



A reappraisal of leaf morphology in *Aponogeton natans* (Aponogetonaceae)

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The aquatic monocotyledon genus *Aponogeton* Linnaeus f. (1781[1782]: 32) (Aponogetonaceae) consists of about 57 species distributed mainly in the tropical or subtropical regions of the Old world (Chen *et al.* 2015). *Aponogeton natans* (Linnaeus 1767: 227) Engler & Krause (1906: 11) is the type species of the genus and occurs in India, Pakistan and Sri Lanka.

During recent field work, which focused exclusively on Sri Lankan *Aponogeton*, we were unable to satisfactorily reconcile our collections of *A. natans* with the morphological descriptions given in several previously published accounts globally. Specifically, none of the Sri Lankan material (collected across the entire island) possessed any truly submersed leaves, which had been described and even illustrated for the species by a number of authors (Bruggen 1985, 1987, Cook 1996, Yadav & Gaikwad 2003, Wijesundara & Shantha Siri 2004, Ali 2008). This inconsistency raised the possibility that the Sri Lankan material might represent a taxon similar to, but distinct from, the Indian populations of *A. natans* (Bruggen 1985). Accordingly, we re-evaluated the earlier literature accounts in light of our recent field observations.

In the field we observed that all of the underwater leaves on the specimens presumed to be *A. natans* actually were developing leaves, which remained erect and unexpanded until they reached the water surface, where they would then mature ultimately either as floating (when inundated) or erect (when not inundated) leaves. Apart from the conflicting “submersed” leaf characters, all of the specimens otherwise completely matched the former descriptions of *A. natans*. Notably, all of the putative *A. natans* material possessed eight-seeded fruits (8 ovules), which is a diagnostic character that distinguishes *A. natans* from the other three indigenous species (all with two-seeded fruits) (Bruggen 1985).

The nomenclatural history of *A. natans* provides some insight into the characterization of this species as a plant with submersed leaves. In 1767, Linnaeus initially recognized the taxon in the genus *Saururus* (not known to possess submersed leaves), but with uncertainty as “*Saururus? natans* L. (1767: 227)” The same plant was recognized later by Carl Linnaeus the Younger as *Aponogeton monostachyus* L.f. (1781 [1782]: 214), which is regarded as an illegitimate, superfluous name (IPNI 2016). The first legitimate nomenclatural combination as an *Aponogeton* species was published by Krause & Engler (1906), who described the taxon as *Aponogeton natans* (L.) Engler & Krause. It is likely that the misconception of submersed leaves in *A. natans* was propagated by a misinterpretation of the Latin description provided by Krause & Engler (1906). In that often-cited work, the foliage of *A. natans* was described as “*Folia primaria submersa, membranacea, tenuiora, posteriora lamina natante instructa;*”, which indicated not that submersed leaves were present (as some might have interpreted), but that the foliage is submersed initially, and develops eventually into floating leaves. This is the same developmental sequence that we have observed in our field studies. Moreover, a comparison of our specimens to the lectotype (designated by Bruggen 1970): — UNKNOWN. Koenig, Johann Gerhard, #s.n. (LINN!), further confirmed that the Sri Lankan material was conspecific with *A. natans*.

At least vegetatively, *A. natans* is close morphologically to *A. crispus* (Bruggen 1985, 1987). During a revision of Sri Lankan Aponogetonaceae, Bruggen (1987) stated: “It is almost impossible to distinguish between sterile specimens of *A. natans* and *A. crispus* if the latter only has floating leaves...”. However, during our study we could readily distinguish *A. natans* by its erect or floating leaves with comparatively short erect/rigid petioles, as opposed to *A. crispus*, whose floating leaves are borne on long, creeping petioles.

The superficial morphological similarity of *A. crispus* and *A. natans* can explain some of the problems associated with illustrations of the latter. An illustration allegedly of “*A. natans*” with submersed leaves (Yadav & Gaikwad 2003) actually resembles *A. crispus* rather than *A. natans*, and apparently is based on a misidentification. Similarly, an image of “*A. crispus*” provided by Wijesundara & Shantha Siri (2004) as Figure 5 unquestionably represents a mature plant of *A. natans*. Other anomalies exist. Even though the leaf characteristics of *A. natans* are rendered well in the illustration of Ali (2008) in Figure 1A, the rootstock is portrayed inaccurately, as it more closely resembles a rhizomatous rather than a tuberous structure.

