Nyctanthes is a member of the Oleaceae

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Abstract. The attributes of Nyctanthes (habit, floral morphology, fruit and seed, stem and leaf anatomy, flower vasculature, embryology, pollen, chromosome number and phytochemistry) are reviewed and found compatible with accommodation of the genus in the Oleaceae, tribe Jasminace. The treatment of Nyctanthes in Verbenaceae or as a separate family does not reflect its true affinities.

Keywords. Nyctanthes; Oleaceae; Verbenaceae; morphology; anatomy; embryology; karyology; phytochemistry.

1. Introduction

Since Airy Shaw (1952) removed Nyctanthes from the Oleaceae to subfamily Nyctanthoideae in the Verbenaceae, information has accumulated on its anatomy, embryology and phytochemistry which enables it to be compared with the range encountered both in the Oleaceae and the Verbenaceae. While most authors consider the characters of Nyctanthes compatible with those of the Oleaceae, Kundu and De (1968) suggest that a new family should be erected for the two species of Nyctanthes, N. arbor-tristis L. and N. aculeata Craib.

The following is a summary of the information now available for comparing Nyctanthes with other members of the Oleaceae, with new data on the anatomy of N. arbor-tristis.

2. Comparison of Nyctanthes with other members of the Oleaceae

2.1 Habit

As mentioned by Airy Shaw (1952), Nyctanthes does not "look" oleaceous. It is a coarse shrub with quadrangular stems and scabrid, dentate leaves; characters which are common in Verbenaceae. However, serrate or dentate leaves are also found in species of Olea, Osmanthus and Myxopyrum. A quadrangular stem is typical of Myxopyrum and is also found in a few Malesian species of Jasminum, such as J. insigne Bl. The thorns on the stem of N. aculeata, however, have no parallel in any genus of the Oleaceae.

The roughness of the upper surface of the leaf is so pronounced that leaves of N. arbor-tristis are used as sandpaper in parts of India where it is indigenous. However, in the Oleaceae Menodora scabra A. Gray has leaves which are equally scabrid.
2.2 Floral morphology

The flower of *Nyctanthes* has between 4 and 9 contorted lobes. *Jasminum, Menodora* and *Schrebera* all have more than 4 lobes (usually between 4 and 8) but these are imbricate. Apart from the aestivation, the flower is typically oleaceous: it is regular with two epipetalous stamens which alternate with the two locules of the ovary. This combination of characters is not found in the Verbenaceae.

Patel (1960) noted that *Nyctanthes* is heterostylous, as is commonly the case in *Jasminum* species. *Schrebera* is also heterostylous. Patel also noted that occasional flowers of both *Jasminum* and *Nyctanthes* have three stamens and trilocular ovaries.

2.3 Fruit and seed

The fruit of *Nyctanthes* is a dry chartaceous capsule which splits into two one-seeded parts. Capsules are also characteristic of *Menodora, Schrebera* and *Syringa*. The seeds are exalbuminous, as in many members of the Verbenaceae and species of *Chionanthus, Noronhea* and *Schrebera* of the Oleaceae.

The testa of *Nyctanthes* is thick and heavily vascularized, a feature shared by *Jasminum* and *Menodora*. In contrast, the testa of the Verbenaceae is non-vascularized (Kapil and Vani 1966). In addition the testa of *Nyctanthes* has the outer layer of large transparent cells typical of the Oleaceae (Taylor 1945) and like in *Menodora* the testa is green and the inner layers of cells contain chloroplasts (original observation).

2.4 Stem anatomy

Earlier accounts of the stem anatomy of *Nyctanthes* are by Fotidar (1939), Majumdar (1941), both dealing with the vascular organization, and Stant (1952) and Kundu and De (1968), whilst Murthy et al (1978) reported on the xylem vessels. In the latter study features of the metaxylem were highlighted, but probably confusion arose with early-formed secondary xylem vessels in some cases, and the lateral wall pitting was erroneously interpreted, rendering this study valueless. In Stant's and Kundu and De's accounts of the xylem the fibres are said to be provided with conspicuously bordered pits and xylem parenchyma is reported to be absent, which is in contrast with our observations, thus rendering the data of questionable value in comparing *Nyctanthes* with Oleaceae and Verbenaceae. We therefore give a new description here, based on the study of four authenticated samples of *N. arbor-tristis*. The description of the xylem is in line with a forthcoming, comprehensive generic wood anatomical survey of the Oleaceae (see Esser and Van der Westen 1983, for a summary of the preliminary results).

