THE MORPHOLOGICAL EVALUATION AND TAXONOMIC VALUE OF THE SPATHE IN NAJAS, WITH DESCRIPTIONS OF THREE NEW ASIATIC-MALAYSIAN TAXA

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1. Introduction

In the course of a revision of the genus Najas for the Flora Malesiana I was confronted with the morphological evaluation of the spathe and with the variability of its occurrence, because this organ has served for the distinction of sections within the subgenus Caulinia.

It appeared of interest to publish the result of this work as a separate precursor as the space available in the Flora will not permit a detailed account.

I have to thank Dr. P. W. Leenhouts for valuable advice and suggestions during the course of the work which was supervised by Prof. Dr. C. G. G. J. van Steenis.

2. Status and taxonomic value of the spathe

Briefly, the gross morphology of a Najas plant is as follows. The sheathed leaves on the stem are placed in pseudowhorls of three. On closer examination each whorl consists of 2 subopposite leaves, the sheath of the lowest leaf overlapping the fully amplexicaulous sheath of the upper one. The latter does not produce any shoot from its axil. The lower leaf, however, produces a shoot in its axil which starts immediately with a new similar pair of leaves of which only one leaf (the upper one) develops to full size and forms the third leaf of the pseudowhorl; the other one is reduced to a small scale of microscopical size bearing a bud in its axil. In sterile shoots this bud is merely vegetative, in fertile shoots the scale together with its bud are replaced by a flower, either male or female, which is consequently almost sessile. This structure has been fully explained by Magnus (1870) and has also been agreed to by Rendle (1899).

The male flower consists of only one stamen on a short stalk lengthening in anthesis; this is, however, interpreted as the pedicel, not as the filament, because the anther is entirely surrounded by an adnate, extremely thin envelope ending into two lobes. This envelope is so closely appressed to the anther that it seems to form one whole with the latter, but according to Magnus (1894) it is partly adherent, partly adnate (l.c. t. xi Fig. 3-4). Consequently the envelope is interpreted as the perianth of the flower.

The female flower consists only of a very short-stalked, naked ovary provided with a longish style ending into 2-3 (-4) stigmatic arms. There is no trace of a perianth similar to that in the male flower.

Both male and female flowers may be surrounded by another, but free envelope which has commonly been called the spathe, a thin, membranous, bottle-shaped organ, often obliquely cut at its toothed apex. In the subg. Najas (consisting of one variable species only, N. marina L.) the spathe is only represented in the male flowers; in subg. Caulinia the spathe may occur in both sexes.

The presence or absence of the spathe in one or both sexes has been accepted as of systematical value for a subdivision of subg. Caulinia. Rendle has distinguished four sections largely based on its presence or absence, viz sect. Spathaceae: both sexes with spathe, sect. Americanae and Euvaginatae: only males with spathe, and finally sect. Nudae: no

spathe in either sex.

The morphological interpretation of the spathe has been subject to dispute. Rendle (1899, p. 383-384) has given a good review of the opinion of various authors about the true nature of the envelopes, i.e. their homology, and their evaluation in comparing the structure as found in Najas with that found in affiliated genera or families, such as Zannichellia, Hydrocharitaceae, Araceae, etc. He concluded: "that they found that the homology of the envelopes is difficult to explain on the ordinary terms of definition of the parts of a flower".

Rendle himself accepts the 2-lipped envelope of the male flower as a perianth; the spathe he finds "simply an outgrowth of the axis which ends in the flower below that flower. It is, I think, comparable with the spathe so characteristic of submerged monocotyledonous waterplants, which may have, moreover, a very similar appearance (e.g. Lagarosiphon, Hydrilla, etc.). It will then correspond, as Magnus suggested, with the cup-like envelope in Zannichellia, which on Campbell's interpretation (1897) becomes a spathe surrounding an inflorescence, as in the Aroids."

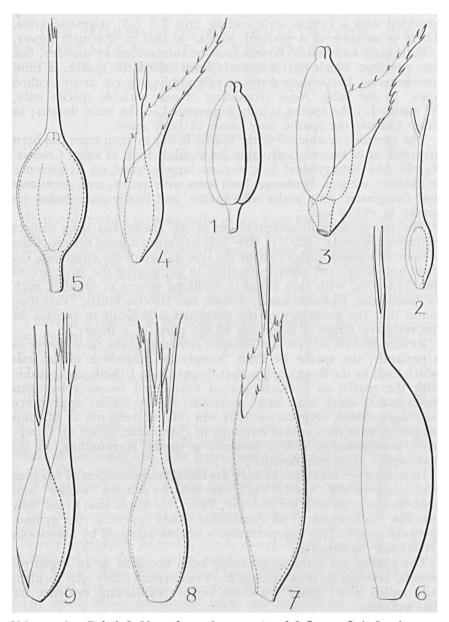
In passing we mention the very deviating interpretation of Magnus who accepted the "spathe" of Zannichellia to contain "ovules" and to be homologous with the ovary in Najas; this would lead to the view that the "inflorescence" of Zannichellia would represent one gymnospermous ovary. This interpretation is neither accepted by SCHUMANN (1894) nor by Rendle.

