

OLEANDRACEAE

(P.H. Hovenkamp, Leiden, The Netherlands & Boon-Chuan Ho, Bonn, Germany)

Oleandraceae Ching ex Pic.Serm., *Webbia* 20 (1965) 745; K.U.Kramer in K.U.Kramer & P.S.Green, eds., *Fam. Gen. Vasc. Pl.* (1990) 190; A.R.Sm. et al., *Taxon* 55 (2006) 718; Hovenkamp & B.C.Ho, *PhytoKeys* 11 (2012) 1. — Type genus: *Oleandra* Cav.

The simple morphology of *Oleandra* has made comparison with other ferns difficult, and its position has been judged to be with Dryopteridaceae or Davalliaceae, where it has been associated in particular with *Nephrolepis* and *Arthropteris* (Copeland 1947; Holttum 1959; Nayar & Bajpai 1978). Holttum (1959) included *Oleandra* with *Nephrolepis* and *Arthropteris* in an informal *Nephrolepis*-group. More recent views (Tryon & Tryon 1982; Kramer 1990; Tryon & Lugardon 1991) exclude *Nephrolepis*, and molecular studies (Kuo et al. 2011; Schuettpelez & Pryer 2007) indicate that these three genera do not form a clade, but that they are each associated with a different clade in the crown leptosporangiates. Here we treat Oleandraceae as a monogeneric family, with the single genus *Oleandra*.

References: Copeland, E.B., *Gen. Fil.* (1947). *Chronica Botanica*, Waltham, Mass. — Holttum, R.E., in C.G.G.J. van Steenis (ed.), *Flora Malesiana, Ser. II*, 1 (1959). Nijhoff, Dr. W. Junk, The Hague, Boston, London. — Kramer, K.U., in K.U. Kramer & P.S. Green (eds.), *Fam. Gen. Vasc. Pl.* (1990). Springer, New York etc. — Kuo, L.-Y., F.-W. Li, W.-L. Chiou & C.-N. Wang, First insights into fern matK phylogeny. *Molec. Phylogenet. Evol.* 59 (2011) 556–566. — Nayar, B.K. & N. Bajpai, Morphology in relation to phylogeny of the Davallioid-Oleandroid group of ferns. *Phytomorphology* 26 (1978) 333–354. — Schuettpelez, E. & K.M. Pryer, Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56 (2007) 1037–1050. — Tryon, A.F. & B. Lugardon, *Spores of the Pteridophyta* (1991). Springer, New York etc. — Tryon, R.M. & A.F. Tryon, *Ferns and allied plants, with special reference to tropical America* (1982). Springer, New York etc.

TAXONOMY

The genus *Oleandra* was described by Cavanilles (1799, 1802) who derived both the genus name and the species name from *Nerium oleander* L. (Apocynaceae). From this it should be clear that he only saw the aerial stems of *Oleandra neriiformis*, of which the forms with distinctly whorled fronds are indeed strongly reminiscent of branches of *Nerium oleander*. *Oleandra* was included in *Aspidium* by Swartz (1801, 1806), but reinstated by Presl (1836) and John Smith (1841, 1842), and the distinctness of the genus has not been questioned by subsequent authors while only one author has preferred to recognize *Oleandra* at subgeneric level (Splitgerber 1840).

There is as much unanimity on the distinctness of the genus as there is uncertainty on the number and distinctness of the species that can be distinguished in *Oleandra*, and many authors who have tried to deal with the genus have commented on the difficulties of species delimitation. Kramer (1990) estimated the number of species to be 40 (“many species are similar in appearance”) and Pichi Sermolli (1965) gives a number of 50 (“the delimitation of the species is not always easy, since some of them show a high degree of polymorphism”). Hovenkamp & Ho (in press) distinguish 9 species in Asia, of which 7 occur in Malesia.

References: Cavanilles, A.J., *Anales Hist. Nat.* 2 (1799). Imprenta real, Madrid. — Cavanilles, A.J., *Descripcion de las plantas* (1802). Imprenta real, Madrid. — Hovenkamp, P. & B.-C. Ho, *Oleandra* (Pteridophyta, Oleandraceae) in Asia. *Blumea* (in press). — Presl, C.B., *Tent. Pterid.* (1836). Theophilus Haase, Prague. — Smith, J., *Enumeration Filicum Philippinarum*. *J. Bot.*, London III (1841) 393–422. — Smith, J., *An arrangement and definition of the genera of Ferns, with observations on the affinities of each genus*. *J. Bot.*, London 4 (1842) 38–70. — Splitgerber, F.L., *Enumeratio Filicum et Lycopodiacearum quas in Surinamo legit F.L. Splitgerber*. *Tijdschr. Natuurl. Gesch. Physiol.* 7 (1840) 411. — Swartz, O., *Genera et species filicum ordine systematico redactarum*. *J. Bot.* (Schrader). Göttingen 1800 (1801). — Swartz, O., *Synopsis Filicum* (1806). Bibliopolii novi academici, Kiel.

MORPHOLOGY AND CHARACTERS

The morphology and anatomy of *Oleandra* has been studied by various authors (Ogura 1939; Wetter 1951; Phillips & White 1967; Sen & Sen 1973; Nayar & Bajpai 1978), mainly with an emphasis on the structure of the rhizome, of which the climbing habit in some species is a striking character.

Much of the variability between species in *Oleandra* is found in the rhizome, but as large parts of the rhizome are usually not preserved in herbarium collections, it is difficult to appreciate and describe this variability. In the Malesian species, rhizomes may be relatively short-creeping, leading to more or less compact clumps of fronds, or more widely creeping. In the latter case, in some species the rhizome appears to be short-lived, decaying less than 1 m behind each growing point, which leads to stands with a scattered growth of plants. In others, the rhizome can be highly persistent, and stands may be extensive, with a dense growth of stems. In plants with this growth form, parts of the rhizome may also grow outwards or upwards from the substrate and form erect or drooping stems, here to be called ‘aerial’ stems, that are often rootless. This is the shrubby growth form that is most often associated with the genus, although it occurs only in a minority of species. Branches are often opposite each other, and then both branches follow the same growth, either downwards (positively geotropic) or upwards (negatively geotropic). The anatomy shows a variably, but often very strongly developed peripheral sclerified sheath, a ground tissue with or without scattered sclerenchyma strands, and a dictyostele.

