

NEPHROLEPIDACEAE

(P.H. Hovenkamp, Leiden, The Netherlands & F. Miyamoto, Kanagawa, Japan)

Nephrolepidaceae Pic.Serm., *Webbia* 29 (1974) 8; K.U.Kramer in K.U.Kramer & P.S.Green (eds.), *Fam. Gen. Vasc. Pl.* (1990) 188. — Type genus: *Nephrolepis* Schott.

In considering this a monogeneric family we follow the treatment in the Families and Genera of Vascular Plants (Kramer 1990). In the past, *Nephrolepis* was considered to be variously allied with *Davallia*, *Oleandra* and/or *Arthropteris* in Nephrolepidaceae, Oleandraceae or Davalliaceae (see Pichi Sermolli 1974 for a concise review), but both molecular phylogenies and morphological data disagree with that position. Molecular phylogenies (Hasebe et al. 1995; Liu et al. 2007; Schuettpelz & Pryer 2008) indicate separate positions for all of these genera, while morphologically, *Nephrolepis* is a highly distinct genus, with the unique character of the very distinctive stolons and although recent studies suggest that it should be aligned with *Lomariopsis* and *Cyclopetlis* (Smith et al. 2006) we here maintain it for the time being in its own family.

References: Hasebe, M., P.G. Wolf, K.M. Pryer, K. Ueda, M. Ito, R. Sano, G.J. Gastony, J. Yokoyama, J.R. Manhart, N. Murakami, E.H. Crane, C.H. Haufler & W.D. Hauk, Fern phylogeny based on rbcL nucleotide sequences. *Amer. Fern J.* 85 (1995) 134–181. — Liu, H.M., X.C. Zhang, W. Wang, Y.L. Qiu & Z.D. Chen, Molecular phylogeny of the fern family Dryopteridaceae inferred from chloroplast rbcL and atpB genes. *Int. J. Pl. Sci.* 168 (2007) 1311–1323. — Schuettpelz, E. & K.M. Pryer, Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56 (2008) 1037–1050. — Smith, A.R., K.M. Pryer, E. Schuettpelz, P. Korall, H. Schneider & P.C. Wolf, A classification for extant ferns. *Taxon* 55 (2006) 705–731.

TAXONOMY

The genus *Nephrolepis* was established by Schott (1834) to accommodate a number of species until then included in *Aspidium*, *Nephrodium* and *Polypodium*, which he distinguished on the basis of the venation pattern and soral position. The genus was quickly adopted by Presl (1836), who further diagnosed it by the presence of articulate pinnae. Presl added a number of species (including a few now no longer included in *Nephrolepis*), and erected the genus *Leptopleuria* for *N. abrupta*, a taxon with an aberrant soral position. The articulated pinnae were accepted as characteristic for the genus by Smith (1841, 1842), who also recognized the correct affinity of *N. abrupta*. The modern circumscription of *Nephrolepis* was attained when Smith (1857, 1866, 1875) distinguished both *Nephrolepis* and *Arthropteris* in the modern sense, using the differences in articulation and the stoloniferous habit of *Nephrolepis* as generic characters. Hooker (1862), mistakenly included *Arthropteris palisotii* (with the misapplied name *N. obliterated*) as a species “peculiar in the genus”, and also introduced the erroneous notion that *N. exaltata* is a pantropical species, thus laying the groundwork for many misidentifications and the misconception that *Nephrolepis* is a particularly difficult genus, expressed by, e.g., Copeland (1947).

In the modern circumscription, *Nephrolepis* is accepted in most recent floristic and horticultural accounts, e.g., Nauman (1985, 1992), Proctor (1989), Hoshizaki & Moran (2001), Mickel & Smith (2004), Hovenkamp & Miyamoto (2005).

References: Copeland, E.B., Gen. Fil. (1947). Chronica Botanica, Waltham, Mass. — Hooker, W.J. Sp. Fil. (1862) 4. Pamplin, London. — Hoshizaki, B.J. & R.C. Moran, Fern growers manual (2001). Timber Press, Portland, Oregon. — Hovenkamp P.H. & F. Miyamoto, A conspectus of the native and naturalized species of *Nephrolepis* (Nephrolepidaceae) in the world. Blumea 50 (2005) 279–322. — Mickel, J.T. & A.R. Smith, The Pteridophytes of Mexico. Mem. New York Bot. Gard. 88 (2004). The New York Botanical Garden, New York. — Nauman, C.E., A systematic revision of the neotropical species of *Nephrolepis* Schott (1985). PhD thesis, The University of Tennessee, Knoxville. — Nauman, C.E., *Nephrolepis*. Fl. Mesoamericana (1992) 286–289. New York. — Presl, C.B., Tent. Pterid. (1836). Theophilus Haase, Prague. — Proctor, G.R., Ferns of Puerto Rico and the Virgin Islands. Mem. New York Bot. Gard. 53 (1989). The New York Botanical Garden, New York. — Schott, H., Gen. Fil. 1 (1834). Wallishausner, Vienna. — Smith, J., Enumeration Filicum Philippinarum. J. Bot. (Hooker) 3 (1841) 393–422. — Smith, J., An arrangement and definition of the genera of ferns, with observations on the affinities of each genus. J. Bot. (Hooker) 4 (1842) 38–70, 146–198. — Smith, J., Cultivated ferns (1857). Pamplin, London. — Smith, J., Ferns: British and foreign (1866). Hardwicke, London. — Smith, J., Historia Filicum (1875). Macmillan & Co., London.

MORPHOLOGY AND CHARACTERS

The morphology of *Nephrolepis* has been studied extensively and in great detail (Heinricher 1907; Sen & Sen 1973; Nayar & Bajpai 1978).

Rhizome

The rhizome system is composed of two different elements: erect, rootless frond-bearing parts and creeping, root-bearing runners. The frond-bearing parts in all Malesian species form well-developed, erect, sometimes aerial trunks, bearing several green fronds at the same time (trunks are poorly developed or virtually absent only in species outside the area). Runners originate from the frond-bearing part, and may be variously developed and branched. Although the morphology of the runners is clearly of a rhizomatous nature, during development of a plant runners and roots appear to be equivalent (Espagnac 1973). The vascular system of the erect part is a dictyostele, while of the runners it is protostelic. In some species further modifications of the runners occur. In *N. cordifolia* (and related non-Malesian taxa) underground tubers may be formed, which are irregularly globose to somewhat elongated, up to a few cm in diameter and densely scaly. From the tubers, new plantlets can be formed, and in times of drought the water reserve in the tubers can be used. In some species (most notably in *N. brownii* and *N. hirsutula*) the parts of the runners close to the erect rhizomes are often stout and stilt-like, propping up the frond-bearing erect stems. In *N. radicans*, the runners are further differentiated. Most conspicuous are the negatively geotropic runners that are thick and scrambling and may form dense thickets. They bear erect frond-bearing branches at more or less regular intervals, from which thin, twining, tendril-like and rootless runners originate, as well as positively geotropic runners that are distinctly thinner than the scrambling ones, and bear roots at the tips or wherever they come into contact with a suitable substrate. In *N. acutifolia* the parts close to the erect rhizomes are frequently branched, forming bush-like structures around the tufts of fronds. The degree to which otherwise unmodified runners bear young plantlets varies, and is highest in *N. lauterbachii*, where young plantlets are often regularly spaced on horizontal runners. The runners, which may reach lengths of several metres, develop

into frond-bearing stems when they are severed from the main plant, thus facilitating colonization and vegetative propagation.

Scales

Scales are most densely set on the rhizome and the basal parts of the stipe, more sparsely on runners and stipes, and in most species very sparse or absent on the lamina of mature fronds. The rhizome scales are usually very similar to the basal scales on the stipe (Plate 1), whereas distinctly different scales occur higher up on the stipe and on the lamina. Here we use the term ‘basal scales’ to distinguish the scales on the rhizome and the base of the stipe from the scales on the upper part of the stipe and the rhachis. The central part of the basal scales is in several species conspicuously dark and appressed (Plate 1a), with the margin fringed with teeth or longer hairs. In other species, the scales are more evenly brown to straw coloured, in which case they are usually also more spreading (Plate 1b). The scales on the upper part of the stipe are often strikingly different, and in some cases an accurate identification may be impossible without the presence of basal scales. Scales on the rhachis (Plate 2) usually are similar to the upper stipe scales but smaller, and may be more deeply dissected. An unusual character is that the scales on the rhachis have their longest extension often directed towards the base of the frond, not towards the apex as have the scales on the rhizome and stipe base, and on the rhachises of virtually all other ferns. The scales on the runners are usually much sparser than on the frond-bearing parts and mostly light brown.

Fronds

Above the stipe, the lamina is in outline usually strongly elongated and strap-shaped. As terminal growth usually appears to have been arrested before a well-formed apex