As a consequence, we have been unable to find any evidence in support of previous reports of submersed leaves in *A.*

natans and attribute such descriptions as misconceptions regarding the actual developmental sequence of floating leaves in this species. It is likely that this erroneous description was propagated by a misinterpretation of the Latin description provided by Krause & Engler (1906). To clarify the nature of the foliage in *A. natans* we provide here a revised morphological description of this taxon along with an illustration (FIGURE 1) and images (FIGURE 2).

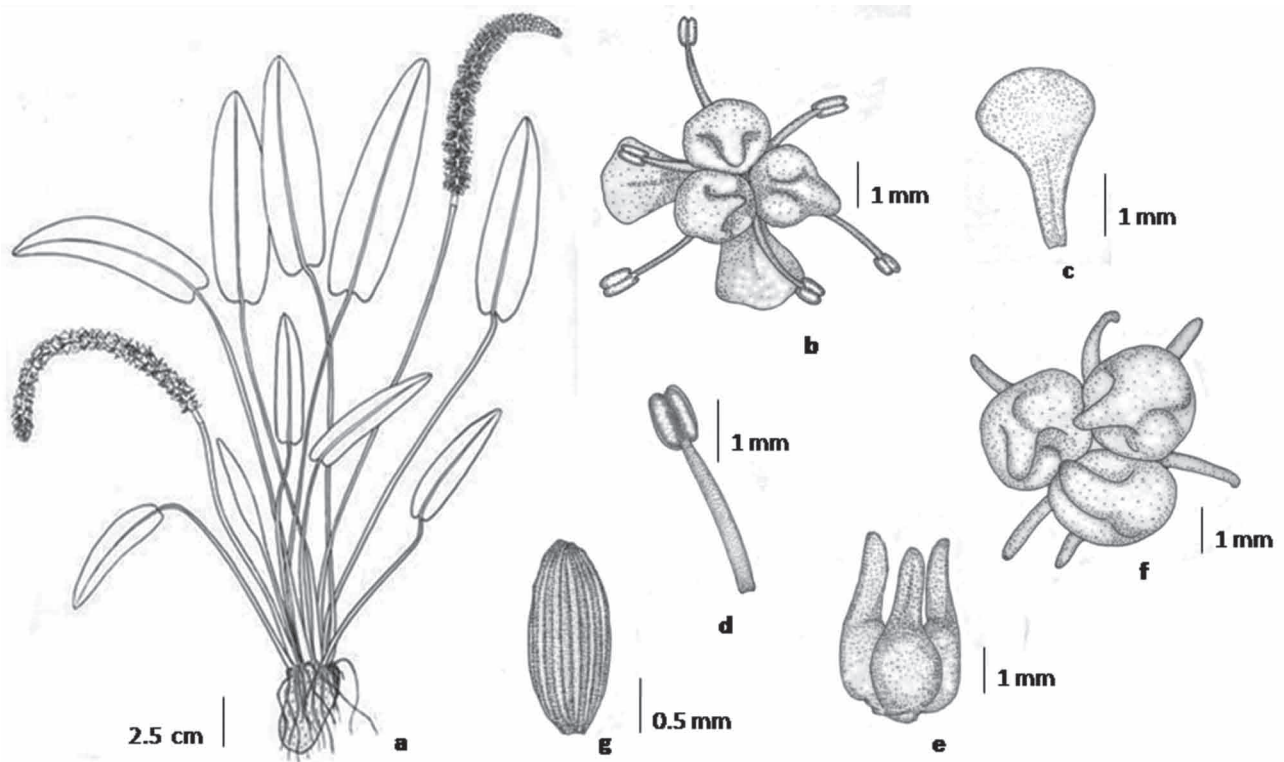


FIGURE 1. *Aponogeton natans*; habit (a), floret (b), tepal (c), stamen (d), gynoecium (e), follicles (f) and seed (g).



FIGURE 2. *Aponogeton natans*; in extremely dry sandy habitat (a), occurring together with other amphibious plants (b), in water logged conditions with erect leaves (c) and with floating leaves (d), inflorescence (e), infructescence (f), floating (g) and erect leaves (h); note the unequal leaf base and the texture.