The rhizome is covered with usually persistent rhizome scales with a peltate attachment. The scales are often strongly thickened near the attachment, and the margin can be nearly entire or densely set with woolly hairs (best visible in young scales) or sessile glands. The scales are strongly appressed or spreading to recurved – in the latter case the recurved parts tend to disappear on older rhizomes, giving the impression of a cover of short, appressed scales.

Roots arise mostly from the ventral side of the rhizome, and may be unbranched for a considerable length. The long unbranched parts have been described as rhizophores, but were identified as real roots by Wetter (1951). Branching associated with the formation of root hairs occurs presumably when the roots are in contact with a suitable substrate, and thus the unbranched parts tend to be more evident in species that creep over the substrate, often at some distance, or over dense cushions of moss, than in species with a subterranean rhizome.

Fronds arise on the rhizome without any apparent regularity, often clustered in more or less distinct whorls or clumps, but on creeping rhizomes often also more widely separated. They do not appear to grow in regular series, but are inserted more or less dorsally on creeping stems, and often on all sides on aerial stems. At a variable position on the stipe, there is a distinct articulation point, where old fronds abscise cleanly. The lamina is uniformly simple in all species, and varies little in shape, except in *O. werneri* where the fronds are distinctly dimorphic, with the fertile fronds or parts strongly contracted. Sori are indusiate with a reniform indusium, and always separate. They are borne dorsally and singly on the veins, at distances from the costa that may vary strongly. Sporangia are long-stalked, often with a number of glandular hairs attached to the distal part of the stalk, just below the capsule. The capsule is of the common Polypodiales type.

The spores of *Oleandra* have been studied with SEM by Liew (1977), Tryon & Lugardon (1991) and Hovenkamp & Ho (in press). The morphology of the spores of the Malesian species is highly variable but essentially uniform, and the variation can be described in terms of a restricted number of parameters.

The spore wall is composed of a smooth exospore, and a thick but hollow and often highly ornamented perispore. The surface of the perispore shows a pattern of coarse folds, a variable ornamentation and a variable degree of perforation. The folds may be broad, narrow, or replaced by elongated fissures, the ornamentation ranges from warty to densely spinose. This surface may be perforated or perforated to varying degrees, exposing an inner structure of numerous narrow cylindrical pillars c. 0.5 μm thick. These pillars are attached to a thin basal layer that adheres closely to the exospore. In the extreme case, the outer surface is so strongly perforated that the entire perispore consists of an open mesh. Within this range of variability, most species that could be studied with an adequate sample of specimens show variability in 2 or more of these parameters, and it is difficult to identify character states that are characteristic for one species, although it appears that *O. sibbaldii* has a more consistently highly perforated perispore than the other species.

The size of the spores of a single specimen varies from c. 35–45 to 60–70 μm , also between specimens of one species.

References: Hovenkamp, P. & B.-C. Ho, *Oleandra* (Pteridophyta, Oleandraceae) in Asia. *Blumea* (in press). — Liew, F.S., Scanning electron microscopical studies on spores of Pteridophytes. 11. The family Oleandraceae (*Oleandra*, *Nephrolepis* and *Arthropteris*). *Gard. Bull. Singapore* 30 (1977) 101–110. — Nayar, B.K. & N. Bajpai, Morphology in relation to phylogeny of the Davallioid-Oleandroid group of ferns. *Phytomorphology* 26 (1978) 333–354. — Ogura, Y., Anatomy and morphology of *Oleandra wallichii* (Hk.) Pr., with some notes on the affinities of the genus *Oleandra*. *J. Jap. Bot.* 9 (1939) 193–211. — Phillips, D.A. & R.A. White, Frond articulation in species of Polypodiaceae and Davalliaceae. *Amer. Fern J.* 57 (1967) 78–88. — Sen, U. & T. Sen, Anatomical relationships between the *Oleandra* and *Nephrolepis* groups. *Bot. J. Linn. Soc., Suppl.* 1 (1973) 155–172. — Tryon, A.F. & B. Lugardon, *Spores of the Pteridophyta* (1991). Springer, New York etc. — Wetter, C., Über die Luftwurzeln von *Oleandra*. *Planta* 39 (1951) 471–475.

KARYOLOGY

Chromosome numbers have been established for the Malesian species *O. musifolia* and *O. neriiformis* (Löve et al. 1977) but not on basis of Malesian specimens. In both species, the number was diploid with $n = 41$. The variability in spore size may be an indication of the presence of different ploidy levels (Harmata & Kornás 1978).

References: Harmata, K. & J. Kornás, Spore morphology in two varieties of *Oleandra distenta* Kunze (Davalliaceae, Filicopsida) from southern tropical Africa. Zesz. Nauk. Univ. Jagiellon. Prace Bot.: 493 (1978) 8–14. — Löve, A., D. Löve & R.E.G. Pichi Sermolli, Cytotaxonomical atlas of the Pteridophyta (1977). Cramer, Vaduz.

DISTRIBUTION

Oleandra is pantropical, but all the individual species are more limited in distribution. Some of the Malesian species extend to Continental Asia, Australia or the Pacific. One is endemic to Borneo, and two are restricted to New Guinea and the surrounding islands.

OLEANDRA

Oleandra Cav., Anales Hist. Nat. 1 (1799) 115; Descr. plant. (1802) 252; Backer & Posth., Varenfl. Jav. (1939) 86; Copel., Gen. Fil. (1947) 90; Fern Flora of the Philippines 1 (1958) 180; Holttum, A revised Flora of Malaya II. Ferns. Ed. 2 (1968) 383; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes (1985) 179; G.H.Bell, Flora of Australia 48 (1998) 445; Lumbreras, Flora Montiberica 28 (2004) 19. — *Aspidium* Sw. subg. *Oleandra* Splitg., Tijdschr. Natuurl. Gesch. Physiol. 7 (1840) 411. — Type: *Oleandra neriiformis* Cav. ('neriiformis').