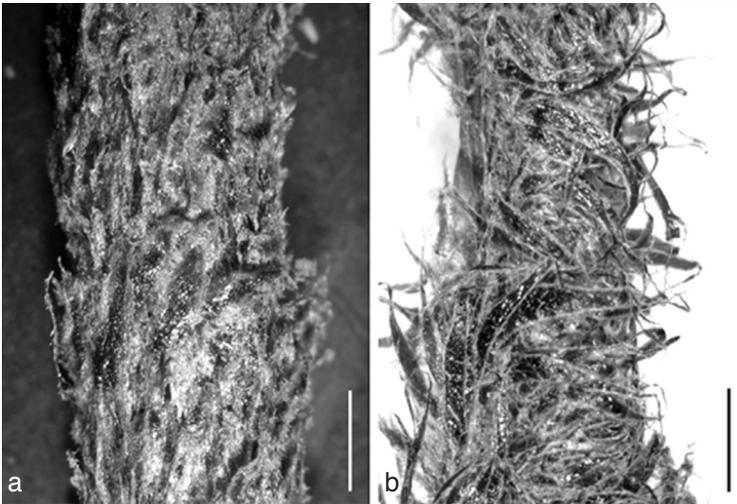
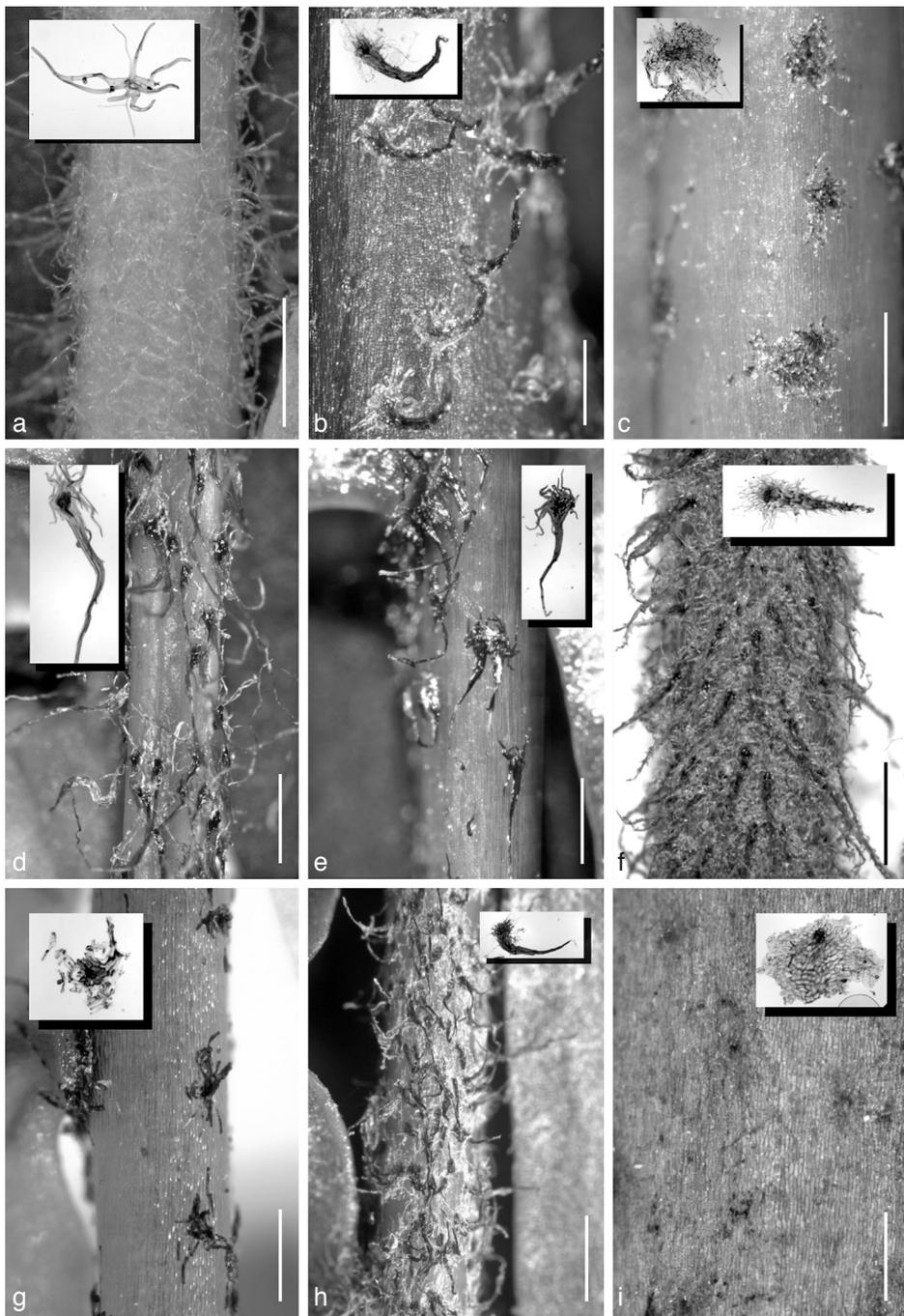


Plate 1. a. *Nephrolepis brownii* (Desv.) Hovenkamp & Miyam., basal scales on stipe appressed; b. *N. biserrata* (Sw.) Schott, basal scales on stipe spreading sideways (a: Hortus Leiden 20000574; b: Croft 62, L). — Scale bar: 1 mm.



develops, the length of the fronds is to some degree indeterminate, and most fronds are never completely unrolled. However, both field observations and cultivated specimens indicate that fronds are not able to grow indeterminately (there appears to be a maximum length of a few metres for fully grown fronds of *N. biserrata*), but the highly exposed and sensitive apex is apparently very sensitive to adverse conditions so that presumably even short spells of such conditions can cause the arrest of apical growth. At the base, the lamina is reduced to various degrees, the lowermost pinnae usually at wider distances from each other than higher upwards. The articulation of the pinnae is often highly functional, and pinnae are often absent from older fronds (as well as from many herbarium specimens). The fronds have an indument composed of hairs and scales. The hairs may be present regularly on the upper surface of the main rhachis and pinna rhachis, but also to varying degrees on both sides of the lamina. In some species, hairiness is more frequent than in others, but it is not possible to evaluate to what degree the presence of hairs is also decided by stage in the life-cycle of a plant. The scales are usually deciduous with age, and persistent only in few species.

Sori

Sori vary from reniform to lunulate or linear, and may also be cup-shaped (Fig. 1). Reniform sori, occurring in the majority of species, may differ in the degree to which the sinus is narrowed. When the sinus is very narrow, the sori may appear to be fully peltate when dry. Lunulate sori, occurring in *N. auriculata* and related taxa are attached with a longer, often concave base. They often open more towards the apex of the pinnae. Sori with a straight or somewhat convex base occur in *N. abrupta* and *N. rosenstockii*, situated close to and opening towards the margin. In *N. acutifolia*, the sori are linear (sometimes interrupted). Cup-shaped sori, attached on base and sides, occur in a marginal position in *N. davalliae*.

Spores

Spore morphology of the Asian species has been studied by Liew (1977) and Tryon & Lugardon (1991). Spores are relatively small (27–35 µm, rarely to 39 µm long), monolete and elongate in outline. The exospore is smooth or weakly sculptured, and the contours of the spore wall are derived from the variably thick perispore only. In

←

Plate 2. a. *Nephrolepis acutifolia* (Desv.) H.Christ, rhachis scales tomentose; b. *N. davallioides* (Sw.) Kunze, rhachis scales with dark apex, directed sideways; c. *N. radicans* (Burm.) Kuhn, rhachis scales without protracted acumen, appressed; d. *N. cordifolia* (L.) C.Presl var. *cordifolia*, rhachis scales with elongated acumen; e. *N. lauterbachii* H.Christ, rhachis scales with elongated, dark acumen; f. *N. hirsutula* (G.Forst.) C.Presl, rhachis scales dense, strongly dentate; g. *N. falciformis* J.Sm., rhachis scales without protracted acumen, dark; h. *N. falcata* (Cav.) C.Chr., rhachis scales very dark, directed sideways; i. *N. obliterated* (R.Br.) J.Sm., rhachis scales appressed, very inconspicuous (a: Anderson 3632, L, inset: Nur 204, L; b: Hortus Leiden, inset: Stone 6075, L; c: Hortus Leiden, inset: Alston 13116, L; d: Hortus Leiden 960313, inset: Van Beusekom & Phengkhlai 3094, L; e: Hortus Leiden 930105, inset: Vink & Schram BW 8623, L; f: Pullen 7584, L, inset: Idjan & Mochtar 917, L; g: Hortus Leiden 960312, inset: De Joncheere 1329, L; h: Hortus Leiden 902014; inset: Elmer 10330, P; i Takeuchi 8915, L, inset: Van Royen 3170, L). — Scale bars: a–c, e, g = 1 mm; d, f, h = 2 mm; i = 0.5 mm.

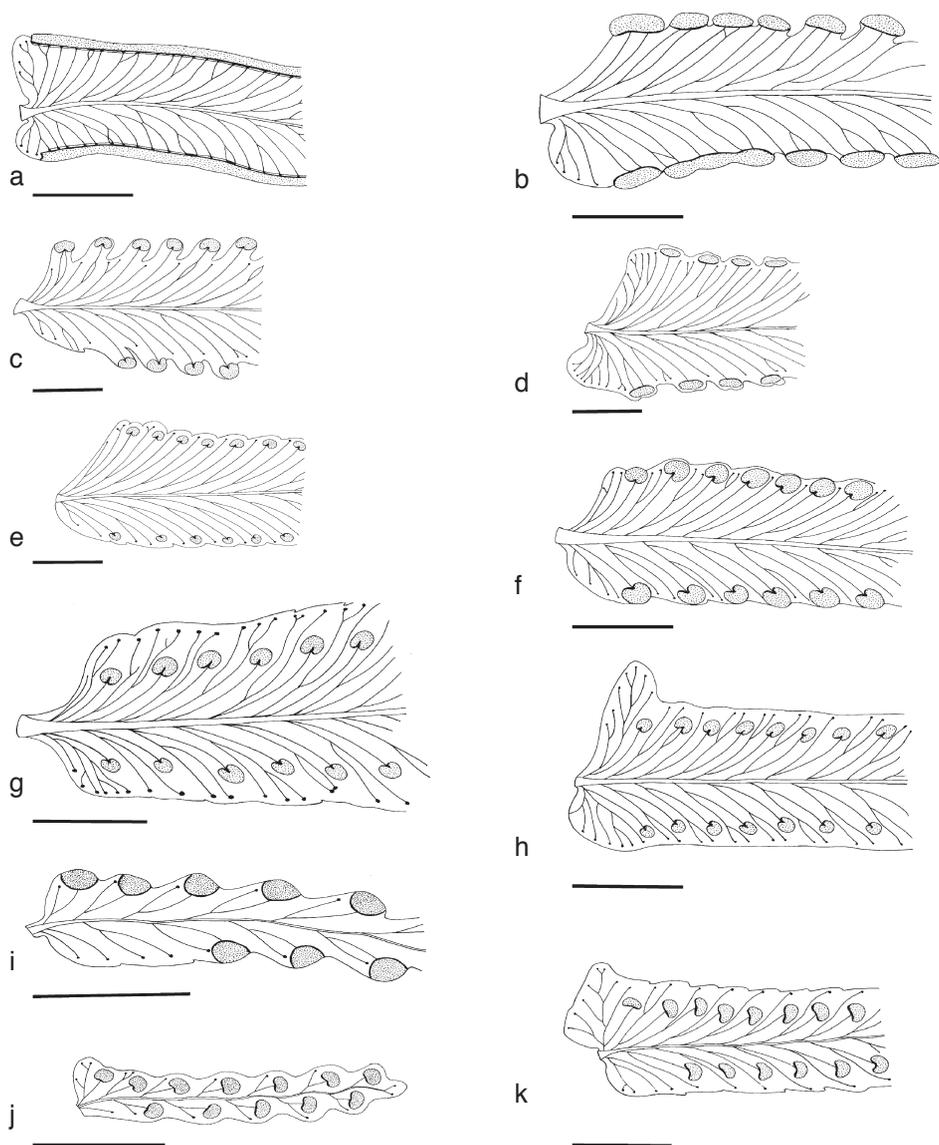


Fig. 1. a. *Nephrolepis acutifolia* (Desv.) H.Christ, sorus marginal, uninterrupted; b. *N. dicksonioides* H.Christ, sori marginal, on more than one vein, mostly separate; c. *N. davallioides* (Sw.) Kunze, sori marginal, on separate teeth; d. *N. abrupta* (Bory) Mett., sori submarginal, protruding slightly; e. *N. oblitterata* (R.Br.) J.Sm., sori submarginal, not protruding; f. *N. brownii* (Desv.) Hovenkamp & Miyam., sori submarginal; g. *N. biserrata* (Sw.) Schott, sori submedial to medial; h. *N. hirsutula* (G.Forst.) C.Presl, sori submedial; i. *N. davalliae* Alderw., sori marginal, cup-shaped; j. *N. cordifolia* (L.) C.Presl var. *cordifolia*, sori medial, lunulate; k. *N. lauterbachii* H.Christ, sori medial, lunulate, pinnae sinuose, attachment 1-sided (a: Surbeck 1035; b: Idjan & Mochtar 283; c: Van Borssum Waalkes 1345; d: Kato & Wiradinata B 6427; e: Van Royen 3170; f: Van Ooststroom 13534; g: Raciborski s.n.; h: Kato et al. C 2082; i: Brass 13296; j: Danser 6176; k: Takeuchi 10769; all L). — Scale bars = 5 mm.

the perispore sculpture, three distinct character states can be distinguished: coarsely rugate-tuberculate, more finely verrucose, and longitudinally rugate.