The spathe has hitherto generally been accepted as an organ sui generis, save for a casual remark by Venkatesh (1956) who incidentally called it a "bract", without further explaining evidence for

that opinion.

It is rather remarkable that Magnus did not pay more attention to the small scale bearing a bud in its axil found at the base of each vegetative shoot connected with the third leaf of each whorl.

Also Rendle, who obviously has considered the possibility that the spathe might be of a leafy nature, expressly stated (1899, p. 382) "that there is no sign of a midrib or of the division of these sac-like outgrowths into leaves."



Najas graminea Del. 1–2. Normal espathaceous $\mathcal J$ and $\mathcal J$ flower. 3–4. Spathaceous $\mathcal J$ and $\mathcal J$ flower found in one specimen with the normal ones. 5. $\mathcal J$ Flower with spathe (all $\mathcal J$ flowers of this specimen, the $\mathcal J$ were espathaceous).— $\mathcal J$. indica (Willd.) Cham. 6–7. Espathaceous and spathaceous $\mathcal J$ flowers of one specimen. 8–9. Spathaceous $\mathcal J$ flowers, found together with espathaceous $\mathcal J$ flowers on one specimen. All $\mathcal J$ 24.— 1–4 Carr 11792 (L), 5 Hook. f. & Th. s.n. (K), 6–7 Gamble s.n. (K), 8–9 Herb. Rottl. (K).

During my work on Najas I have seen many hundreds of sheets and examined a couple of thousands of flowers and have come across some specimens of Najas graminea Del., a species which normally has naked flowers (Fig. 1-2) but in which occasionally some flowers are provided with an envelope which is intermediary between a spathe and a leaf. Fig. 3-4.

These envelopes have in common with the spathe that they are at least partly closed and have no midrib, and no sheath-like auricles (which are obviously suppressed through the connation of the leaf margins).

They have in common with leaves that they are green, elongated,

and possess intravaginal scales as in normal leaves.

Besides I have observed in two specimens from Asia, which are in all other respects agreeing with N. graminea, a further stage which nearly approaches that of a normal spathe. In a sheet marked "Ass. Malariol. Publ. Health No. 1" (BM) from Burma one male flower was naked, the three others had a completely closed spathe but with a very thin and relatively long cylindric neck. In another Indian specimen marked "Hook. f. & Th." p.p. (K) all flowers had such a

long-necked spathe. Fig. 5.

The variability in occurrence of the spathe just mentioned in N. graminea is more clear in N. indica (Willd.) Cham. As I have published earlier (1960) the type of Caulinia indica Willd. had been erroneously described as being female; all flowers are male and have in this species almost invariably only a spathe in male flowers. In Malaysia the female flower is always naked but in Indian specimens the female flowers have occasionally also a spathe (Fig. 6-9), or more rarely, all female flowers on one specimen are provided with it. Besides, there occur in these occasional specimens intermediary stages between spathe and leaf (Fig. 7, 9), in that the adaxial, spathaceous incision at the apex of the spathe runs down to less than halfway (Fig. 7) or almost to the base of the female flower (Fig. 9). In all I have found 6 sheets of N. indica in which spathes are found on female flowers, viz (with an occasional spathe): Madras, leg. Gamble (K), Lawson 12856 (K), Penins. Or. Herb. Rottlerianum (K), and (all ♀ flowers with a spathe): Tranquebar, Soc. Unit. Frat. (BM), Behar, Hook. f. & Th. (K), Sambalpur, Mooney 3785 (K).

A similar occasional development of a spathe I have observed in N. tenuifolia R. Br. subsp. pseudograminea (W. Koch) De Wilde in which normally the δ flower is enclosed by a spathe but the $\mathfrak P$ flower is naked. A collection from Java (leg. C. Schröter & J. H. Coert 454, in L) possessed many δ and $\mathfrak P$ flowers. One of the latter flowers was beyond anthesis, and the nearly ripe fruit was enclosed by a spathe with a short neck spathaceously incised to about halfway the neck.