Ophiopteris Reinw., Sylloge plantarum novarum ... 2 (1825) 3. — Type: *Ophiopteris verticillata* Reinw. = *Oleandra neriiformis*.

Neuronia asplenioides D.Don, Prodr. Fl. Nepal. (1825) 6. — Type: *Neuronia asplenioides* D.Don = *Oleandra wallichii*.

Terrestrial, epilithic or epiphytic, creeping or scrambling ferns. *Rhizome* scaly, roots scattered, often with long rhizophore-like proximal parts, fronds scattered or in whorls, on stipe-like phyllopodia, dehiscing at a slightly thickened articulation point. *Fronde* stipitate, lamina simple, margin entire, veins distinct, somewhat raised on both sides, 1–2 times forked at or near the costa, costa often with narrow scales, lamina and veins often with acicular or capitate hairs. *Sori* in one, often irregular row on each side of the costa, with a more or less reniform, glabrous or hairy indusium. *Sporangia* stalked, stalk often with a number of sessile or stalked glands below the sporangium, sporangium body glabrous, spores monolete, perispore with broad wings, sometimes highly perforate, or echinate, massive.

KEY TO THE SPECIES

- 1a. Rhizome with stiff, erect to pendent rootless aerial branches 2
- b. Rhizome creeping 4
- 2a. Fronds strongly dimorphic, scattered on the rhizome or somewhat clustered on short side branches **7. O. werneri**

- b. Fronds monomorphic or slightly dimorphic, often in whorls of 5–10 fronds . . . 3
- 3a. Lamina thick, coriaceous, costa below with copious, conspicuous, 3–4 mm long pale to brown scales **1. *O. coriacea***
- b. Lamina thin, papyraceous when dry, costa below mostly with few or inconspicuous scales **4. *O. neriiformis***
- 4a. Rhizome in older parts not entirely covered with scales; scales with squarrose acumen and entire or distinctly glandular margin 5
- b. Rhizome entirely covered with overlapping scales, scales with appressed or spreading apex, usually with non-glandular cilia 6
- 5a. Rhizome scales with gradually narrowed apex, stipe 0.5–4.5 cm long, costa and stipe often with distinct dark coloration **5. *O. sibbaldii***
- b. Rhizome scales with abruptly narrowed apex, stipe to 2–3 mm long, costa and stipe without dark coloration below **6. *O. vulpina***
- 6a. Phyllopodia very short, inconspicuous, much shorter than the stipe, sori mostly in a closely costal single row **3. *O. musifolia***
- b. Phyllopodia longer, position of sori variable **2. *O. cumingii***

1. *Oleandra coriacea* Copel.

Oleandra coriacea Copel., J. Straits Branch Roy. Asiat. Soc. 63 (1912) 72. — Type: *Moulton s.n.* (SAR?, n.v.), Borneo.

Rhizome with creeping parts unknown, aerial stems unbranched and rootless, 2–3 mm thick (when dry), bearing in cross-section with a distinct sclerified peripheral sheath and few, scattered sclerified strands, not white waxy, fronds in weak to distinct clusters of 4–6. *Scales* persistently covering the rhizome, peltate, 5–70 by 0.5–1 mm, appressed (sometimes spreading), dark, shining with pale to brown margin and acumen, margin ciliate especially when young. *Fronds* monomorphic; phyllopodia short, usually less than 5 mm high, stipe 1–1.5 cm long, without dark coloration, with up to 1 mm long glandular hairs and often small, appressed scales; lamina 13–30 by 1.2–3.3 cm, linear, base narrowly cuneate to rounded, apex acuminate to caudate with cauda to 1.5 cm, texture coriaceous; costa and veins on lower surface densely hairy with up to 1 mm long, acicular hairs, costa without dark coloration, with copious, conspicuous, 3–4 mm long pale to brown scales, upper surface more glabrous, mostly hairy on the costa only, with similar hairs and with less copious scales. *Sori* in a single more or less irregular medial row, separated from the costa by a 2–7 mm wide sterile zone, indusium distinct, c. 1.5 mm wide, glabrous or glandular. *Sporangial stalk* with glands below the sporangium. *Spores* with coarse confluent ridges, areolae with short pointed excrescences, perispore hollow, with internal baculae, outer layer distinctly perforated.

Distribution — In *Malesia*: Borneo: Sarawak, Brunei, Kalimantan Timur.

Ecology — Terrestrial in montane forest, mainly on ridges and in summit vegetation, 1100–2200 m altitude.

Notes — 1. Creeping and rooting parts of the rhizome are absent in all collections seen, but presumably present, as in *O. neriiformis*.

2. Much more coriaceous than *O. neriiformis*, and with copious large pale costal scales and long hairs especially on lower surface. The sori are consistently medial, with firm indusia that are often clearly glandular on their surface.

2. *Oleandra cumingii* J.Sm.

Oleandra cumingii J.Sm., J. Bot. (Hooker) 3 (1841) 413; Copel., Polypod. Phil. Isl. (1905) 49; Fern Fl. Philipp. 1 (1958) 184; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 324. — Type: *Cuming 60* p.p. (holo K; iso B, BM, SING, US*), Luzon.

Oleandra scandens Copel., Philipp. J. Sci. 46 (1931) 218; Fern Fl. Philipp. 1 (1958) 184. — Type: *Elmer 6513* (US*), Baguio.

Rhizome short- to long creeping, 3–8 mm thick, little branched and not forming extensive stands, in cross-section with or without scattered sclerified strands, sometimes white waxy in the older parts; roots scattered, sometimes with unbranched aerial parts; fronds scattered or more or less tufted. *Scales* persistently covering the rhizome, peltate, 4–9 by 5–1.5 mm, appressed, acumen with dark centre and lighter acumen and margin, margin ciliate especially when young. *Fronde*s monomorphic, phyllopodia (1–)3–10 cm high, stipe 2–12 cm long, without dark coloration, glabrous or hairy with catenate to acicular up to 2 mm long hairs, lamina to c. 40 by 2–4.5 cm, base narrowly cuneate to truncate, apex acute to long-acuminate, texture thin-chartaceous, both surfaces and margin with catenate or acicular hairs 0.2–1 mm long, usually more densely on lower surface, costa without dark coloration, on lower surface without or with few, pale to dark scales. *Sori* close to or scattered up to 2 mm from the costa, indusium distinct, 1–2 mm wide, densely hairy with short or long hairs. *Sporangial stalk* with glands below the sporangium. *Spores* with broad or narrow confluent ridges, surface variably ornamented with small pustules to narrow spines, perispore hollow, with internal baculae, outer layer not or finely perforated, sometimes fissured along the ridges.