Coarsely rugate-tuberculate spores occur in the majority of species. Spores with this character have tubercles of varying degree of dispersion, which may be fused into irregular ridges, but the degree to which the tubercles or rugae are distinct and prominent may vary even within a species. The size of the individual tubercles or the corresponding width of the ridges varies between 2 and 2.5 μm . In the finely verrucose type the individual tubercles are smaller (mostly 1–1.5 μm), often more dispersed and less often coalescing into irregular ridges. Spores with this character occur in *N. brownii*, *N. hirsutula* and *N. radicans*, but this character is not always clearly distinct from the previous one. The longitudinally ridged spores have coarse rugae more or less regularly orientated in the length of the spore. They occur only in *N. dicksonioides* and do not show any intermediates to the other types.

References: Espagnac, H., Les axes polymorphes de *Nephrolepis biserrata*. Analyse expérimentale du déterminisme de leurs structures. *Ann. Sci. Nat., Bot.* 12 (1973) 223–286. — Heinricher, E., Zur Kenntnis der Farngattung *Nephrolepis*. *Flora* 97 (1907) 43–75. — Liew, F.S., Scanning electron microscopic 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. — 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 Verlag, New York.

KARYOLOGY AND HYBRIDIZATION

Basic chromosome number is 41 for all species investigated so far, and most species appear to contain diploids only, with additional tetraploids reported in two species (Löve et al. 1977; Tindale & Roy 2002): in *N. hirsutula* in South India (probably this record refers to *N. brownii*) and in *N. pectinata* in Jamaica. Hybridization under natural circumstances occurs occasionally (Nauman 1979), but is probably far less common than sometimes supposed; the rampant hybridity suggested by some authors can probably for a large part be explained by an incomplete understanding of the natural species. In cultivation, most of the variation being offered on the market is due to the occurrence of vegetative ‘sports’ (Benedict 1916) and artificial hybridization plays a minor role, if any at all.

References: Benedict, R.C., The origin of new varieties of *Nephrolepis* by orthogenetic saltation. *Bull. Torrey Bot. Club* 43 (1916) 207–234. — Löve, A., D. Löve & R.E.G. Pichi Sermolli, *Cytotaxonomical atlas of the Pteridophyta* (1977). Cramer, Vaduz. — Nauman, C.E., A new *Nephrolepis* hybrid from Florida. *Amer. Fern J.* 69 (1979) 65–70. — Tindale, M.D. & S.K. Roy, A cytotaxonomic survey of the Pteridophyta of Australia. *Austral. Syst. Bot.* 15 (2002) 839–937.

DISTRIBUTION

The genus as well as a small number of species are pantropical, but most species have a more limited distribution in either Southeast Asia or Tropical America. The phylogeny and biogeography were analyzed by Hennequin et al. (2010) who found that the Neo-

tropical and Paleotropical species form two distinct clades, with the widespread species *N. abrupta*, *N. biserrata*, *N. cordifolia* and *N. undulata* nested in the Paleotropical clade. Brown & Brown (1931) state for all species of *Nephrolepis* that they can “reasonably be considered as aboriginally introduced” in Southeast Polynesia. If true, that would suggest a contact between the native population on Hawaii with Caribbean tribes to explain the occurrence of *N. exaltata* on Hawaii.

References: Brown, E.D.W. & F.B.H. Brown, Flora of Southeastern Polynesia. II. Pteridophytes. Bernice P. Bishop Mus. Bull. 89 (1931). — Hennequin, S., P. Hovenkamp, M.J.M. Christenhusz & H. Schneider, Phylogenetics and biogeography of *Nephrolepis* – a tale of old settlers and young tramps. Bot. J. Linn. Soc. 164, 2 (2010) 113–127.

CULTIVATION

Various cultivars of *Nephrolepis* are among the most popular ferns in cultivation, with most forms currently cultivated presumably derived from the American *N. exaltata* cv. ‘*bostoniensis*’ (Benedict 1915, 1916a, b, 1922). Before ‘*bostoniensis*’ was discovered as a source for cultivars, cultivated forms appear to have been mostly derived from Southeast Asian species. Both *N. duffii* T.Moore, introduced from Duke of York’s Island, and *N. rufescens* var. *tripinnatifida* appear to be derived from *N. hirsutula*. Despite the popularity of cultivars of *N. exaltata*, there are no indications that any of these are escaping or naturalizing on a significant scale in the Malesian area.

References: Benedict, R.C., *Nephrolepis*: a description of the species and horticultural varieties, with a general discussion of the genus. In: Bailey’s Standard Cyclopedia of Horticulture IV (1915) 2131–2135. — Benedict, R.C., Some horticultural fern variations. Amer. Fern J. 6 (1916a) 8–15. — Benedict, R.C., The origin of new varieties of *Nephrolepis* by orthogenetic saltation. Bull. Torrey Bot. Club 43 (1916b) 207–234. — Benedict, R.C., The origin of new varieties of *Nephrolepis* by orthogenetic saltation. II. Regressive variation of reversion from the primary and secondary sports of *Bostoniensis*. Amer. J. Bot. 9 (1922) 140–157.

NEPHROLEPIS

Nephrolepis Schott, Gen. Fil. 1 (1834) pl. 3; Backer & Posth., Varenfl. Jav. (1939) 88; Copel., Gen. Fil. (1947) 90; Fern Fl. Philipp. 1 (1958) 184; Holttum, Revis. Fl. Malaya 2, 2nd ed. (1968) 372; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes (1985) 170; G.H.Bell, *Nephrolepis*. Fl. Australia 48 (1998) 440; Hovenkamp & Miyam., Blumea 50 (2005) 279. — Type: *Nephrolepis exaltata* (L.) Schott.
Leptopleuria C.Presl, Tent. Pterid. (1836) 136, pl. 5, f. 9–11. — Type: *Leptopleuria abrupta* (Bory) C.Presl.

Terrestrial or epiphytic ferns, bearing basifix, pseudopeltate or peltate scales on all parts. *Rhizome* consisting of long creeping or pendent protostelic runners bearing roots and erect dictyostelic radial stems bearing fronds and runners. *Fronde*s not articulated to the rhizome, stipitate, pinnate, often not forming an apical pinna or segment, scales on fronds often inconspicuous or deciduous, catenate hairs sometimes present. *Pinnae* articulated to the midrib, sessile, often with unequal base, margin usually crenate or serrate, apex rounded to acuminate, venation free, 1–2(–3) times furcate except in the most basal vein-group, free veins ending before the margin in a hydathode. *Sori* terminal on the acroscopic vein-branch (rarely innervated by 2 veins), medial to marginal,

indusiate, indusium reniform to lunulate or linear, glabrous. *Sporangia* long-stalked, glabrous, 0.2–0.24 by 0.15–0.18 mm, with (11–)13(–16) indurated annulus cells. *Spores* 27–35(–39) μm , elongate, monolete, brown, variously verrucate to tuberculate or rugose.

IDENTIFICATION AND KEY TO THE SPECIES

Nephrolepis has a reputation of being difficult. It is certainly the case that identification of juvenile plants may be difficult, as there may be considerable differences between juvenile and mature plants, also when the juvenile plants are ‘outliers’ established from runners. Accordingly, when identifying or collecting *Nephrolepis* specimens it is preferable to take a single frond from a well-established clump than an entire small ‘outlier’ plant even though the latter may more neatly fit on a herbarium sheet.

In a few cases species may be part of a complex in which delimitation between the various elements is difficult, e.g. between the taxa around *N. cordifolia* (*N. undulata*, outside Malesia also *N. cordifolia* var. *pumicicola*, *N. flexuosa*, *N. pectinata*). However, on the whole, most species are appreciably different and identification of complete fronds of mature plants will present little difficulty in the great majority of species.

To facilitate the identifications of more fragmentary, sterile, material, the following list of ‘spot characters’ may be useful.