In my opinion these observations can only lead to one conclusion, viz that the spathe of *Najas* is homologous with a normal leaf, namely the lower one of each axillary sessile pair which is in sterile shoots normally developed as a minute scale. This is strengthened by the fact that the intermediary stages just-mentioned, and the normal

spathe are all toothed at the apex as are the leaves. Consequently the flower must be interpreted as axillary.

The observations lead also to another conclusion, viz that the occurrence of a spathe or its absence seems to be of less systematical value than attributed to it in the past and it is my feeling that the distinction of sections based on it is artificial.

In my opinion the distinction of subgenera is also overrated because of the great resemblance of N. marina to the other species of Najas; I prefer to return to the old opinion of two sections instead of two subgenera.

DESCRIPTION OF THREE NEW TAXA OF MALAYSIAN NAJAS

Najas malesiana De Wilde, nov. sp. — N. bengalensis Horn af Rantzien, Act. Bot. Gotob. 18: 192, 193, 1950, in clav., descr. angl., ad int., nom. inval. — N. graminea var. minor Rendle et var. angustifolia Rendle, Trans. Linn. Soc. Lond. II, Bot. 5: 426, 427. 1899.

Planta ad c. 15 cm alta, internodiis in partibus inferioribus 1-3 cm \times 0,5-0,8 mm. Folia (12-) 19 (-25) mm longa, basi laminae (0,4-) 0,5-0,7 (-0,9) mm lata; lamina plana, apice obtusa vel acutiuscula, circa 3 mm infra apicem 0,25-0,5 mm lata, margine in utroque latere denticulis inconspicuis (20-) 25-30 (-60) munito, denticulis singulis praecipue e spinis compositis, spinis fuscis (0,05-) 0,1 (-0,25)mm longis. Costae latitudo c. 1/20 eius laminae; cavitates septati confines longitudinales latitudinem occupantes usque ad dimidiam partis dimidiatae laminae attingentem. Vaginae, auriculis inclusis, (1,5-) 2-2.5 (-3.0) \times 1-2.5 mm, in utroque latere spinulis (2-) 6-14 munitae, margine interiore auriculi spinuli 0-4 praedito. Auriculi elongatotriangulares vel linguiformes, interdum incurvati, 0,5-0,8 (-1,1) mm × 0,3-0,8 mm, integri, raro leviter lobati. Saepe 3 flores ♀ diversae aetatis cum uno flore 3, masculino femineum appresso, vel 3 solitarius, floribus masculinis spathella destitutis. Anthera 1-locellata, ellipticooblonga, interdum apicem versus contracta, $0.6-1.0 \times 0.15-0.3$ mm; perianthis lobuli saepe inconspicui. Pedicelli 0,2-0,4 mm; in floris maturitate c. 1 mm longi; spathella in floribus Q absens. Flores Q raro usque ad c. 0,3 mm pedicellati, (1,2-) 1,5 (-1,8) mm longa, ovarium $0.4-0.8 \times 0.2-0.3$ mm. Stylus 0.25-0.5 mm longus, stigmatibus 2(-1?), 0.3-0.6 mm longis. Semina (0.9-) 1-1.5 \times (0.35-) 0.4-0.5 mm usque ad 1,5–1,8 \times 0,5–0,6 mm. Testa areolata, areolis subquadrangularibus vel 5-6-angulatis, in seriebus 16-26 longitudinalibus confertis, seriebus e areolis 24-30 compositis.

Holotypus: Sumatra, W. Meijer 5772 (L).

India. East Bengal: Griffith 5609/1 (BM).

BURMA. Pegu: Kurz 3310 (BM).

LOWER SIAM. Setul: Ridley, March 1910 (SING).

Indo-China. Tourane: Clemens 4213 (BM).

MALAY PENINSULA. Wellesley: in rice fields, Dec. 1895, Ridley (SING), Pahang: Pekan, in pool, 20 Aug. 1889, Ridley (SING), ditto, May 1896, Ridley (BM). Selangor: May 1896, Ridley 7830, doubtful because sterile (SING). Malacca: Griffith s.n. (herb. J. Gay) (K); Griffith 5609/6 (K). Singapore: stream, Tanglin, Febr. 1889, Ridley (SING); Garden lake, 1894, Ridley 8946 (BM).

Sumatra. Eastcoast Res. Asahan: Sg Piring, 1936, F. Schneider (ZT), ditto, Aek Kwasan, F. Schneider (ZT). Westcoast Res.: Bukittinggi, Karbouwengat (Karbou canyon), W. Meijer 5772 (L).