Distribution — South China, Indochina (Laos, Thailand); in *Malesia*: Peninsular Malaysia; Lesser Sunda Islands: Flores, Timor Leste; Philippines: Luzon.

Ecology — Terrestrial or on rocks, cliffs and roadsides in open forest, to c. 1200 m altitude.

Note — *Oleandra cumingii* is a variable assemblage of fairly widely scattered forms, in many characters intermediate between *O. musifolia* and the non-Malesian *O. undulata*. From *O. musifolia* it differs in the elongated phyllopodia and the distinctly tomentose indusia and lower surface of the lamina. The differences, however, are often slight and bridged by some specimens with an intermediate character combination.

3. *Oleandra musifolia* Blume

Oleandra musifolia Blume, Enum. Pl. Javae (1828) 141 (*'Aspidium musaefolium'*). — *Oleandra musaefolia* C.Presl, Epimel. Bot. (1849) 42; Ching, Fl. Reipubl. Popularis Sin. 2 (1959) 321. — *Oleandra musifolia* C.Chr., Index Filic. 466 (1906); Backer & Posth., Varenfl. Jav. (1939) 87; R.M.Tryon, Rhodora 102 (2000) 434, f. 4. — Type: *Blume s.n.* (L), Java, Gedeh.

Aspidium lomatosus Kunze, Bot. Zeitung (Berlin) 11 (1848) 238. — *Oleandra lomatosus* C.Presl, Epimel. Bot. (1849) 43. — Type: *Zollinger s.n.* (n.v.), Java.

Aspidium moritzii Kunze, Bot. Zeitung (Berlin) 11 (1848) 238; (1851) 348. — *Oleandra moritzii* C.Presl, Epimel. Bot. (1849) 42. — Type: *Zollinger 1306B* (lecto L, L0317415), Java.

* Specimens seen only as on-line images, provided either directly through the database of the holding institute or via JSTOR, <http://plants.jstor.org>.

Oleandra geniculata Alderw., Bull. Jard. Bot. Buitenzorg 16 (1914) 23. — Type: *Docters van Leeuwen s.n.* (BO?, n.v.), Java.

Oleandra benguetensis Copel., Philipp. J. Sci. 46 (1931) 217; Fern Fl. Philipp. 1 (1958) 183. — Type: *Elmer 6286* (US*), Baguio.

Rhizome creeping, 5–8 mm thick, often supported above the substrate by unbranched stilt-like roots, dorsiventrally flattened, (strongly compressed, 4–6 mm wide when dry), with up to 10 cm long, curved internodes (only occasionally straight and then often much longer) terminating in a cluster of a few fronds, with an innovation just below this cluster, lateral branches usually basal on the internodes, in opposite pairs; all parts in cross-section without or with few sclerified strands, white waxy in the older parts; roots scattered, with long unbranched aerial parts. *Scales* persistently covering the rhizome, peltate, 5–10 by 1–1.5 mm, appressed, with dark centre and lighter brown acumen and margin, margin ciliate especially when young and with sessile glands. *Fronds* monomorphic, phyllopodia short, usually less than 5(–15) mm high, often hidden by the scales, stipe 0.5–4 cm long, without dark coloration, with short, glandular hairs; lamina to 60 by 4.2 cm, linear, base cuneate to truncate or more or less rounded, apex acute to long-acuminate, texture thin-chartaceous, both surfaces with catenate, often glandular hairs 0.2–0.5 mm long; costa without dark coloration, on lower surface with inconspicuous, 1–3 mm long brown scales. *Sori* mostly in a single regular row close to the costa, sometimes more scattered over a 2–5 mm wide zone close to the costa or at a distance of up to 3 mm, indusium distinct, 1.5–2 mm wide, glabrous or glandular, sometimes setose. *Sporangial stalk* with glands below the sporangium. *Spores* with coarse confluent ridges, areolae with short pointed excrescences, perispore hollow, with internal baculae, outer layer not or hardly perforated.

Distribution — Southern India, Sri Lanka, South China, Thailand; in *Malesia*: Java; Lesser Sunda Islands; Philippines: Luzon, Sulawesi; Australia: Queensland.

Ecology — Mostly terrestrial or on rocks, less often as low trunk epiphyte, in various types of forest, often disturbed, up to c. 2000 m altitude.

Notes — 1. Variability: Density of hairs is variable, as is the distance of the sori to the costa.

2. *Oleandra musifolia* is distinguished from *O. cumingii* mainly by the short phyllopodia (long in *O. cumingii*). Incomplete collections are easily confused also with *O. neriiformis* but can often be recognized by the flat, softer rhizome usually without sclerenchyma strands (rhizome more rigid, rounded, with sclerenchyma strands in *O. neriiformis*) and by the catenate hairs with capitate apex (more acicular, not capitate in *O. neriiformis*). Distinguishing these two species on basis of juvenile material may be difficult, and is often impossible, while it may not be clear from herbarium material that the material is juvenile.

4. *Oleandra neriiformis* Cav.

Oleandra neriiformis Cav., Anales Hist. Nat. 2 (1799) 115 ('*neriformis*'); Descr. Pl. 252 (1802); Backer & Posth., Varenfl. Jav. (1939) 87; Copel., Fern Fl. Philipp. 1 (1958) 182; Brownlie, Pterid. Fl. Fiji (1977) 156; R.M.Tryon, Rhodora 102 (2000) 430. — *Aspidium neriiforme* Sw., Syn. Fil. (1806) 42. — Type: *Née s.n.* (MA, n.v.), Mauban.