*Indumentum* of glandular capitate and unicellular eglandular hairs (cf. 2.5a). *Cork* subepidermal. *Cortex* parenchymatous and with irregularly shaped crystals. Cortical bundles at the four stem corners inverted (i.e., with the phloem on the internal side) to almost centric (figure 1), with a thin sheath of perivascular fibres confined to the internal side. *Perivascular sclerenchyma* of the central cylinder fibrous (phloem fibres). *Secondary phloem* with groups of stone cells and minute, irregularly shaped to acicular crystals in the parenchyma cells. *Secondary xylem* diffuse-porous, vessels numerous, predominantly in long radial multiples (of up to 8 vessels), diameter 30–85 µm; vessel member length ca 490 (300–890) µm; perforations simple in oblique end walls;
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Figures 1 and 2. Nyctanthes arbor-tristis. 1. Stem cross-section showing cortical bundle (above) and secondary xylem (below) with radial vessel multiples (× 125). 2. Tangential longitudinal section of wood showing ray cells and libriform fibres (× 510).

Intervessel pits alternate, nonvestured, 4–5 μm in diameter. Vessel-ray and vessel-parenchyma pits similar but half-bordered. Vasicentric tracheids very rarely present. Fibres thin- to medium thick-walled, ca 800 (470–1180) μm long, with minutely bordered to almost simple pits more numerous in the radial than in the tangential walls (libriform fibres, figure 2). Parenchyma very scanty apotracheal diffuse and paratracheal, in 3–4-celled strands. Rays 1–3-seriate; near the pith almost exclusively uniseriate and exclusively composed of upright cells; in thicker stems towards the periphery also with 2–3-seriates and including procumbent central cells (heterocellular, or heterogeneous type 1). Primary xylem in the internodes in an almost continuous cylinder. Pith composed of thin-walled, lignified parenchyma cells.

Most characters of the above description are of common occurrence in the Oleaceae. Wood with vessels for a large proportion in multiples and with libriform fibres is typical for a group of genera including Chionanthus, Comoranthus, Forestiera, Fraxinus, Haenianthus, Noronhia, Olea and Schrebera (Esser and Van der Westen 1983). Affinity of Nyctanthes with the Verbenaceae is less likely because most species of the latter family are characterized by septate fibres.
The phloem anatomy of *Nyctanthes* is also compatible with Oleaceae on account of its stone cell groups (cf. Zahur 1959). Cortical bundles in the corners of quadrangular stems are also typical for the oleaceous genus *Myxopyrum*, although in the latter they are fully centric (a minor, gradual difference with *Nyctanthes*).

Thus stem anatomy supports an oleaceous rather than a verbenaceous alliance of *Nyctanthes*.

2.5 Leaf anatomy

2.5a Leaf architecture: In a recent paper Mohan and Inamdar (1983) demonstrated that *Nyctanthes* showed similarities with Oleaceae in all aspects of leaf architecture and venation.

2.5b Indumentum: Stant (1952) described two main types of hairs for *Nyctanthes*: glandular hairs (found on both surfaces) which have a slightly depressed unicellular stalk and a head of four cells (figure 3), and unicellular trichomes (which are more frequent abaxially but are longer adaxially) having a base of eight adjacent cells which protrudes from the surface (figures 3 and 4). The former hair type is common among species of the Oleaceae, the latter is unusual especially for its length and raised hair base. The cells forming part of the hair base complex at the adaxial side are strongly sclerified and give the impression of being silicified in addition (original observation); the number of cells around the unicellular hair varies somewhat (6–9) and other cells around and below this ring (local hypodermis) are also sclerified and probably silicified. These unicellular trichomes give the upper surface its scabrid texture. The scabrid hairs of *Menodora scabra* are much shorter and hooked and have only a slightly raised base (original observation).