Borneo. North Borneo: Gibbs 2820 (BM); Jesselton, Clemens 9699 (BO). South-

east Borneo: Bandjermasin, Motley (BM).

JAVA. Bogor, Inst. Plantenziekten 1 (BO); Tjitjadas, van Steenis 5402.

SOUTH CELEBES. Kendari, Lepo-lepo, Beccari s.n. sheet number 11810A, pro parte (FI); Lasao, Kjellberg 1186 (BO).
Philippines. Luzon: Manila, Loher 1590 (K); San Francisco del Monte, Loher

1587 (K).

South Moluccas. Tanimbar Is.: Jamdena, Buwalda 4506 (L).

Notes. The species is easily distinguished from \mathcal{N} , graminea Del. and other species of the former section Nudae by the small, 1-celled anthers and the small seeds.

I have not perpetuated the epithet bengalensis as it has appeared that the species is more abundantly represented in Malaysia.

Because of their poor condition I have not designated as holotype one of the specimens used by Rendle for the description of his varieties. Other good fertile specimens are Singapore, Garden lake, Ridley (BM) and North Bornco, Jesselton, Clemens 9699.

Najas graminea Del. var. robusta De Wilde, nov. var.

Planta validior, usque ad 50 cm longa, internodiis inferioribus (1,6-) 2-2,25 mm diam. Cortex caulis e struebus cellularum numerosis compositus, cavitatibus a struebus minime duobus sibi sejunctis. Folia 50-60 mm longa, apud basin laminae 3-4 mm lata, in parte superiore circa 3 mm infra apicem circa 1,2 mm lata, marginibus spinulis inconspicuis 160–185 obsitis. Vagina, auriculis inclusis, (4–) 7,5 (–10,5) \times (4–) 6,2 (-8,5) mm, in utroque latere spinulis (15–) 30 (-50) munita. Auriculae elongato-triangulares, subincurvatae, (2-) 4 (-5,5) \times (0,8–) 1 (-1,5) mm. Flores (?plerumque) solitarii. Antherae 4-locellatae, ellipticae (vel oblongae), (1,5–) 1,7 – 1,8 (-2,0?) \times 0,8–1 mm. Flores Q c. 3,5 mm longis; ovarium c. 0,9 \times 0,35 mm; stylus c. 1 mm; stigmata c. 1,6 mm longa. Semina ignota.

Holotypus: Ins. Wetar, J. Elbert 4521 (K; isotype L).

Notes. There is no other material known of this variety. The new variety is clearly distinct from the normal form by the coarse habit, the thick stem, long, wide leaves, etc.

Najas marina L. var. sumatrana De Wilde, nov. var.

Planta usque ad 70 cm longa, internodiis in partibus inferioribus 3-7 cm \times 0,9-1,4 mm, dense spinulosis (spinulis 15-20 per aream 2 mm metientem, plerisque ad et paulum infra nodos insertis). Folia 35-45 mm longa; lamina ad basin 2-2,3 mm lata, c. 3 mm infra apicem latitudine c. 1,8 mm, plana, tenuis, in sicco translucida, apice acuta vel obtusiuscula, in utroque latere secundum marginem spinulis 30-40 conspicuis, in parte infima (2 mm longa) saepe inermis; foliorum superficies inferior totidem spinulis munita quam margines, in superficie superiore spinulis paucioribus et plerisque spinulis ad costam confertis, spinulis elongato-conicis 0,75–1 mm longis sursum curvatis, eorum cellula apicali c. 0,15 mm longa fusca cellulis brunneis pluribus inserta. Foliorum vagina 3–3,5 \times 4–4,5 mm, in utroque latere secundum marginem spinulis 7–10 munita, superficie inferiore in parte apicali multispinulosa. \mathcal{E} Flores ignoti. \mathcal{E} Flores 2,5–3 mm longi; ovarium c. 1 \times 0,6 mm; stylus 0,6–0,8 \times 0,1 mm; stigmata 2 vel 3, c. 1,2 mm longa; semina 4–4,4 \times 2,5 mm.

Holotypus: Ins. Sumatra, Lake of Manindjau, E. Jacobson s.n. (L; isotypus BO).

Note. Though it will appear that among the more than one dozen varieties of *N. marina* some may appear to be superfluous, the present one seems to be worthy of distinction. It is clearly distinct by its long, narrow, flat, and thin leaves with very numerous spines along the margin and the midrib; the sheath and stem are similarly densely spinulose.

REFERENCES