Pinnae

Attachment 1-sided — *lauterbachii*

Acroscopic base very conspicuously auricled — *brownii*, *hirsutula*

Base narrowed on both sides — *biserrata*

Basiscopic base conspicuously auricled — *cordifolia*, *undulata*

Margin deeply incised — *davallioides*, *dicksonioides*

Lamina indument

Tomentose-flocculose — *acutifolia*

Scaly, persistent — *brownii*, *hirsutula*

Soft-hairy — *biserrata*

Rhachis indument

Appressed isodiametric scales — *obliterata*, *radicans*

Dense, rufous scales — *abrupta*, *hirsutula*

Dense, pale scales — *brownii*, *cordifolia*

Dense, dark scales — *davallioides*, *falcata*, *lauterbachii*

Dense, scale, ‘scabrous’-looking — *davalliae*

Sparse, inconspicuous or absent — *falciformis*, *obliterata*

Highly dissected scales, appearing as downy tomentum — *acutifolia*

KEY TO THE SPECIES

- 1a. Indusia broad, lunulate, or linear 2
- 1b. Indusia reniform, with wide or narrow sinuses 8

- 2a. Sori medial to submarginal 3
 b. Sori marginal 5
- 3a. Pinnae with acute apex; rhachis scales hyaline **15. N. undulata**
 b. Pinnae with rounded or obtuse apex; rhachis scales light brown to dark 4
- 4a. Rhachis scales dark; pinna-base fully 1-sided, basiscopically base narrowly cuneate; basal scales with entire acumen **12. N. lauterbachii**
 b. Rhachis scales light brown; pinna-base slightly to strongly unequal, basiscopically rounded or cordate; basal scales usually with denticulate acumen **5. N. cordifolia**
- 5a. Sori linear; basal scales squarrose, with light brown central part **2. N. acutifolia**
 b. Sori round or elongated; basal scales appressed, spreading or sometimes squarrose, with rufous central part 6
- 6a. Indusium attached at base and sides; basal scales dull, with microscopic marginal glands around the scale, with entire or dentate acumen; rhachis scales dark, with entire or dentate acumen **6. N. davalliae**
 b. Indusium attached at broad base; basal scales shining, without marginal glands, with ciliate or fimbriate acumen; rhachis scales hyaline to rufous, with ciliate acumen. 7
- 7a. Pinna apex acuminate to caudate; pinna margin in basal part entire **8. N. dicksonioides**
 b. Pinna apex rounded, obtuse or acute; pinna margin in basal part crenate **1. N. abrupta**
- 8a. Plants scrambling, runners modified into thick scrambling ones and thinner, tendril-like or root bearing ones; rhachis scales distinctly bullate when dry **14. N. radicans**
 b. Plants not scrambling, runners not modified; rhachis scales flat when dry 9
- 9a. Basal scales spreading or squarrose 10
 b. Basal scales appressed with light brown central part; pinna-base equal or slightly unequal; rhachis scales appressed or spreading **3. N. biserrata**
- 10a. Basal scales dull; rhachis scales very sparse or sparse, appressed, without a distinctly protracted acumen; scales on lamina absent or sometimes present . . . 11
 b. Basal scales shining; rhachis scales dense to very dense, spreading to squarrose, with a well-developed protracted acumen; scales on lamina usually persistent . 12
- 11a. Rhachis scales very sparse, inconspicuous, hyaline; pinnae not auricled; sori marginal **13. N. oblitterata**
 b. Rhachis scales sparse, dark and conspicuous when present; pinnae slightly to distinctly auricled; sori submarginal **10. N. falciformis**
- 12a. Sterile pinnae strongly auricled; basal scales with distinct, wide hyaline margin 13
 b. Sterile pinnae auricled or not; basal scales with hyaline margin narrow or present in lower part only 14
- 13a. Hairs on upper side of costae absent; rhachis scales rufous, with strongly dentate acumen; sori submarginal **11. N. hirsutula**
 b. Hairs on upper side of costa present; rhachis scales hyaline or light brown (rarely rufous), with nearly entire acumen; sori submedial **4. N. brownii**
- 14a. Rhachis scales dark, with entire acumen; lamina base strongly reduced; pinna-base strongly unequal, acrosopically truncate, slightly to distinctly auricled; sori submarginal, not on teeth. **9. N. falcata**

- b. Rhachis scales hyaline or with a dark, acicular, often ciliate acumen; lamina base truncate; pinna-base slightly unequal, acroscopically emarginate to cuneate, not auricled; sori marginal, often on separate teeth **7. *N. davallioides***

1. *Nephrolepis abrupta* (Bory) Mett.

Nephrolepis abrupta (Bory) Mett., Fil. Hort. Bot. Lips. (1856) 99; J.Sm., Hist. Fil. (1875) 227; Hovenkamp & Miyam., Blumea 50 (2005) 288. — *Dicksonia abrupta* Bory, Voy. Iles Afrique (1804) 187, pl. 30. — *Leptopleuria abrupta* (Bory) C.Presl, Tent. Pterid. (1836) 137, pl. 5, f. 9–11. — Type: *Anon. s.n., s.d.* (holo P; iso K, L), Réunion.

Habit, rhizome morphology. Runners 1–2 mm thick, branching angle divaricate. Scales on runners dense, spreading or squarrose. Tubers absent. *Fronds* to 200 cm long (or much longer), 15–19 cm wide, stipe 30–35 cm long. Lamina base strongly reduced, tapering over 20–60 cm, basal pinnae 1–1.2 cm long, 2.5–6 cm distant, middle pinnae slightly to strongly falcate (mostly the cauda only is falcate). Sterile pinnae 3–13 by 0.8–2.8 cm (usually distinctly triangular, narrowed gradually from base to apex), leathery, base strongly unequal, basiscopic base cordate (strongly, sometimes somewhat auriculate), acroscopic base cuneate, truncate, rounded or cordate (always less distinctly cordate than the basiscopic base), not or slightly auricled (usually distinctly dilated, but not auricled), margin in basal part finely crenate, towards apex crenate, apex rounded, obtuse or acute. Fertile pinnae 3.2–14 by 0.7–1.8 cm, differing from sterile pinnae in the margin being incised between sori but not beyond the attachment. *Indument.* Basal scales pseudopeltate, spreading, 5.5 by 1 mm, central part rufous, shining (translucent), hyaline margin absent, marginal glands absent, margin in basal part fimbriate, acumen fimbriate, transition to rhachis scales abrupt or basal scales persisting to high up. Rhachis scales sparse or dense, with a well-developed protracted ciliate acumen, appressed or spreading, light brown or rufous. Scales on lamina absent. Hairs on lamina absent or present, short, dense. *Sori* marginal, 14–34 pairs on fully fertile pinnae, elongated, not impressed. Indusium broad, attached at broad base. — **Fig. 1d.**

Distribution — Indian Ocean: Madagascar, Comores, Réunion; in *Malesia*: Peninsular Malaysia, Borneo.

Habitat & Ecology — In the Malesian part of its range epiphytic or terrestrial, on limestone, 200–400 m altitude; outside Malesia often in pioneer vegetation on recent lava flows.

Note — *Nephrolepis abrupta* is somewhat similar to *N. dicksonioides* and has been confused with that species, from which it differs in more triangular pinnae, gradually narrowed from the base towards the apex, the fertile pinnae not incised beyond the sori, so that the sori are protruding from the margin, not on distinct teeth, indusium not reaching margin, innervated by 1, rarely 2 veins, rhachis scales more strongly lacerated. The pinnae often appear to stand in a plane at right angles to the rhachis. They are usually glabrous, but may be densely short-hairy all over the lamina, with hairy and glabrous fronds sometimes occurring on the same plant. Plants from the non-Malesian part of the range are often much more compact and densely scaly, but this habit is not preserved in cultivation.

2. *Nephrolepis acutifolia* (Desv.) H.Christ

Nephrolepis acutifolia (Desv.) H.Christ, Fil. Saras. III (1895) 243; Backer & Posth., Varenfl. Jav. (1939) 89; Copel., Fern Fl. Philipp. 1 (1958) 189; Holtum, Revis. Fl. Malaya 2, 2nd ed. (1968) 375; Tagawa & K.Iwats., Fl. Thailand 3 (1985) 171; Hovenkamp & Miyam., Blumea 50 (2005) 289. — *Lindsaya acutifolia* Desv., Prodr. Fam. Foug. (1827) 312. — Type: *Anon. s.n.* (P? not found), Mascarenes. *Isoloma lanuginosa* J.Sm. in Hook., Gen. Fil. (1842) pl. 102. — *Lindsaya lanuginosa* (J.Sm.) Hook., Sp. Fil. (1846) 210. — Type: *Wallich 154* (holo K; iso BM), East Indies. *Nephrolepis lindsayae* H.Christ, Fil. Nov. (1898) 837. — Type: *Schneider s.n.* (P), Sumatra. *Nephrolepis niphoboloides* Alderw., Bull. Jard. Bot. Buitenzorg II (1913) 18. — Type: *Koorders 61* (BO), Java. *Nephrolepis marginalis* Copel., Philipp. J. Sci., Bot. 12 (1917) 49. — Type: *Topping 1632* (n.v.), Borneo.

Habit, rhizome morphology. Plants forming tufts of 4–8 fronds. Runners densely branching at \pm right angles, forming ‘bushes’ around the base of the plants, 1–3 mm thick (distinctly tapering to thinner ends). Scales on runners dense (especially at the base), spreading to squarrose. Tubers absent. *Fronde*s 150 cm long or more to 15 cm wide, stipe 15–18 cm long. Lamina base strongly reduced, tapering over 50 cm or more, basal pinnae 0.6–1 cm long, 3–3.5 cm distant, middle pinnae straight or slightly falcate. Sterile pinnae 6–8 by 1.5–1.9 cm, base slightly to strongly unequal, basiscopic base truncate, rounded or cordate, acroscopic base truncate, not auricled, margin in basal part entire, apex acute. Fertile pinnae 6–7 by 0.8–1.1 cm, different from sterile pinnae somewhat auricled as acroscopic base. *Indument.* Basal scales basifix or pseudopeltate, squarrose to reflexed, often inserted on a short spine, 3.5 by 0.5 mm, central part light brown, dull, hyaline margin absent, marginal glands present around the scale, margin in basal part ciliate, acumen dentate (teeth often unicellular), apex uniseriate, often somewhat zigzag. Rhachis scales dense, often caducous, with a well-developed protracted acumen, spreading, hyaline or light brown, acumen ciliate, without a distinct central lamina, forming a floccose cover. Scales on lamina usually persistent, forming a tomentum similar to that on rhachis. Hairs on lamina absent, costa absent. *Sori* marginal, linear (sometimes interrupted), not impressed. Indusium linear, attached at broad base. — **Fig. 1a; Plate 2a.**

Distribution — Africa (Madagascar to Ivory Coast) to Indochina (Burma, Thailand); in *Malesia*: Throughout; Australia and the Pacific (Solomon Isl., Marshall Isl., Samoa, Guam, Caroline Isl.: Ponape).

Habitat & Ecology — At low elevations (sea level up to 200 m). Usually epiphytic, often in coastal vegetation (on mangroves), also on oil palms, coconut trees, and on cliff faces.

Note — The runners in this species are strongly branched around the erect rhizomes, with branches at angles of 60–90° forming a dense bush around the rhizome. Otherwise, the marginal, elongated sori and the tomentose indument make this an easy species to recognize.