- Aspidium pistillare* Sw., J. Bot. (Schrader) (1801) 30. — *Oleandra pistillaris* C.Chr., Index Filic. Suppl. 3 (1934) 132; Holttum, Flora of Malaya. II Ferns (1954) 386; X.C.Zhang, Ching Mem. Vol. (1999) 91. — Type: *Unknown s.n.* (S, n.v.), Java (teste Sw. 1806).
- Ophiopteris verticillata* Reinw., Syll. Pl. Nov. 2 (1825) 3. — Type: *Reinwardt? s.n.* (L), Java.
- Aspidium bantamense* Blume, Enum. Filic. 2 (1828) 141. — *Aspidium micranthum* Blume, Enum. Filic. (1828) 141. — *Oleandra bantamense* Kunze, Bot. Zeitung (Berlin) 9 (1851) 349. — *Oleandra micrantha* Kunze, Linnaea 9 (1851) 349. — Type: *Kuhl & Van Hasselt s.n.* (L), Java.
- Aspidium neriiforme* Sw. var. *salaccens* Blume, Enum. Pl. Javae (1828) add. et emend. — *Aspidium salaccense* Blume, Enum. Filic. (1828) 140. — *Oleandra neriiformis* Cav. var. *salaccensis* Kunze, Bot. Zeitung (Berlin) 9 (1851) 348. — Type: *Blume s.n.* (L), Java.
- Blechnum colubrinum* Blanco, Fl. Filip. (1837) 834. — *Oleandra colubrina* (Blanco) Copel., Polypod. Phil. Isl. (1905) 48; Merr., Sp. Blancoan. (1918) 43; Copel., Fern Fl. Philipp. 1 (1958) 181. — Type: *Unknown*.
- Aspidium phyllarthron* Kunze, Bot. Zeitung (Berlin) 6 (1848) 237. — *Oleandra phyllarthron* C.Presl, Epimel. Bot. (1849) 42. — Type: *Zollinger 1306* (L, L0317564), Java.
- Oleandra mollis* C.Presl, Epimel. Bot. (1849) 41; Fée, Gen. Fil. (1852) 304. — Type: *Cuming 94* p.p. (holo PRC, n.v.; iso BM, L, SING, US*), Luzon.
- Oleandra hirtella* Kunze, Farrnkräuter (1850) 70. — *Oleandra neriiformis* Cav. var. *hirtella* Hook.f., Sp. Fil. 4 (1862) 156. — Type: *Miquel? s.n.* (L?, not found), Java.
- Oleandra neriiformis* Cav. var. *brachypus* Hook.f., Sp. Fil. (1862) 156. — Type: *Norris s.n.* (K, n.v.), Malay Archipelago.
- Oleandra cumingii* J.Sm. var. *tahitense* Hook.f., Sp. Fil. (1862) 159. — Type: *Greville s.n.* (K, n.v.), Tahiti.
- Oleandra ciliata* Kuhn, Linnaea 36 (1869) 126. — Type: *Cuming 48* (holo B), Aneiteum.
- Oleandra cuspidata* Baker, Malesia 3 (1886) 44. — Type: *Beccari s.n.* (K), New Guinea, Arfak.
- Oleandra colubrina* (Blanco) Copel. var. *membranacea* Copel., Philipp. J. Sci., Bot. 3 (1908) 32. — Type: *Copeland PPE57* (holo MICH; iso K, PNH, UC), Mt Maquiling.
- Oleandra colubrina* (Blanco) Copel. var. *nitida* Copel., Philipp. J. Sci., Bot. 3 (1908) 33. — *Oleandra nitida* Copel., Fern Fl. Philipp. 1 (1958) 181; Amoroso & Pava, Philipp. J. Sci. 120 (1991) 423. — Type: *Copeland 1474* (lecto US*), Mt Apo.
- Oleandra oblanceolata* Copel., Philipp. J. Sci., Bot. 7C (1912) 64. — Type: *Brooks 115* (MICH), Borneo.
- Oleandra colubrina* (Blanco) Copel. var. *membranacea* Brause, Bot. Jahrb. Syst. 56 (1921) 119. — Type: *Whitford 999* (B, n.v.), Mt Banajao.
- Oleandra maquilingsis* Copel., Philipp. J. Sci. 46 (1931) 217; M.G.Price, Philipp. Agric. 57 (1974) 42; P.M.Zamora & Co, Guide Philipp. Fl. Fauna (1986) 145; Amoroso & Pava, Philipp. J. Sci. 120 (1991) 423. — Type: *Matthew s.n.* (lecto MICH), Luzon.
- Oleandra archboldii* Copel., Philipp. J. Sci. 73 (1940) 346. — Type: *Brass 13002* (n.v.), New Guinea.
- Oleandra subdimorpha* Copel., J. Arnold Arbor. 24 (1943) 441. — Type: *Brass 6886* (GH, n.v.), New Guinea.
- Oleandra clemensiae* Copel., Philipp. J. Sci. 81 (1952) 12; Fern Fl. Philipp. 1 (1958) 182. — Type: *Clemens 16494* (holo MICH; iso UC*), Philippines.
- Oleandra herrei* Copel., Philipp. J. Sci. 81 (1952) 12; Fern Fl. Philipp. 1 (1958) 182. — Type: *Herre s.n.* (UC*), Philippines.
- Oleandra malasianum* S.R.Ghosh, J. Bombay Nat. Hist. Soc. 80 (1984) 630. — Type: *Cantor-Wallich 2235* (CAL, n.v.), Penang.