Inamdar (1967) in a detailed study of the hairs of a few species of *Jasminum* and of *N. arbor-tristis* described eight hair types for *Nyctanthes*. Of these only the fusiform eglandular type was not found in the four *Jasminum* species he examined. Unicellular trichomes are therefore not unique to *Nyctanthes* as is also apparent from Metcalfe and Chalk's (1950) account of the Oleaceae.

2.5c Stomata: The stomata of *N. arbor-tristis* are anomocytic, and thus typical of the family Oleaceae.

2.5d Foliar sclereids: Rao (1947) and Kundu and De (1968) reported the presence of sclerosed palisade cells in *N. arbor-tristis*, which occur as isolated cells or in groups of a few cells. These are short rod-like cells with thick walls and a narrow lumen. Foliar sclereids have been found in most representatives of the Oleaceae (Rao and Das 1979) but not in all (Solereder 1899); those of *Nyctanthes* are, however, atypical in not showing intrusive growth. Stant (1952) did not observe any mesophyll sclereids. In our material presence or absence varies with the specimen, probably related to absolute age of the leaf. Examination of a series of six leaves from a developing shoot showed that sclerosed palisade cells are only present in leaves which are fully expanded.

2.5e Crystals: Crystals are not present in the leaf of either species of *Nyctanthes* (Stant 1952; Kundu and De 1968; our own study). Although common in many species, they are
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Figures 3 and 4. Nyctanthes arbor-tristis. Drawings from SEM micrographs. 3. Abaxial leaf surface with vein and long unicellular hairs. Note also glandular hairs (arrows) and stomata (× 230). 4. Adaxial surface showing hairs which cause the scabrid texture of the leaf (× 190).

not invariably present in species of Oleaceae. For example, examination of 15 species of Chionanthus showed that crystals were present in only seven of these species (Kiew and Che Su 1982). It may be noted in passing that the type of crystals found in some of the stem material (see §2.4) is compatible with Oleaceae, which often have minute acicular or irregularly shaped crystals in both stem and leaf.

2.5f Petiole: The crescent-shaped vascular system of the petiole in Nyctanthes which is flanked by two or three pairs of lateral traces (Fotidar 1939; Majumdar 1941; Stant 1952; Kundu and De 1968; and our own study) is also common in members of the Oleaceae (Metcalfe and Chalk 1950; Kiew 1983).
2.6 Flower vasculature

Joshi and Fotidar (1940) investigated the course of the vascular system from the pedicel into the ovule. For *Syringa*, *Olea* and *Ligustrum* they found that the ovule received a single bundle which ran unbranched and ended in the chalaza. In *Jasminum* and *Nyctanthes* the crescent-shaped ovular trace divided into two bundles in the funicle and then further divided until the vascular system of the ovule consisted of about 25 to 30 bundles in the integument. Kshetrapal and Tiagi (1970) noted that this strong integumentary vascular system is not encountered in the Verbenaceae.

2.7 Embryology

Kapil and Vani (1966) reported that *Nyctanthes* differs from the Verbenaceae in two important characters. Firstly, the antipodal cells of *Nyctanthes* are small and ephemeral, whereas in the Verbenaceae they are large and persistent. Secondly, following the system of Sourges, the embryogeny of *Nyctanthes* is of the Megarchetype III of Second Period, whereas that of Verbenaceae is Megarchetype IV of First Period. *Jasminum* is the same as *Nyctanthes* for these two characters. Devi (1975) also found that the embryology of *Nyctanthes arbor-tristis* and species of *Jasminum* is basically similar.

2.8 Pollen

Saxena (1975) described the pollen of *Nyctanthes* as having a thick, subtectate sexine with winding muri and wide lumen (with a maximum diameter of over 8 μm) and provided with luminal bacules. He stated that he had not found this type of pollen in his investigation of 286 species in 77 genera of the Verbenaceae. Kundu and De (1968) noted that *Nyctanthes* pollen resembled the pollen of *Jasminum* to some extent, the latter also having a reticulate surface pattern.