3. *Nephrolepis biserrata* (Sw.) Schott

Nephrolepis biserrata (Sw.) Schott, Gen. Fil. 1 (1834) ad. pl. 3; Brack., U.S. Expl. Exped. 16. Filic. (1854) 213; Merr., Sp. Blancoan. (1918) 43; Backer & Posth., Varenfl. Jav. (1939) 92; Copel., Fern Fl. Philipp. 1 (1958) 187; Holtum, Revis. Fl. Malaya 2, 2nd ed. (1968) 380; Hovenkamp &

- Miyam., *Blumea* 50 (2005) 290. — *Aspidium biserratum* (Sw.) Sw. in Schrad., *J. Bot.* 1800 (1801) 32; *Syn. Fil.* (1806) 46. — *Hypopeltis biserrata* (Sw.) Bory in Bél., *Voy. Indes Or.* (1833) 65. — *Lepidonevron biserratum* (Sw.) Fée, *Gen. Fil.* (1852) 301. — *Nephrodium biserratum* (Sw.) Desv., *Prodr. Fam. Foug.* (1827) 253; C.Presl, *Reliq. Haenk.* (1830) 31. — Type: *Groendal s.n.* (S, n.v.), Mauritius.
- Tectaria fraxinea* Cav., *Descr. Pl.* (1801) 250. — Type: *Nee s.n.* (BM, fragm., MA), Philippines.
- Aspidium acutum* Schkuhr, 24. *Kl. Linn. Pfl.-Syst.* (1804) 32, t. 31; Sw., *Syn. Fil.* (1806) 46. — *Nephrodium acutum* (Schkuhr) C.Presl, *Reliq. Haenk.* (1830) 31. — *Hypopeltis palmoides* (Schkuhr) Bory in Bél., *Voy. Indes Or.* (1833) 50, nom. superfl. — *Nephrolepis acuta* (Schkuhr) C.Presl, *Tent. Pterid.* (1836) 79; Baker, *Syn. Fil.* (1867) 301. — Type: Schkuhr (1804) 32, t. 31.
- Aspidium ensifolium* Schkuhr, 24. *Kl. Linn. Pfl.-Syst.* (1804) 32, t. 32; Sw., *Syn. Fil.* (1806) 46; Blume, *Enum. Pl. Javae* (1828) add. et emend. — *Nephrolepis ensifolia* (Schkuhr) C.Presl, *Tent. Pterid.* (1836) 79. — Type: Schkuhr (1804) 32, t. 32.
- Aspidium splendens* Willd., *Sp. Pl.* 5 (1810) 220; Blume, *Enum. Pl. Javae* (1828) 147. — *Nephrolepis splendens* (Willd.) C.Presl, *Tent. Pterid.* (1836) 79; Brack., *U.S. Expl. Exped.* 16. *Filic.* (1854) 212; J.Sm., *Hist. Fil.* (1875) 227. — Type: *D. Klein* (Willdenow herb. 19740, B), Ceylon.
- Aspidium gibbosum* Willd., *Sp. Pl.* 5 (1810) 222. — *Nephrodium gibbosum* (Willd.) Gaudich. in Freyc., *Voy. Uranie, Bot.* (1828) 338. — *Nephrolepis gibbosa* (Willd.) C.Presl, *Tent. Pterid.* (1836) 79. — Type: *Nee ? s.n.* (Willdenow herb. 19743, B).
- Nephrodium rufescens* Schrad., *Ill. Fil.* (1824) 896. — *Aspidium rufescens* (Schrad.) Kunze in Mart. *Fl. Bras.* 1, *Beibl.* (1839) 34. — *Lepidonevron rufescens* (Schrad.) Fée, *Gen. Fil.* (1852) 301. — *Nephrolepis rufescens* (Schrad.) Wawra, *Bot. Ergebn.* (1866) 200, t. 201. — Type: *Anon. s.n.* (herb. Mart., BR), locality unknown.
- Nephrodium timoriense* Desv., *Prodr. Fam. Foug.* (1827) 253. — Type: *Anon. s.n.* (P).
- Polypodium palmoides* Bory in Bél., *Voy. Indes Or.* (1833) 50. — Type: *Bélanger s.n.* (P), Java.
- Hypopeltis amygdalina* Bory in Bél., *Voy. Indes Or.* (1833) 64. — Type: *Bélanger s.n.* (P), Java.
- Nephrolepis depauperata* de Vriese, *Ned. Kruidk. Arch.* 1 (1846) 9. — Type: *Reinwardt 1680* (L), Java.
- Nephrolepis zollingeriana* de Vriese, *Ned. Kruidk. Arch.* 1 (1846) 10. — Type: *Zollinger 146* (L).
- Nephrolepis macrophylla* C.Presl, *Epimel. Bot.* (1851) 43. — Type: *Cuming 22* (holo PRC; iso BM), Philippines.
- Nephrolepis acuta* (Schkuhr) C.Presl var. *laurifolia* H.Christ, *Bot. Jahrb. Syst.* 23 (1897) 355. — *Nephrolepis laurifolia* (H.Christ) Proctor, *Mem. New York Bot. Gard.* 53 (1989) 262. — Lectotype (Proctor (1989) 262): *Reinecke 1-d* (B? n.v.; iso L).
- Nephrolepis persicifolia* H.Christ, *Nova Guinea, Bot.* 8 (1909) 159. — Type: *Versteeg 1017* (holo P; iso BO, K, L), New Guinea.
- Nephrolepis pilosula* Alderw., *Bull. Jard. Bot. Buitenzorg II*, 8 (1913) 18. — Type: *Amdjah 542* (BO).
- Pteris signata* Merr., *Sp. Blancoan.* (1918) 43. — Type: Unknown.
- Nephrolepis dayakorum* Bonap., *Notes Pteridol.* (1918) 399. — Type: *Native collector? 70* (holo P; iso BM, fragm.), Borneo.

Habit, rhizome morphology. Plants forming tufts of 3–5 fronds. Runners 1–2.5 mm thick, branching angle divaricate. Scales on runners very sparse to dense, spreading or squarrose. Tubers absent. *Fronde*s 120–160 by 19–25 cm, stipe 29–42 cm long. Lamina base truncate, tapering over 40–50 cm, basal pinnae 3.5–4 cm long, 4.5–5 cm distant, middle pinnae straight or slightly falcate (or somewhat recurved). Sterile pinnae 8–11 by 1.5–2 cm, herbaceous, thick or leathery, base equal or slightly unequal, basiscopic base cuneate, truncate or rounded, acroscopic base cuneate or truncate, slightly to distinctly auricled, margin in basal part crenate, towards apex serrate or dentate, apex obtuse, acute or acuminate. Fertile pinnae 9–15 by 0.9–1.3 cm, more strongly serrate than the sterile pinnae. *Indument.* Basal scales pseudopeltate, spreading (often somewhat falcately curved), 5 by 0.8 mm, central part light brown, shining, hyaline margin

present in lower part only, marginal glands present around the base, small, margin in basal part fimbriate, acumen dentate, apex entire. Rhachis scales sparse or dense, spreading, hyaline or light brown, with a well-developed protracted entire acumen. Scales on lamina usually persistent. Hairs on lamina absent or sometimes present, costa sometimes present. *Sori* submarginal or medial, 50 pairs on fully fertile pinnae, round, not impressed. Indusium reniform, with narrow sinus, attached at sinus. — **Fig. 1g; Plate 1b.**

Distribution — Pantropical; in *Malesia*: Throughout.

Habitat & Ecology — Usually in lowlands (sea level up to 750 m, rarely higher, to 1500 m), in open, disturbed situations, occasionally in forest; epiphytic or terrestrial. In Kalimantan covering large tracts of recently burned forest.

Cultivation — Plants with repeatedly furcate pinnae have been collected on Celebes and Java, both possibly from cultivation, and most likely belonging to this species. A similarly furcate form was described by Moore (Gard. Chron. 1873: 13) as *N. davalloides* var. *furcans*. Furcate forms of *N. biserrata* are quite regularly fertile, which may serve to distinguish them from similar forms of *N. exaltata*. A form with irregularly cristate/furcate pinnae was once collected on Sarawak.

Notes — 1. *Nephrolepis biserrata* is very variable in frond size, shape of pinna-base, width of pinnae, hairiness, and to a lesser degree position of the sori. In Malesia, pubescent forms occur mainly on Borneo, where they seem to be increasing as a result of recent forest fires – the burnt areas are quickly covered with a dense mat of sterile specimens of this form – and on New Guinea.

2. Here we follow the traditional, wide circumscription of *N. biserrata*, which includes all *Nephrolepis*-forms with clearly inframarginal to medial sori with narrow sinus. Other rather constant characters are the basal stipe scales, which are uniformly narrow, concolorous and spread out sideways in one direction and the generally fairly large size of the plants. However, it is possible that in this circumscription a number of cryptic species are included. Herbarium studies may not be able to resolve these species partly for the usual reasons: lack of complete, well-documented specimens.

4. *Nephrolepis brownii* (Desv.) Hovenkamp & Miyam.

Nephrolepis brownii (Desv.) Hovenkamp & Miyam., *Blumea* 50 (2005) 293. — *Nephrodium brownii*

Desv., *Mém Soc. Linn. Paris* 6 (1827) 252. — Type: *R. Brown* 20 (holo BM; iso K), Australia.

Nephrodium regulare Desv., *Mém Soc. Linn. Paris* 6 (1827) 252. — Type: *Anon. s.n.* (P), Timor.

Aspidium floccigerum Blume, *Enum. Pl. Javae* (1828) 147. — *Nephrolepis floccigera* (Blume) T.Moore, *Index Fil.* (1857) 92; Baker, *Syn. Fil.* (1867) 302; Backer & Posth., *Varenfl. Jav.* (1939) 93. — Type: *Anon. s.n.* (L? not found), Moluccas.

Aspidium schkuhrii Blume, *Enum. Pl. Javae* (1828) 147. — Type: *Kuhl & Van Hasselt s.n.* (L), Java.

Davallia multiflora Roxb., *Calcutta J. Nat. Hist.* 4 (1844) 515, pl. 31. — *Nephrolepis multiflora* (Roxb.)

C.V.Morton, *Amer. Fern J.* 48 (1958) 309; Proctor, *Mem. New York Bot. Gard.* 53 (1989) 265. — Type: *Roxburgh s.n.* (BR), India.

Nephrolepis tomentosa Alderw., *Bull. Jard. Bot. Buitenzorg* II, 1 (1911) 11. — Type: *Koorders 24101b* (holo BO; iso L), Java.

Nephrolepis pubescens Copel., *Philipp. J. Sci.* 81 (1952) 12; *Fern Fl. Philipp.* 1 (1958) 187. — Type: *BS 11539* (MICH), Philippines.

