. *lanceolata* from Mt. Bukhansan, Kyoungkido, and var. *pilosa* from Jinchunkun, Choongchungbukdo. *F. saxatilis* var. *pilosa* was found from Imsilgun, Chollabukdo later, but its name was erroneously reported as *F. saxatilis* (Cultural Heritage Administration website). Beside these endemic taxa, *F. viridissima* was introduced from China and widely cultivated in Euisungkun, Kyungsangbukdo for a medicinal purpose. *F. suspensa* was also introduced from China and cultivated for an ornamental purpose (Lee, 1984).

From the study of Korean *Forsythia* (Lee, 1984), the present author understood that the endemic taxa were found to be grouped into two: *F. koreana* complex including *F. koreana*

only and *F. nakaii* complex (this term was not used in the original paper) including *F. nakaii*, *F. ovata*, and *F. saxatilis* and its varieties. The former is characterized by long petiole (although slightly overlapping with the latter complex), more yellowish petals, broad floral tube and lobes, long sepals (above the half of the floral tube), and reddish and 4-ridged twigs, whereas the latter by short petiole, whitish yellow petals, narrow floral tube and lobes, short sepals (shorter than a quarter of the floral tube), and grayish and round twigs. Pollen characters of the former is congruent with morphological groupings by having thin muri, many minute reticula inserted among big reticula, and many granules on the lumen bottom, whereas those of the latter by thin to thick muri, few or no minute reticula inserted among big reticula, and few or no granules on the lumen bottom. The introduced species from China such as *F. suspensa* and *F. viridissima* can be included within the *F. koreana* complex based on exomorphological and pollen characters.

Among the *F. nakaii* complex, *F. nakaii* was regarded to be the most primitive because it has somewhat erect habit. The primitive nature was also found from the thick muri of the reticulate pollen surface. By the studies on *Forsythia* conducted later by many authors, the above hypothesis was never proven, mainly because *F. nakaii* was not included and in many studies *F. saxatilis* was probably mis-identified. For example, Lim and Ko (1989), Kim (1999), and Lee et al. (2011) did not include *F. nakaii* and *F. saxatilis*; what they used is dubious since the present author has never seen the type species of *F. saxatilis* var. *saxatilis* (autonym) except its varieties, *F. saxatilis* var. *lanceolata* and var. *pilosa*. Possibly the misidentification is thought to be made in Kim and Hong (1984) and Yeom et al. (1984) in the same reason. They mentioned *F. saxatilis* was collected at Kwanak Arboretum but the present author has never seen *F. saxatilis* there. It is guessed that materials the above authors used may be *F. saxatilis* var. *lanceolata* or less probably var. *pilosa*.

What is the problem in the identification of *F. saxatilis*? *F. saxatilis* var. *saxatilis* described from Mt. Bukhansan (Nakai, 1921) has broadly ovate to cordate leaves with hairs beneath. The present author verified the type specimens of *F. saxatilis* at Tokyo University (TI). Since the beginning of the present author's study of *Forsythia*, he has never seen the type species in the field as well as in the botanical garden, but found and described two varieties: var. *lanceolata* and var. *pilosa*. Both has the same shape of flower as *F. saxatilis* var. *saxatilis*, but their leaves are lanceolate. The difference between var. *lanceolata* and var. *pilosa* is that the latter has more hairs. Somebody may ask if the hairiness of the two varieties are continuous. Believe

or not, the difference between the two are so obvious and there is no way to be confused each other. In addition, their distribution is different: var. *lancolata* at Bukhansan and possibly Kwanaksan and var. *pilosa* at Jinchun and Imsil.