2.9 Chromosome number

The somatic chromosome number of *Nyctanthes* has been recorded as 44 (Bolkhorskhikh et al 1969) and as 46 (Kundu and De 1968). Both these numbers occur in the Oleaceae: 2n = 44 is recorded for *Menodora scabra* (Taylor 1945, who also recorded 2n = 22 for two other species of *Menodora*) and *Ligustrum ibota*, *L. japonicum* and *L. tschonoskii*, *Osmanthes fortunei* and *O. sandwicensis*, as well as *Syringa amurensis*, *S. emodii*, *S. josikaea*, *S. persica* and *S. vulgaris* (Bolkhorskhikh et al 1969); while 2n = 46 is reported from eight genera of the Oleaceae, viz. *Chionanthus* (including *Linociera*), *Fraxinus*, *Ligustrum*, *Nestegis*, *Olea*, *Osmanthus*, *Picconia* and *Schrebera* (Bolkhorskhikh et al 1969).

In contrast, of more than 200 species of the Verbenaceae surveyed only three species have 2n = 44 (*Lantana camara*, *L. horrida* and *L. indica*) and one species, *Clerodendron thomsonae*, has 2n = 46.

2.10 Phytochemistry

Das and Rao (1966) compared the phenolic acids of *Nyctanthes arbor-tristis* with a few species of the Oleaceae and the Verbenaceae. Of the 13 phenolic acids investigated,
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eight were common to both families. Nyctanthes had caffeic acid present, which occurs in the Verbenaceae but only as a trace in the Oleaceae. In common with other members of the Oleaceae investigated, O-pyrocatechuic acid, phloretic acid and syringic acid were absent (they are present in the Verbenaceae) while ferulic acid was present in large amounts in both Nyctanthes and other members of the Oleaceae, but was present as only a trace in the Verbenaceae studied.

Hegnauer (1969) on the basis of mannitols, agreed that Nyctanthes is closer to the Oleaceae than the Verbenaceae. Harborne and Green (1980) found that Nyctanthes has the two common flavones of the family Oleaceae.

3. Discussion

The grounds for transferring Nyctanthes to the Verbenaceae are primarily its habit (its quadrangular stems and scabrid, dentate leaves) which is more commonly encountered in members of the Verbenaceae. However, species with these characters are also found in the Oleaceae. Apart from habit, there are no other characters which support its position in the Verbenaceae while evidence based on floral morphology, characters of the testa and integument, vegetative anatomy, embryology and palynology, chromosome number and phytochemistry all confirm its affinity with the Oleaceae.

Among the genera of the Oleaceae, Nyctanthes shows most similarity to Jasminum, Menodora and Schrebera (table 1) and, with Myxopyrum it shares a similar habit (quadrangular stem with cortical bundles in the corners and dentate leaves) as well as having ascending ovules.

The grouping of similar genera in the Oleaceae has been obscured by the division of the family into two subfamilies. Sensu Knoblauch (1892), subfamily Jasminoideae was small and consisted of three genera, Jasminum, Menodora and Nyctanthes, and subfamily Oleoideae was larger and more diverse and included the remaining 18 genera. Johnson (1957) reversed this situation by confining the subfamily Oleoideae to Tribe Fraxineae and Tribe Oleace. As he commented subfamily Jasminoideae then became "merely a convenient and capacious pigeonhole for everything that is excluded from the

<table>
<thead>
<tr>
<th>Characters of Nyctanthes</th>
<th>Menodora</th>
<th>Jasminum</th>
<th>Schrebera</th>
</tr>
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<tbody>
<tr>
<td>More than 4 corolla lobes</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Flowers sweet scented and open in evening, night</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Seed ascending</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Endosperm scanty or absent</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Integument and testa strongly vascularized</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Testa chloropyllous</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaves scabrid</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Fruit a capsule</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Heterostylos</td>
<td>?</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Vessels mostly in multiples</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Libriform fibres</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

Total number of shared characters 8 6 6

+ = presence; - = absence; ? = not known
Oleoideae." More detailed consideration of the genera he had removed to subfamily Jasminoideae, namely Schrebera (Harborne and Green 1980) and Myxopyrum (Kiew 1983) show them to be more closely related to Tribe Oleaeae. In fact neither subfamily can accommodate the range of diversity shown by the genera of the Oleaceae and it is more meaningful to abandon the use of the subfamilies altogether and to revert to the practice of Bentham and Hooker (1876) of using tribes of equal standing which can be arranged to show the relationship between them.