Habit, rhizome morphology. Plants forming tufts of 5 or 6 fronds. Runners often forming stilts supporting the upright rhizome, 1.5–2.5 mm thick, branching angle divaricate. Scales on runners sparse, appressed or spreading. Tubers absent. *Fronde* 70–130 by 10–12 cm, stipe 14–37 cm long. Lamina base more or less strongly reduced, tapering over 25–35 cm, basal pinnae 1.5–2 cm long, 2–5 cm distant, middle pinnae straight or slightly falcate. Sterile pinnae 6 by 1.4 cm, base slightly to strongly unequal, basiscopic base rounded or cordate, acroscopic base truncate, strongly auricled (usually with a narrow auricle), margin in basal part entire or crenate, apex acute. Fertile pinnae 5.5–7 by 0.9 cm, with more distinctly serrate margin than the sterile pinnae. *Indument.* Basal scales peltate, appressed, 3.5 by 1.3 mm, central part dark brown or blackish, shining, hyaline margin wide, distinct, marginal glands absent, margin in basal part ciliate, acumen ciliate. Rhachis scales dense, spreading, hyaline or light brown, with a well-developed protracted entire or ciliate acumen (ciliate in the lower part). Scales on lamina usually persistent, often also persistent on upper surface. Hairs on lamina absent, on costa constantly present. *Sori* marginal or submarginal (rarely), 25–27 pairs on fully fertile pinnae, round. Indusium reniform, with narrow sinus, attached at sinus. — **Fig. 1f; Plate 1a.**

Distribution — Widespread in Tropical Asia. India, Sri Lanka, China (south only: Guangdong, Hainan, Hong Kong), Taiwan, Japan: Ryukyu Isl., Bonin Isl.; Indochina; in *Malesia*: Peninsular Malaysia, Java, Lesser Sunda Islands, Borneo, Philippines, Celebes, Moluccas?, New Guinea; New Caledonia, Australia: Queensland; New Zealand: Kermadec Isl.; Pacific: Fiji, Pitcairn; Rapa; Society Isl.; Cook Isl.; Tonga. Introduced in Tropical America and the Hawaiian Islands.

Judging by the distribution of early collections, almost certainly native in Malesia, but dubiously elsewhere. It is certainly introduced in America, where it is spreading as a weed and classified as an invasive species in Florida (<http://www.fleppc.org/Plantlist/03list.htm>).

Habitat & Ecology — Common at low to middle elevations (sea level to 1700 m), usually terrestrial, also epiphytic, both in forests and open vegetation (roadsides, riverbanks, open thickets), often weedy.

Note — This species has often been confused with *N. hirsutula*. Characters to distinguish these two species are discussed under *N. hirsutula*. Similar scales and costal indument is found in *N. acuminata*, which is, however, easily distinguished by the rhachis indument including at least some scales with a dark acicular apex.

5. *Nephrolepis cordifolia* (L.) C.Presl

Nephrolepis cordifolia (L.) C.Presl, Tent. Pterid. (1836) 79; Baker, Syn. Fil. (1867) 300; Backer & Posth., Varenfl. Jav. (1939) 91; Copel., Fern. Fl. Philipp. 1 (1958) 186; Holtum, Revis. Fl. Malaya 2, 2nd ed. (1968) 379; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 172; Hovenkamp & Miyam., Blumea 50 (2005) 294. — *Polypodium cordifolium* L., Sp. Pl. (1753) 1089. — *Aspidium cordifolium* (L.) Sw., J. Bot. (Schrader) 1800 (1801) 32; Syn. Fil. (1806) 45. — Lectotype (Verdcourt 1996): *Ekman H11627* (K), Hispaniola.

Polypodium auriculatum L., Syst. Nat. (1759) 1326, nom. rej. — *Nephrolepis auriculata* (L.) Trimen, J. Linn. Soc., Bot. 24 (1888) 152; Verdc., Taxon 45 (1996) 540. — Lectotype (Verdcourt 1996): *Herb. Hermann s.n.* (BM), Ceylon.

Aspidium tuberosum Bory in Willd., Sp. Pl. 5 (1810) 234. — *Nephrodium tuberosum* (Bory) Desv., Mém Soc. Linn. Paris 6 (1827) 252. — *Nephrolepis tuberosa* (Bory) C.Presl, Tent. Pterid. (1836) 79. — Type: *Anon. s.n.* (B-Willd., L, P), Réunion.
Nephrolepis rhizodes Kunze, Bot. Zeitung (Berlin) 6 (1848) 236. — Type: *Zollinger 2526* (L).

a. var. *cordifolia*

Habit, rhizome morphology. Plants forming tufts of 3–7 fronds. Runners 0.5–1.5 mm thick, branching angle divaricate. Scales on runners very sparse to dense, spreading or squarrose (occasionally). Tubers present or absent. *Fronde*s to 40–120 by 2–6 cm, stipe 4–15 cm long. Lamina base strongly reduced, tapering over 10–25 cm, basal pinnae 4–10 cm long, 0.7–1.7 cm distant, middle pinnae slightly to distinctly falcate. Sterile pinnae 1–3.3 by 3–9 mm, herbaceous, thick, base slightly to strongly unequal, basiscopic base rounded or cordate, acroscopic base cordate, distinctly to strongly auricled, margin in basal part dentate, towards apex deeply dentate, apex rounded or obtuse. Fertile pinnae 1.6–3.2 by 0.4–0.8 cm, otherwise similar to sterile ones. *Indument.* Basal scales pseudopeltate, spreading, 8 by 1 mm, central part light brown, dull, margin in basal part irregularly lacerate, not hyaline, towards apex denticulate, without marginal glands, apex narrow, not long uniseriate. Rhachis scales sparse or dense, spreading, light brown, with lacerate base and a well-developed protracted entire acumen. Scales on lamina absent. Hairs on lamina absent or sometimes present, costa absent. *Sori* medial, 6–15 pairs on fully fertile pinnae, elongated, not impressed. Indusium lunulate or broad, attached at broad base. — **Fig. 1j; Plate 2d.**

Distribution — Pantropical. In *Malesia*: Throughout.

Habitat & Ecology — In *Malesia* mostly at middle elevations (800–2000 m), occasionally higher (collections from lower elevations are probably from cultivated plants), often in submontane or ridge forest, mostly terrestrial (often on rotting logs), rarely epiphytic; rarely in fully open situations. Outside *Malesia* in subtropical areas often growing at lower elevation.

Cultivation — Often cultivated and possibly as garden escape in some localities, but not thriving when cultivated in lowland tropical gardens.

Note — Scaly tubers are produced mainly on underground runners – the aerial parts appear to form tubers more sporadically. In cultivation, the tubers can be observed to shrivel and disappear when plants are kept dry – in nature the presence may be similarly dependent on periods of moist conditions. For these reasons, it is impossible to use herbarium collections to assess the frequency with which tubers are formed. Their presence seems to be uncorrelated to other characters, but more observations are needed.

6. *Nephrolepis davalliae* Alderw.

Nephrolepis davalliae Alderw., Bull. Dép. Agric. Indes Néerl. 21 (1908) 2; Hovenkamp & Miyam., Blumea 50 (2005) 297. — Type: *Versteeg 1675* (holo BO; iso L), New Guinea.
Nephrolepis schlechteri Brause, Bot. Jahrb. Syst. 49 (1913) 24. — Type: *Schlechter 19639* (BM, K, L, P), New Guinea.

Habit, rhizome morphology. Plants forming tufts of 3–8 fronds. Runners 1–1.5 mm thick (polished), unbranched. Scales on runners sparse, spreading or squarrose. Tubers

absent. *Fronde*s 50–115 cm long (or more), 4–8 cm wide, stipe 8–15 cm long. Lamina base reduced, tapering over 20–25 cm, basal pinnae 1.2–2.7 cm long, 1.2–1.5 cm distant, middle pinnae straight or slightly falcate. Sterile pinnae 2–4.3 by 0.4–0.7 cm, leathery, base equal or slightly unequal, basiscopic base truncate or rounded, acroscopic base cuneate or truncate, not to slightly auricled, margin in basal part crenate, towards apex serrate, apex acute. Fertile pinnae 1.8–4.7 by 0.3–0.6 cm, with a more longly drawn out apex than the sterile pinnae. *Indument*. Basal scales pseudopeltate, appressed or spreading, 3.5 by 0.3–0.7 mm, central part rufous, dull, margin not hyaline, in basal part irregularly lacerate (protrusions most unicellular), in acumen entire or dentate (remotely, with 2-celled teeth), marginal glands present around the scale. Rhachis scales with a well-developed protracted acumen, appressed or spreading (sometimes recurved), dark, acumen entire or dentate. Scales on lamina usually persistent (more so on the upper surface), small, more or less stellate/lacerate. *Sori* marginal on teeth, 7–14 pairs on fully fertile pinnae, round or elongated, protruding on adaxial surface. Indusium broad, attached at base and sides. — **Fig. 1i.**

Distribution — *Malesia*: Moluccas, New Guinea, New Britain.

Habitat & Ecology — Montane or ridge forest, 500–2150 m, rarely lower, epiphytic or terrestrial, often forming large stands covering open places.

Note — Easily recognized by the leathery texture of the lamina, with indistinct veins, and the marginal sori, each opening to the anterior side of a separate tooth, covered with a cup-shaped indusium.

7. *Nephrolepis davallioides* (Sw.) Kunze

Nephrolepis davallioides (Sw.) Kunze, Bot. Zeitung (Berlin) 4 (1846) 460; Baker, Syn. Fil. (1867) 302; Holttum, Revis. Fl. Malaya 2 (1954) 634; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 172; Hovenkamp & Miyam., Blumea 50 (2005) 298. — *Ophioglossum acuminatum* Houtt., Nat. Hist. (1783) 49. — *Aspidium davallioides* Sw., J. Bot. (Schrader) 1800 (1801) 33; Blume, Enum. Pl. Javae (1828) 148. — *Nephrodium davallioides* (Sw.) Desv., Mém Soc. Linn. Paris 6 (1827) 254. — *Nephrolepis acuminata* (Houtt.) Kuhn, Ann. Mus. Bot. Lugduno-Batavi 4 (1869) 286; Backer & Posth., Varenfl. Jav. (1939) 93; Holttum, Revis. Fl. Malaya 2, 2nd ed. (1968) 378, nom. illeg. non C.Presl 1836. — Type: Plate in Houttuyn.

Nephrodium deparioides Bory in Bél., Voy. Indes Or. (1833) 59. — Type: *Belanger s.n.* (P), Java.

Nephrolepis pendula de Vriese, Ned. Kruiddk. Arch. 1 (1846) 8, nom. illeg. non J.Sm. 1842a. — Type: *Reinwardt 1564* (L), Celebes.

Nephrolepis serrata Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 34. — Type: *Kornassi 626* (BO), Ceram.