Rhizome with main stems creeping or ascending, 3–8 mm thick, creeping parts sparsely rooting, branches often in opposite pairs, ascending parts rootless, at base propped up by downwards directed branches, ultimately aerial, erect or pendent; branches

* See note p. 128.

single or in opposite pairs, mostly directly above a frond cluster, all parts in cross-section with a peripheral sclerified sheath and scattered sclerified strands, white waxy in the older parts, fronds on creeping parts few, scattered, on aerial parts in more or less dense, often whorled clusters and branches. *Scales* persistently covering the rhizome, peltate, 4–6.5 by 1–1.5 mm, appressed to squarrose, with dark centre and lighter margin and acumen, margin ciliate. *Fronde*s monomorphic or weakly dimorphic, phyllopodia very short or up to 15 mm long, stipe very short or up to 3.5 cm, without dark coloration; fertile lamina 12–43 by 0.5–4.5 cm, base very gradually narrowed to narrowly truncate, then often somewhat lyrate, apex acuminate or to c. 2 cm caudate; sterile, if present, usually slightly shorter and wider, to 36 by 5.5 cm; texture thin-chartaceous, costa and lamina on lower surface without dark coloration, glabrous or with up to 2 mm long hairs, costa often with up to 2 mm pale to dark narrow scales. *Sori* in a single row close to the costa, or more scattered over a 2–5 mm wide zone close to or at a distance of up to 4 mm from the costa, indusium inconspicuous to distinct, to c. 1.5 mm wide, glabrous to hairy. *Sporangial stalk* with glands below the sporangium. *Spores* with coarse confluent ridges, surface pustulose or with pointed excrescences, outer layer variably perforated. — **Fig. 1.**

Distribution — Himalayas (India: Assam, Bengal; China: Xizang), Indochina, throughout *Malesia*; Pacific Islands (Fiji, Samoa).

Ecology — Terrestrial or epiphytic, in various types of forests, in open places, often making up a significant part of summit or ridge scrub. Sea level to 2200 m altitude.

Variability

With its wide-creeping and persistent rhizome, *O. neriiformis* may form extensive and probably long-lived stands, which, when collected a number of times over a long period, may give the impression of the presence of a locally abundant species with highly constant and distinct combination of characters. I expect this is at least partly the basis for the multitude of local species that have been described, and that I all include in *O. neriiformis*. Another reason may be the presence of juvenile plants, in which the rhizome is not characteristically developed, and which may have much more softly hairy fronds than well-developed plants, blurring the distinctions to *O. musifolia* and *O. cumingii*.

The following characters or character complexes in particular are variable:

1. Place of the stipe articulation. The phyllopodium may be distinctly longer than the very short stipe, or a distinctly elongated stipe may be present equal to or longer than the phyllopodium.
2. Length and density of lamina hairs. Although the presence or length of lamina hairs is usually highly variable, some forms have constantly and distinctly longer hairs.
3. Location of soral zone. Sori may be located in a narrow zone close to the costa, or in a more irregular zone at some distance from the costa, thus always leaving a distinct sterile zone between costa and sori.
4. Indusium. The presence of an indusium is rarely constant over an area. It may vary from distinct and often firm to inconspicuous (then often hairy) or absent.
5. Costal scales. Some forms have uniformly pale and flat costal scales, some almost uniformly narrow, dark scales, other forms have more variation in this character.

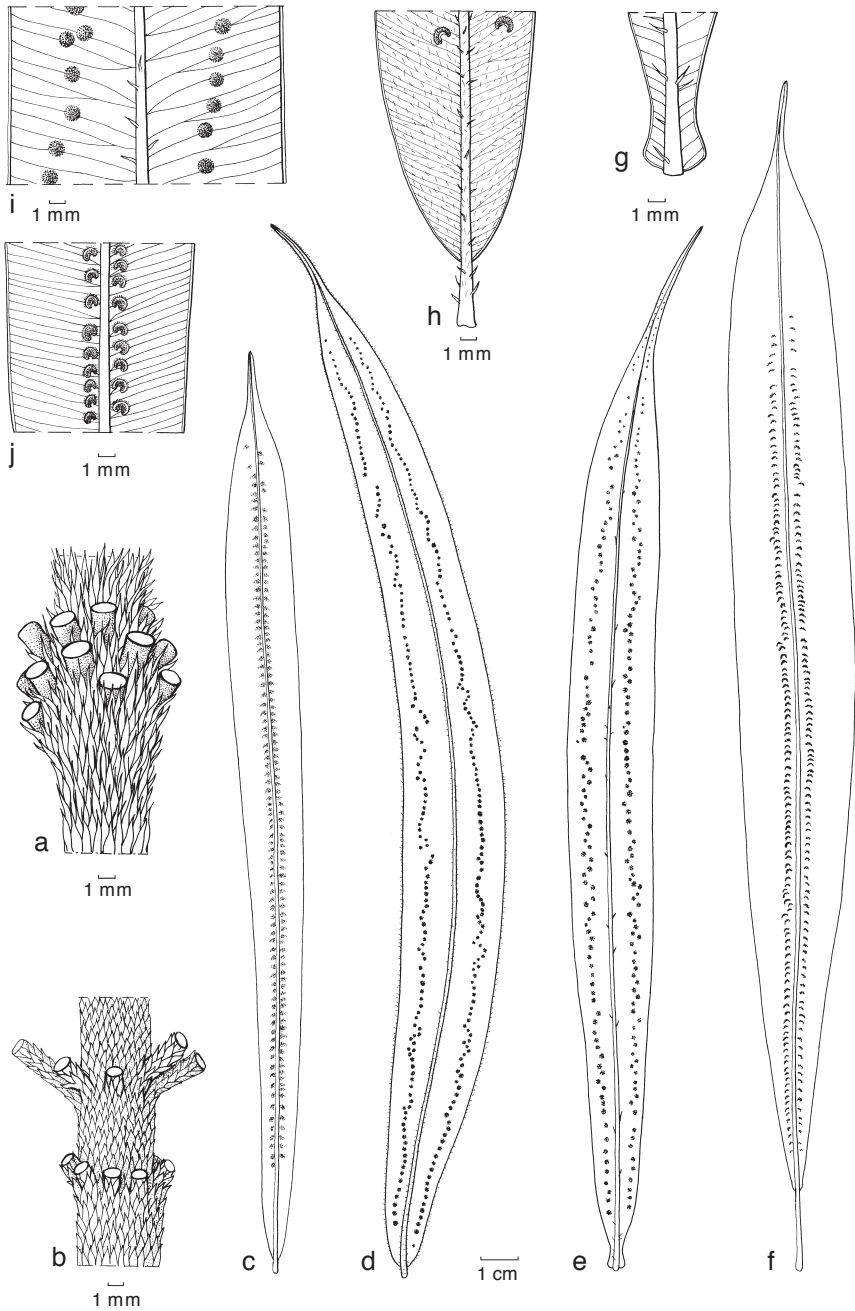


Fig. 1. *Oleandra neritiformis* Cav. a, b. Aerial erect rhizome with whorls of phyllopodia; c–e. fertile fronds; g. lyrate lamina base; h. rounded lamina base; i. medial sori, without conspicuous indusia; j. costal sori, with conspicuous indusia (a: Chew, Corner & Stainton 298; b, c, l: Chew 942; d: Copeland s.n., 29 Jan. 1933; e, g, i: Brass 23016; f: Croft 66; h: Van Balgooy 5223; all L.) Drawing by Anita Walsmit Sachs.