Bentham and Hooker (1876) recognized four tribes: Jasmineae (equivalent to Knoblauch's subfamily as it contained the same genera, Jasminum, Menodora and Nyctanthes); Syringae, Fraxineae and Oleineae. Johnson (1957) described four additional tribes: Fontanesieae H. Taylor & L. Johnson (split from Fraxineae); Forsythieae H. Taylor ex L. Johnson (split from Syringae); Schrebereae L. Johnson (split from Syringae) and Myxopyreae (split from Oleaeae). These four tribes were accommodated within his capacious subfamily Jasminoideae. Syringa was placed next to Lithustrum in Tribe Oleaeae.

Since Airy Shaw (1952) transferred Nyctanthes to subfamily Nyctanoideae in the Verbenaceae, many authors (Das and Rao 1966; Kapil and Vani 1966; Kshetrapal and Tiagi 1970; Mohan and Inamdar 1983; Saxena 1975; Thorne 1983) have considered that it should be retained in the Oleaceae and Devi (1975) has suggested subfamily rank for Nyctanthes in the Oleaceae, as does Thorne (1983). Kundu and De (1968) accorded Nyctanthes family status.

Accepting that Nyctanthes belongs to the Oleaceae, it is nevertheless unique for this family possessing a corolla which is truly contorted and a two-seeded schizocarp. What then should be its position within the Oleaceae? Should it join Jasminum and Menodora in Tribe Jasmineae or should it be given tribal or even subfamily rank?

It is always possible to argue that a particular genus possesses unique characters that would merit tribal rank, but this would defeat the purpose of suprageneric ranking which aims to reflect relationships between genera. If a monogeneric tribe or subfamily is erected for Nyctanthes on grounds of its habit and fruit type, then it is equally justified to erect a monogeneric tribe for Jasminum (which is unique in the Oleaceae for its climbing habit combined with the possession of pinnate leaves and bilobed berries), for Menodora, and so on for other genera.

However, this is unnecessary as table 1 indicates that Nyctanthes shares an array of characters with Jasminum and Menodora, and can therefore easily be accommodated within tribe Jasmineae sensu Bentham and Hooker as is also shown in §4. The differences in wood anatomy between Nyctanthes and the other two genera of the Jasmineae indicate a higher level of specialization of Nyctanthes. In other tribes similar differences in the level of wood specialization also occur (Esser and Van der Westen 1983, and in preparation).

Table 1 also indicates that Schrebera (in Tribe Schrebereae) is more similar to Tribe Jasmineae than are the other tribes. It will, however, be interesting to see if further chromosome counts of Nyctanthes confirm 2n = 44 (as n = 11 is the base number for Menodora) or 2n = 46 (n = 23 is the base number for Schrebera).

4. Taxonomy

Tribe Jasmineae Bentham & Hooker f.
Bentham & Hooker f. (1876) Gen Plant. 2 672.
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Subfamily Jasminoideae Knobl. (1892) in E and P. Pflanzenfam. 4, 2 13
Subfamily Nyctanthoideae (Verbenaceae) Airy Shaw (1952) Kew Bull. 272

Small trees, shrubs or climbers. Leaves simple, 1-, 3-pinnatisect or imparipinnate, sometimes scabrid. Corolla rather large with well-developed tube, 4–12 lobes, usually white or yellow, sweet-scented and opening in evening or night. Fruit bilobed, either fleshy or dry, or a schizocarp. Seed ascending, with thick, strongly vascularized testa. Endosperm scanty or absent.

Chromosome number: Jasminum n = 13, 14; Menodora n = 11; Nyctanthes n = 22, 23.

Key to the genera

1. Stem quadrangular, corolla lobes contorted, fruit a 2-seeded schizocarp, not bilobed ...................................................... Nyctanthes

1. Stems terete, corolla lobes imbricate, fruit bilobed, not a schizocarp

2. Fruit a bilobed berry. Shrubs or climbers with pinnate, tri- or unifoliate leaves

2. Fruit a bilobed capsule. Shrubs with simple or 1–3-pinnatisect leaves

.......................................................... Jasminum

.......................................................... Menodora

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