***Aponogeton natans* (L.) Engler & Krause (1906: 11)**

Tuber up to 2.3 cm Ø. Leaves floating or erect up to 16 × 3 cm; base cordate, mostly unequal, seldom cuneate; apex (narrowly) cuneate with a blunt tip; parallel main nerves 5 or 7(not prominent). Peduncle up to 38 cm, not thickening towards the inflorescence. Spathe up to 15 mm, caducous. Inflorescence with one spike up to 12 cm long, densely flowered, seldom laxly flowered, scentless. Flowers turned towards all directions. Tepals 2, spatulate, 1.8–3 × 1–1.9 mm, purple, 1-nerved. Stamens 6, 2–4.2 mm; filaments not widened towards the base. Ovaries 3, up to 4 × 1.6 mm; ovules c. 8. Infructescence c. 15 cm, very dense. Folical up to 4×1.6 mm, smooth and inflated with a very long (up to 1 mm) terminal beak. Seeds c. 1.9 × 0.7 mm with a double testa: outer one loose, winged, transparent and reticulately veined, inner one brown, closely fitting the embryo. Embryo c. 1.5 × 0.5 mm.

Acknowledgement

Financial assistance provided by the University of Peradeniya, Sri Lanka (University Research Grant RG/2014/38/S) to DY is gratefully acknowledged. Authors wish to thank different herbaria for providing information on voucher material of *A. natans*, especially Central National Herbarium, Botanical Survey of India; Natural History Museum, Linnean Society of London, The Museum of Evolution Herbarium, Uppsala University and Menaka Ariyaratne for her assistance in the field.

References

- Ali, S.I. (2008) Contribution to the family Aponogetonaceae from Pakistan. *Pakistan Journal of Botany* 40: 1–3.
- Bruggen, H.W.E. van (1970) Revision of the genus *Aponogeton* (Aponogetonaceae). *Blumea* 18: 477–478.
- Bruggen, H.W.E. van (1985) Monograph of the genus *Aponogeton* (Aponogetonaceae). In: *Bibliotheca Botanica* Heft 137. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, pp. 14–26.
- Bruggen, H.W.E. van (1987) Aponogetonaceae. In: Dassanayake, M.D. & Fosberg, F.R. (Eds.) *A Revised Hand Book to the Flora of Ceylon, Vol. VI*. Amerind Publishing, New Delhi, pp. 3–16.
- Chen, L., Grimm, G.W., Wang, Q. & Renner, S.S. (2015) A phylogeny and biogeographic analysis for the Cape-Pondweed family Aponogetonaceae (Alismatales). *Molecular Phylogenetics and Evolution* 82: 111–117.
<http://dx.doi.org/10.1016/j.ympev.2014.10.007>
- Cook, C.D.K. (1996) *Aquatic and Wetland Plants of India*. Oxford University Press, New York, pp. 48–49.
- IPNI (2016) *The International Plant Names Index*. Available from: <http://www.ipni.org> (accessed 30 March 2016)
- Krause, K. & Engler, H.G.A. (1906) Aponogetonaceae. In: *Das Pflanzenreich. Regni Vegetabilis Conspectus*. Heft 24. IV.13. Wilhelm Engelmann, Leipzig, p. 11.
- Linnaeus, C. (1767) *Mantissa Plantarum. Generum editionis VI et specierum editionis II*. Laurentii Salvii, Holmiae [Stockholm], 227 pp.
- Linnaeus, C. (1781 [1782]) *Supplementum Plantarum Systematis Vegetabilium Editionis Decimae Tertiae, Generum Plantarum Editiones Sextae, et Specierum Plantarum Editionis Secundae. Editum a Carolo a Linné*. Impensis Orphanotropei, Brunsvigae, pp. 32–33.
- Wijesundara, D.S.A. & Shantha Siri, J.G. (2004) *Some selected aquatic ornamental plants of Sri Lanka: a simplified guide to identification of Aponogeton (Kekatiya), Lagenandra (Ketala) and Cryptocoryne (Atiudayan)*. National Science Foundation of Sri Lanka, Colombo, Sri Lanka, pp. 4–14.
- Yadav, S.R. & Gaikwad, S.P. (2003) A revision of the Indian Aponogetonaceae. *Bulletin of Botanical Survey India* 45: 39–76.