Kim and Kim (2011) included *F. nakaii* and obtained the result in which *F. nakaii* is a sister to *F. ovata*, and *F. japonica* comes at their base. The present author agrees to this result, because *F. japonica* has also broadly ovate to cordate leaves (Makino, 1914) and *F. saxatilis* (Nakai, 1942) was originally reported as *F. japonica* variety (Nakai, 1919), i.e. all belonging to the *F. nakaii* complex on the present author's criteria. But the present author doubts the result in which *F. saxatilis* is nested with *F. koreana* and *F. suspensa* in the same clade. *F. koreana* and *F. suspensa* have common features well distinguished from *F. nakaii* complex including *F. saxatilis*. As mentioned above, *F. koreana* and *F. suspensa* belong to the *F. koreana* complex and *F. nakaii* to the *F. nakaii* complex. Since the present author thinks that as far as *F. saxatilis* is obviously distinct from *F. koreana*, their identification is dubious and the result (Kim and Kim, 2011) is not easily acceptable.

A new discovery and challenges to the *Forsythia* studies

The present author and his colleagues in the laboratory of plant molecular systematics at Sungkyunkwan University, found *F. ovata* at another locality besides Mt. Sorak, and *F. ovata* again living along with *F. saxatilis* var. *saxatilis* in the other locality. *F. saxatilis* var. *saxatilis* is marvelously alive! It was really astonishing to see *F. saxatilis* var. *saxatilis*, because the author has thought it was extinct. However, the coexistence of the two taxa raised a new question what is the difference between the two except the hairiness. Since they belong to the same *F. nakaii* complex, other characters except the hairiness are the same, at least to the present author. The hairiness of *F. nakaii* complex is common but does not seem to be requisite. Therefore, it would need an intensive study to differentiate the two or merge them to one if not differentiated. Molecular techniques would be helpful to contribute for the elucidation of the problem.

If this problem is solved, the next question arises if there is other differences except the leaf shape between *F. saxatilis* var. *saxatilis* and its two varieties. The present author described the two varieties because they have hairs on the lower surface of leaves, although their leaf shape is lanceolate. Thus an arising question is if broadly ovate-leaved *F. saxatilis* var. *saxatilis* and *F. ovata* are distinct from lanceolate-leaved *F. saxatilis* var. *lancolata* and var. *pilosa*.

It would be interesting to study further on the *Forsythia* taxonomy as follows: Is *F. nakaii* a basal group of *Forsythia* species? *F. nakaii* is thought to be primitive because of an erect habit and the small and homogeneous reticula with thick muri. In the plant taxonomy, there is a general rule in which a common character is primitive (Estabrook, 1977; Frohlich, 1987). In *Forsythia*, the stems of most species are not erect but first ascending and later bending down, and the somewhat erect habit of *F. nakaii* is thought to be primitive. As a palynologist the present author thinks that the pollen surface character is an important basis to assume primitive to derived states. Because the widely reticulate surface more efficiently facilitates the absorption of stigmatic fluid and the penetration of pollen tube through stigma and style (Lee, 1978, 1988, 1989), the direction toward reticulation would be favored and thus *F. nakaii* is primitive. Further studies to verify the primitiveness of *F. nakaii* would be necessary.

If *F. nakaii* is proven to be the most primitive among the species of *Forsythia*, Korean peninsula becomes known as another center of origin of the genus. It was found that Korean peninsula is the center of origin of *Lycoris* (Lee and Kim, 1987), but many people, even plant taxonomists, do not recognize this fact well. It would be wonderful to see a phylogeny of *Forsythia* starting from a Korean endemic *F. nakaii* at the base of the tree someday.

As reviewed above, in spite of numerous researches of the Oleaceae, there are still left many issues to be solved in the phylogeny and taxonomy of the subfamilies and tribes of the family and Korean taxa of *Forsythia*. It is suggested that the correct identification of the species be needed to elucidate the relationships especially among the *Forsythia* species as well as the above levels. Whatever the levels are studied, more samples and more techniques should be used than ever used. Taxonomists should continuously search for evaluating the phylogeny and amending the infrafamilial classification systems of the family until a natural system, if there is (Lorch, 1961), is made, although we do not know when the dream comes true (Cronquist, 1969).

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