Habit, rhizome morphology. Plants forming tufts of 4 or 5 fronds. Runners 1–2 mm thick, branching angle narrow. Scales on runners very sparse to dense, appressed. Tubers absent. *Fronde*s 110–210 cm long (or more), 26–38 cm wide, stipe 23–45 cm long. Lamina base truncate, tapering over 25–30 cm, basal pinnae 4–12 cm long, 3.5–12 cm distant, middle pinnae slightly to distinctly falcate. Sterile pinnae 14–18 by 1.7–2.4 cm, base slightly unequal, basiscopic base cuneate, truncate or rounded, acroscopic base emarginate or slightly cuneate, not auricled, margin in basal part crenate to serrate, towards apex more distinctly serrate, apex acuminate or caudate with cauda to 3 cm long. Fertile pinnae 14–28 by 1.1–1.4 cm, base often more narrowly cuneate and

margin more deeply incised (to 2–3.5 mm) than the sterile pinnae. *Indument*. Basal scales peltate, appressed, 3 by 1 mm, central part dark brown, shining, margin in basal part hyaline, fimbriate, in acumen fimbriate, near apex entire, marginal glands present around the base. Rhachis scales dense, with a well-developed protracted acumen, spreading or squarrose, hyaline, acumen ciliate (acumen of larger scales composed of a long, sclerified subular protrusion). Scales on lamina usually persistent, sparse, present on lower surface only. Hairs on lamina absent, costa absent. *Sori* marginal (on teeth), 28–50 pairs on fully fertile pinnae, round, not impressed. Indusium reniform, with narrow sinus, attached at sinus. — **Fig. 1c; Plate 2b.**

Distribution — *Malesia*: Sumatra, Peninsular Thailand, Peninsular Malaysia, Java, Borneo, Celebes, New Guinea.

Habitat & Ecology — Common in forests at middle elevations (800–1600 m), rarely lower (200 m) or higher (up to 2100 m). Usually in forest, terrestrial, often on roadside or stream banks; more often epiphytic, often on trunks.

Note — Typical specimens have deeply dissected fertile pinnae, with sori nearly marginal, on separate teeth, and the lamina between the sori cut to c. 1/2. However, many specimens (especially from the eastern part of the range) have less deeply divided pinnae, and such specimens can easily be confused with other species. They can best be distinguished by the rhachis indument, which consists of scales with a narrow, dark acumen, sometimes needle-like, often directed sideways towards the upper surface. Hairs are sometimes present on the upper surface of the costae, usually near the base only.

8. *Nephrolepis dicksonioides* H.Christ

Nephrolepis dicksonioides H.Christ, Verh. Naturf. Ges. Basel 11 (1895) 241; Holtum, Revis. Fl. Malaya 2, 2nd ed. (1968) 376; Hovenkamp & Miyam., Blumea 50 (2005) 300. — *Dicksonia nephrolepioides* H.Christ, Verh. Naturf. Ges. Basel 11 (1895) 241. — Type: *Sarasin 1030* (P, n.v.), Celebes. *Nephrolepis rosenstockii* Brause, Bot. Jahrb. Syst. 49 (1913) 25. — Type: *Schlechter 16494* (K, L, P), New Guinea.

Habit, rhizome morphology. Plants forming tufts of 2 or 3 fronds. Runners 1.5–2 mm thick, branching angle divaricate. Scales on runners dense, spreading. Tubers absent. *Fronde*s 200 cm long (or more), 16–18 cm wide, stipe 33–35 cm long. Lamina base strongly reduced, tapering over 30 cm, basal pinnae 1.2–2.5 cm long, 4–6 cm distant, middle pinnae slightly to distinctly falcate. Sterile pinnae 9.5–11 by 1.6–2 cm, leathery, base strongly unequal, basispic base rounded or cordate, acroscopic base cuneate or truncate, not auricled, margin in basal part entire, towards apex crenate or serrate, apex acuminate or to 1.5–2.5 cm caudate. Fertile pinnae 10–15 by 0.6–1.2 cm, different from sterile pinnae in the margin deeply incised between the sori, especially towards pinna-apex, and the apex more gradually narrowed to a 2.5–4 cm long cauda. *Indument*. Basal scales pseudopeltate, spreading, 5 by 2–2.5 mm, central part rufous, shining, marginal glands absent, margin not hyaline, in basal part ciliate or fimbriate, in acumen ciliate or fimbriate. Rhachis scales dense, with a well-developed protracted acumen, appressed (inconspicuous), hyaline or light brown, acumen ciliate. Scales on lamina absent. Hairs on lamina and costa absent. *Sori* marginal (or nearly marginal),

often on dilated teeth, especially towards the pinna-apex, 20–32 pairs on fully fertile pinnae, elongated (sometimes confluent near the base of the pinna), not impressed. Indusium broad, attached at broad base. — **Fig. 1b.**

Distribution — *Malesia*: Celebes, Moluccas, New Guinea; Solomon Islands.

Habitat & Ecology — Terrestrial, on rocks, or epiphytic. Disturbed places in lower montane forest, in ridge forest or disturbed secondary forest, 400–1900 m.

Note — *Nephrolepis dicksonioides* has been confused with *N. abrupta* and *N. acuminata*. It has fertile pinnae similarly incised as typical specimens of *N. acuminata*, and marginal sori similar to those of *N. abrupta*, but differs from both in the indusium having a broad base, innervated by 2 or 3 veins. The apex of the sorus-bearing tooth is often dilated. From *N. abrupta* it can also be distinguished by the shape of the pinnae: the fertile ones are more constantly deeply divided, the sterile ones more distinctly acuminate, narrowing to a distinct cauda from c. halfway.

9. *Nephrolepis falcata* (Cav.) C.Chr.

Nephrolepis falcata (Cav.) C.Chr., Dansk Bot. Ark. 9 (1936) 15, pl. 1, f. 5–9; Copel., Fern Fl. Philipp. 1 (1958) 188; Hovenkamp & Miyam., Blumea 50 (2005) 302. — *Tectaria falcata* Cav., Descr. Pl. (1801) 250. — Type: *Née s.n.* (holo MA, n.v.; iso BM), Philippines.

Nephrolepis barbata Copel., Fragm. Fl. Philipp. 3 (1905) 178. — Type: *Copeland 1286* (MICH), Philippines.

Habit, rhizome morphology. Runners 1–1.5 mm thick, branching angle narrow. Scales on runners very sparse or sparse, appressed. Tubers absent. *Fronds* 65–200 cm long (or more), 7–10 cm wide, stipe 10–34 cm long. Lamina base strongly reduced, tapering over 20–35 cm, basal pinnae 0.7–1 cm long, 1.5–3.5 cm distant, middle pinnae distinctly to strongly falcate. Sterile pinnae 4–8 by 1–1.4 cm, herbaceous, thick, base strongly unequal, basiscopic base rounded, acroscopic base truncate, slightly to distinctly auricled, margin in basal part crenate, dentate or serrate, apex acute to (indistinctly) 1 cm caudate. Fertile pinnae 4.8–8 by 0.7–1.2 cm, otherwise similar to sterile ones. *Indument.* Basal scales peltate, appressed, 2 by 0.5–1 mm, central part blackish, shining, hyaline margin narrow, marginal glands absent, margin in basal part irregularly lacerate or ciliate, acumen ciliate. Rhachis scales dense, with a well-developed protracted acumen, squarrose to recurved, dark, with entire acumen. Scales on lamina usually persistent, with a long, narrow, entire, acicular acumen. Hairs on lamina and costa absent. *Sori* submarginal, 19–29 pairs on fully fertile pinnae, round, not impressed. Indusium reniform, with narrow sinus, attached at sinus. — **Plate 2h.**

Distribution — *Malesia*: Philippines: Luzon, Samar, Negoro, Mindanao.

Habitat & Ecology — Few data. Reported from lowlands to high elevations, 300–2500 m, in forest and in severely disturbed areas, epiphytic or terrestrial.

Note — Similar in pinna shape and position of the sori to *N. falciformis*, but differs in the very dark, dense, squarrose rhachis scales; the denser and more persistent lamina scales, and the absence of hairs on the costae. Juvenile specimens of *N. davallioides* may have a similar rhachis indument and may then be impossible to distinguish from sterile fronds of *N. falcata*.

10. *Nephrolepis falciformis* J.Sm.

Nephrolepis falciformis J.Sm., Ferns Brit. For. (1866) 287; Hovenkamp & Miyam., Blumea 50 (2005) 303. — Type: *Anon. s.n.* (BM), Borneo.

Nephrolepis thomsonii Alderw., Bull. Jard. Bot. Buitenzorg II, 24 (1917) 2. — Type: *Thomson 690* (holo BO; iso L), New Guinea.

Nephrolepis cordifolia (L.) C.Presl var. *calcareo* H.Christ, Nova Guinea, Bot. 8 (1909) 158. — Type: *Versteeg 1614 (1603?)* (BO, K), New Guinea.

Nephrolepis falcata auct. non (Cav.) C.Chr.: Holttum, Revis. Fl. Malaya 2, 2nd ed. (1968) 381; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 176.

Habit, rhizome morphology. Plants forming tufts of 2–4 fronds. Runners 1–2 mm thick, frequently branched, branching divaricate. Scales on runners sparse, appressed. Tubers absent. *Fronde* 150–200 cm long (or more), 9–14 cm wide, stipe 16–45 cm long. Lamina base reduced, tapering over 20–50 cm, basal pinnae 1.5–2.5 cm long, 4.5–5 cm distant, middle pinnae usually strongly falcate (basal and apical pinnae usually far less so). Sterile pinnae 5–6 by 1.1–1.8 cm, herbaceous, thick (often conspicuously pale green when dry), base strongly unequal, basiscopic base rounded, acroscopic base truncate, slightly to distinctly auricled, margin in basal part entire or crenate, apex acute or acuminate. Fertile pinnae 5.3–8 by 1–1.3 cm, with a more distinctly dentate margin than from sterile pinnae. *Indument.* Basal scales peltate, appressed, 3.5 by 1 mm, central part dark brown, dull, hyaline margin wide, distinct, ciliate throughout, marginal glands absent. Rhachis scales sparse, without a distinctly protracted acumen, appressed, dark, conspicuous especially when dry. Scales on lamina sometimes present, very small, inconspicuous. Hairs on lamina absent, on costa sometimes present, few (usually forming a small group of scattered hairs near the base). *Sori* submarginal, 21 or 22 pairs on fully fertile pinnae, round, slightly impressed. Indusium reniform, with narrow sinus, attached at sinus. — **Plate 2g.**

Distribution — Sri Lanka, Indochina; in *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Celebes, Moluccas, New Guinea.

Habitat & Ecology — At low to middle elevation, sea level to 800 m, rarely higher, in forests, often in shade, also in open places, terrestrial or epiphytic.

Cultivation — Despite the fact that it appears to be more restricted to forest than many of the other species of *Nephrolepis*, many of the *Nephrolepis* plants that are planted as garden or roadside plants in lowland areas in Indonesia appear to belong to this species. Collections from the Botanic Garden in Bogor go back to the early part of the 20th century, these plants may well be the source of the cultivated plants.