Geographic variation and local forms

Over most of the distribution area, two forms can often easily be distinguished locally, on basis of the relative length of phyllopodium and stipe. Stipitate forms have short phyllopodia, elongated stipes (thus the articulation is positioned at the base of the phyllopodium/stipe), the lamina gradually narrowed towards the base, and sori relatively close to the costa. The other form is characterized by longer phyllopodia, stipes short or absent (thus the lamina appearing sessile with regard to the articulation), usually a truncate lamina base (although the lamina directly above the base may be strongly narrowed, the base is still suddenly contracted, and often somewhat lyrate) that is clearly set off against the stipe, and sori in a more variable position, in some cases almost at the margin. However, other characters, such as indument, or indusium are independently variable and often show similar states in the two forms in the same area.

Java, Sumatra

On Java and Sumatra, there is no clear distinction between stipitate and sessile forms, as both stipe and phyllopodium length are strongly variable and extremes are not sharply separated. In Backer & Posthumus (*Varenflora voor Java*, 1939), all are taken together as *O. neriiformis*.

Peninsular Malaysia, Southern Thailand

In collections from the Malay Peninsula the difference between stipitate and sessile forms is associated with differences in hairiness of the lamina and position of the sori.

Holtum (*Rev. Flora Malaya II. Ferns*, 1968) also distinguishes these two forms, on basis of the same characters, but notes that they are not sharply distinct, nor ecologically sharply separated, although he cites a difference in altitudinal preference. The scant label data I have seen indicate no differences in preference for epiphytism vs terrestrial, or for altitude.

Borneo

On Borneo, the two forms also differ in hairiness of lamina, but not in the position of the sori, which are usually more or less closely costal. Here, the stipitate form is almost exclusively reported as epiphyte, the other form as terrestrial. Both forms tend to have narrower, darker costa-scales than in other areas. Completely glabrous forms such as are most common on Java and Sumatra are not found on Borneo. The sessile form has been described as *O. oblanceolata* Copel.

Philippines

On the Philippines, distinctly stipitate forms represent a small minority of all collections. The two forms here do not show any difference in degree of hairiness and position of the sori, but share a distinctly hairy lamina and more copious, pale, flat rachis-scales than the forms in other areas.

Copeland (*Fern Fl. Philipp.* 1958) distinguishes *O. neriiformis* from the short-stipitate form, and within the latter a number of species, based on details of indument: *O. herrei*, with paleate costa, *O. colubrina*, with setose costa and hairy lamina, *O. nitida*,

with setose costa and glabrescent lamina. We find that although the density of costal scales varies strongly (it seems to be negatively and weakly correlated with the density of setae), scales can be found on all specimens, and the density of hairs on the lamina varies strongly. We see no basis on which these characters could lead to the distinction of clear groups.

Celebes, Moluccas

South of the Philippines, two forms co-occur on Celebes and the Moluccas, while the stipitate form extends to the Solomon Islands and Vanuatu. Both forms here share rather indistinct indusia, which may be shortly setose.

Kato (J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14, 4 (1989)), distinguishes the specimens from Ceram with very small, setose indusia as *O. cuspidata*, but we find that this represents only the extreme state of variability.

New Guinea and surrounding islands

The stipitate form that extends eastwards from Celebes co-occurs, on the main island of New Guinea, with a sessile form that is often distinctly dimorphic and has sori often quite distant from the costa.

5. *Oleandra sibbaldii* Grev.

Oleandra sibbaldii Grev., Ann. Mag. Nat. Hist. 1 (1848) 327; Copel., Fern Fl. Philipp. 1 (1958) 183; Brownlie, Pterid. Fl. Fiji (1977) 157; R.M. Tryon, Rhodora 102 (2000) 436, f. 7. — *Oleandra cumingii* J.Sm. var. *sibbaldii* Baker, Syn. Fil. (1867) 303. — Type: *Sibbald s.n.* (E, barcode E00417634, n.v.), Tahiti.

Oleandra tricholepis Kunze, Bot. Zeitung (Berlin) 9 (1851) 349. — Type: *Hupe s.n.* (LZ, probably destroyed), Borneo.

Oleandra gracilis Copel., Univ. Calif. Publ. Bot. 12 (1931) 397, t. 52b; Philipp. J. Sci. 73 (1940) 347. — Type: *Keysser 74* (UC), New Guinea.

Oleandra crassipes Copel., Philipp. J. Sci. 73 (1940) 347, t. 2. — Type: *Brass 12109* (holo UC; iso BO, L), New Guinea.

Rhizome long-creeping or pendulous, sparsely branching, 1.5–4.5 mm thick, in cross-section without or with few scattered sclerified strands, very strongly white waxy, fronds scattered, roots with distinct unbranched parts. *Scales* deciduous, exposing the rhizome in older parts, peltate, (3–)5–15(–18) by (0.3–)0.4–0.9(–1.2) mm, usually widest above the attachment, squarrose, reddish brown, margin entire or more or less densely set with sessile glands, acumen attenuated, long filiform apex. *Fronds* monomorphic; phyllopodia distinct, (0.3–)0.8–4(–5.7) cm high, stipe (0.3–)0.5–3.5(–4.5) cm long, often with dark coloration on abaxial side; lamina to (4.5–)15–40(–58) by 1–4(–6) cm, widest in middle part, base attenuate to cuneate, sometimes rounded, rarely truncate, sometimes asymmetric, apex acuminate or up to 3 cm caudate, texture membranous to coriaceous, both sides sparsely to densely set with catenate hairs to c. 0.5 mm long; costa on lower surface often with dark-coloration, on both surfaces with scales, scales on lower surface often abundant, to 6(–11) by 1(–1.2) mm, pale to dark brown, on upper surface scarce, inconspicuous. *Sori* inframedial, leaving a distinct 1–4 mm wide sterile zone between costa and soral zone, sometimes as much as 12 mm

from costa, indusium firm, to 1 mm wide, hairy. *Sporangial stalk* with glands below the sporangium. *Spores* with an irregular mesh-like network of up to 10 μm high folds, finely papillose with spinules up to c. 4 by 1 μm , perispore baculate, outer layer much perforated.

Distribution — Eastern Malesia to Vanuatu, Fiji, Western Samoa, Tahiti. In *Malesia*: Borneo: Sabah, Sarawak; Philippines: Mindanao; Sulawesi; Moluccas; New Guinea.

Ecology — Epiphytic, epilithic, or less commonly terrestrial (> 1500 m), climbing or sprawling among bryophytes and other epiphytes, or pendulous from mossy tree branches; commonly collected from mossy forest. Altitude to 600 m (Marquesas and Tahiti) or 1000–3000 m above sea level.

Note — The dark colour on the abaxial surface of the costa is often very conspicuous, extending on the stipe, thus rendering the stipe conspicuously bicolorous.

6. *Oleandra vulpina* C.Chr.

Oleandra vulpina C.Chr., Dansk Bot. Ark. 9 (1937) 68. — Type: *Ledermann 7652* (BM), New Guinea.

Rhizome long-creeping, c. 3 mm thick, sparsely branching, not glaucous, roots with unbranched parts; in cross-section with weakly developed sclerified sheath and few scattered sclerenchyma strands, fronds scattered, 3–6 cm distant. *Scales* scattered, not covering the rhizome, peltate, to 5 by 0.5 mm, appressed at the base, with a narrow squarrose acumen, dark brown near attachment, lighter towards margin, margin densely set with glands and multicellular hairs terminating in a gland. *Fronds* monomorphic, phyllopodia 6–7 mm long, with scales as the rhizome but less dense and short fine glandular hairs; stipe 2–3 mm long, without dark coloration on abaxial side, bearing short fine glandular hairs; lamina linear-lanceolate, 20–17.5 by 3–4 cm wide, base cuneate, apex short caudate, tips up to 1 cm long, margin undulate, weakly cartilaginous, texture papyraceous, all parts with to 0.5 mm long catenate glandular hairs, or with longer, to 1.5 mm, acicular hairs; costa abaxially without dark coloration, with hairs like the stipe and with small scales; veins terminating in a weakly developed hydathode before the margin. *Sporangial stalk* with glands below the sporangium. *Sori* in an irregular row 2.5–6 mm from the costa, indusium round-reniform, c. 0.5 mm across, fugacious at very early stage. *Spores* not seen.

Distribution — *Malesia*: New Guinea.

Ecology — Scandent on trunk of Sago palm in garden, or in forest, at 975 m altitude.

Vernacular name — Taingelem (Wapi language, Miwaute).

Note — Distinct from *O. sibbaldii* in the rhizome and costa scales. Rhizome scales are darker in colour with pale-coloured margin, apices long subulate, margin strongly ciliated with glandular hairs. In addition, the rhizome of *O. vulpina* is not glaucous. The indusia are very small and shrivel at a very young stage but are distinct when present in the numerous setose hairs.

7. *Oleandra wernerii* Rosenst.

Oleandra wernerii Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 5 (1908) 40; Copel., Philipp. J. Sci. 73 (1940) 347; R.M.Tryon, Rhodora 102 (2000) 433, f. 3. — Type: *Werner 12* (lecto L 'Rosenstock 28', here selected), New Guinea.

Oleandra dimorpha Copel., Philipp. J. Sci. 60 (1936) 111. — Type: *Brass 2916* (holo MICH), San Christoval.

Rhizome with main stems creeping, scrambling or pendent, 2–3 mm thick, sparsely rooting, mostly terete when dry; all parts in cross-section with a peripheral sclerified sheath and scattered sclerified strands, white waxy in the older parts, fronds scattered on creeping parts, fronds more closely together but not densely clustered on aerial parts. *Scales* covering the rhizome, peltate, 3–4 by 0.5–1 mm, somewhat squarrose, with dark centre and lighter margin and acumen, margin ciliate especially when young. *Fronde* strongly dimorphic, phyllopodia short, usually less than 5 mm high, stipe 0.5–2.5 cm, without dark coloration, especially upwards with up to 2 mm long hairs; fertile lamina 27–56 by 0.5–1(–1.7) cm, base and apex narrow, sterile 17–30 by 2.2–5.7 cm, base mostly cuneate, apex distinctly 2–3.5 cm caudate; texture chartaceous, costa and lamina on lower surface glabrous or with up to 2 mm long hairs, costa without dark coloration, like the stipe with up to 2 mm long brown scales. *Sori* in a single row on both sides of the costa, indusium firm, 1–3 mm wide, glabrous. *Sporangial stalk* with glands below the sporangium. *Spores* with coarse confluent ridges, areolae with short pointed excrescences, perispore hollow, with internal baculae, outer layer not or hardly perforated.

Distribution — In *Malesia*: Moluccas, New Guinea; Vanuatu.

Ecology — Commonly epiphytic, on trunks or in crowns, less often terrestrial or on rocks, erect, scrambling or pendent, in various types of forest, most frequently in montane or mossy forest, on ridges, up to c. 2000 m altitude.

Notes — 1. As with *O. neriiformis*, rhizome morphology is probably more complicated than can be inferred from the mostly aerial unbranching parts making up most of the collected material.

2. Hairiness is very variable, and while there is no sharp distinction between hairy and glabrous forms, it is noteworthy that hairy forms tend to occur at especially the western extreme of the distribution area, with less hairy forms near the eastern extreme, and glabrous forms mostly on the mainland of New Guinea.