Notes — 1. A fairly distinct species, most easily recognizable by the strongly falcate median pinnae and the strikingly light colour (fresh plants are bright green, dry specimens often, but not always, a pale yellowish brown). The degree to which the pinnae are falcate strongly varies within a single frond, with the median fertile pinnae often very pronouncedly falcate, with the apex frequently curved back somewhat towards the midrib, but the more basal and apical pinnae usually only slightly or not at all falcate. The sori are mostly nearly marginal, some hairs are usually present on the upper surface of the costae especially near the points of attachment, often forming a rather characteristic sparse tuft. The scales on rhachis are small and sparse, but rather conspicuous due to the dark colour.

2. A distinct form occurs on New Guinea, which differs from the typical form in a number of aspects: fronds long, slender, often stated to be pendent, often many in a tuft, strongly narrowed at base to strongly reduced (semicircular) basal pinnae, middle pinna relatively small and not strongly falcate; rhachis and fronds nearly glabrous, scales where present small. Typical plants of this form are at first sight similar to *N. cordifolia*, and have been distinguished as *N. thomsonii* and *N. cordifolia* var. *calcareo*. However, as all the characters that distinguish this form from typical *N. falciformis* show a very gradual transition between the two extreme states, we prefer to deal with it informally under this species.

11. *Nephrolepis hirsutula* (G.Forst.) C.Presl

Nephrolepis hirsutula (G.Forst.) C.Presl, Tent. Pterid. (1836) 79; Brack., U.S. Expl. Exped. 16. Filic. (1854) 211; Backer & Posth., Varenfl. Jav. (1939) 92; Copel., Fern Fl. Philipp. (1958) 188; Holtum, Revis. Fl. Malaya 2, 2nd ed. (1968) 382; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 177; Hovenkamp & Miyam., Blumea 50 (2005) 304. — *Polypodium hirsutulum* G.Forst., Fl. Ins. Austr. (1786) 81; Nicolson & Fosberg, The Forsters and the Botany of the Second Cook Expedition (2003) 136. — *Aspidium hirsutulum* (G.Forst.) Sw., J. Bot. (Schrader) 1800 (1801) 32; Syn. Fil. (1806) 45, 241; Blume, Enum. Fl. Javae (1828) 146. — *Polystichum hirsutulum* (G.Forst.) Bernh., J. Bot. (Schrader) 1801 (1803) 16. — *Lepidonevron hirsutulum* (G.Forst.) Fée, Mém. Foug., 5. Gen. Fil. (1852) 301. — *Nephrodium hirsutulum* (G.Forst.) Desv., Mém. Soc. Linn. Paris 6 (1827) 253; C.Presl, Reliq. Haenk. (1830) 32. — Type: *Forster* 278 (BM), without locality.

Nephrolepis duffii T.Moore, Gard. Chron. n.s. 9 (1878) 622, f. 113; Backer & Posth., Varenfl. Jav. (1939) 89. — Type: *Anon. s.n.* (K), in cult. Hort. Veitch.

Aspidium pilosum Langsd. & Fisch., Pl. Voy. Russes Monde (1810) 14, t. 16. — *Nephrolepis pilosa* (Langsd. & Fisch.) C.Presl, Tent. Pterid. (1836) 79. — Type: *Langsdorff s.n.* (BM).

Nephrodium multifidum A.Rich., Voy. Astrolabe 2 (1834) xxxix. — *Nephrolepis multifida* (A.Rich.) Mett., Fil. Hort. Bot. Lips. (1856) 100. — Type: *Lesson (Astrolabe) s.n.* (P).

Habit, rhizome morphology. Plants forming tufts of 4–8 fronds (or more). Runners often forming stilts supporting the erect rhizome, 1–2 mm thick, branching angle narrow. Scales on runners sparse or dense, appressed or spreading. Tubers absent. *Fronds* 90–210 by 15–20 cm, stipe 32–80 cm long. Lamina base reduced, tapering over 15–30 cm (or more), basal pinnae 3.5–8 cm long, 2–5 cm distant, middle pinnae straight (sometimes recurved). Sterile pinnae 8–10 by 1.2–1.6 cm, herbaceous, thick, base strongly unequal, basiscopic base truncate or rounded, acroscopic base truncate, strongly auricled (with narrow auricle), margin in basal part entire, towards apex crenate, apex acute. Fertile pinnae 7.5–11 by 0.9–1.1 cm, more strongly crenate than the sterile pinnae. *Indument.* Basal scales peltate, appressed, 1.5–23.5 by 1 mm, central part dark brown or blackish, shining, hyaline margin wide, ciliate, marginal glands, absent apex obtuse. Rhachis scales very dense, with a well-developed protracted acumen, spreading or squarrose, rufous, acumen strongly dentate. Scales on lamina usually persistent. Hairs absent from lamina and costae. *Sori* submarginal to nearly medial, 24–33 pairs on fully fertile pinnae, round, not impressed. Indusium reniform, with open sinus, attached at sinus. — **Fig. 1h; Plate 2f.**

Distribution — Indochina; in *Malesia*: Throughout; Australia: Queensland; Pacific islands.

Habitat & Ecology — Usually at low elevations, sea level to 500 m, rarely to 1000 m, at forest margins and other disturbed places, often in coconut plantations, apparently preferring light shade, terrestrial, only rarely reported as epiphyte.

Cultivation — Before *N. exaltata* ‘bostoniensis’ was discovered as source of cultivars, *N. hirsutula* appears to have been the species that gave rise to some of the more popular cultivated forms such as var. *tripinnatifida* and possibly also *N. duffii*, both of which may still be found in lowland tropical gardens. Many of these forms appear to originate from the Eastern part of the range of *N. hirsutula* (New Guinea, New Britain, Duke of York Island, Fiji Islands), where specimens have been collected without any indication of being cultivated there. *Nephrolepis duffii* is characterized by small, deeply furcate or paired pinnae, and often forked frond apices.

Specimens with marginally proliferous pinnae have been collected on the Philippines and on Sumatra and may have been in cultivation there.

Lacerate forms were collected from cultivated plants on Java between 1927 and 1934.

Note — *Nephrolepis hirsutula* differs from *N. brownii* (*N. multiflora* auct.), with which it has been extensively confused, in the sori placed less close to the margin, sometimes nearly medial; the dense, rufous rhachis scales with very strongly dentate acumen; and the glabrous upper surface of costae. In contrast, *N. brownii* has usually sparser, paler rhachis scales, with a longer, nearly always entire narrow apex. The combination of the rufous, dense, rhachis indument and glabrous upper surface of the costae is characteristic for *N. hirsutula*, while the position of the sori is more variable. In case of doubt, the glabrous upper costa-surface is usually decisive.

12. *Nephrolepis lauterbachii* H.Christ

Nephrolepis lauterbachii H.Christ, Rel. Weinland. (1901) 456; Hovenkamp & Miyam., Blumea 50 (2005) 305. — Type: *Lauterbach 578* (P?, n.v.), New Guinea.

Nephrolepis humatoides Alderw., Nova Guinea, Bot. 14 (1924) 33. — Type: *Lam 2047* (BO), New Guinea.

Habit, rhizome morphology. Plants forming tufts of 5 or 6 fronds. Runners often proliferous, 0.5–1 mm thick (or thinner), branching angle narrow. Scales on runners sparse, spreading. Tubers absent. *Fronde*s 25–34 by 3–4 cm, stipe 3–8 cm long. Lamina base strongly reduced, tapering over 8–10 cm, reduced basal pinnae 0.9–1.1 cm distant, middle pinnae straight. Sterile pinnae 1.4–2 by 0.3–0.5 cm, leathery, base fully 1-sided, basiscopic base narrowly cuneate, acroscopic base emarginate, cuneate or truncate, distinctly auricled, margin in basal part crenate, towards apex deeply dentate or incised, apex rounded or obtuse. Fertile pinnae 2 by 0.3–0.4 cm, more sinuose between the sori than the sterile pinnae. *Indument.* Basal scales peltate or type of attachment indistinct, spreading, 4 by 0.25 mm (or less), central part light brown, dull, margin not hyaline, in basal part irregularly lacerate, in acumen entire, without glands, apex acumen narrow, often sinuous, tapering to a long narrow apex. Rhachis scales sparse (often caducous), with a well-developed protracted acumen, spreading, dark (distinctly darker than the basal scales), acumen entire. Scales on lamina absent. Hairs on lamina absent. *Sori* submarginal or medial, elongated. Indusium lunulate, attached at broad base. — **Fig. 1k; Plate 2e.**

Distribution — *Malesia*: Moluccas, New Guinea; Solomon Islands.

Habitat & Ecology — At middle elevations, 900–2200 m, rarely at lower altitudes, from 250 m upwards, epiphytic or epilithic, in montane forest, often mossy or ridge forest.

Notes — 1. Typical *N. lauterbachii* has small pinnae (< 2 cm long), with a sinuous upper margin, at least the middle pinnae distinctly dimidiate, with the attachment at the basal corner. Often the upper pinnae are caducous, therefore plants often have long whip-like bare rhachises in older fronds. Although runners are frequently collected, bulbils are very rarely present, and then very small. Many collections have young plantlets at more or less regular intervals on main runners that are slightly thicker than the other ones.

2. *Nephrolepis lauterbachii* can best be distinguished from *N. cordifolia* by the rhachis scales, which are distinctly darker than the basal scales. In *N. cordifolia*, rhachis scales and basal scales have the same pale to light brown colour. For the distinction from the South American *N. pectinata*, see under that species.

13. *Nephrolepis obliterata* (R.Br.) J.Sm.

Nephrolepis obliterata (R.Br.) J.Sm., J. Bot. (Hooker) 4 (1842) 197; Fée, Mém. Foug., 5. Gen. Filic. (1852) 319; Hovenkamp & Miyam., Blumea 50 (2005) 306. — *Nephrodium obliteratum* R.Br., Prodr. Fl. Nov. Holland (1810) 148. — *Aspidium obliteratum* Spreng., Syst. Veg. 4 (1827) 99. — *Arthropteris obliterata* (R.Br.) J.Sm., Ferns Brit. For. (1866) 163; Hist. Fil. (1875) 225. — Type: *Banks s.n.* (BM), Australia.

?*Nephrolepis saligna* Carruth. in Seem., Fl. Vit. (1873) 361. — Type: *Seemann 743* (BM), Fiji.

Habit, rhizome morphology. Plants forming tufts of 3 or 4 fronds. Runners 1–2 mm thick, branching angle divaricate. Scales on runners very sparse or sparse, appressed or spreading. Tubers absent. *Fronds* 100–170 cm long (or more), 12–33 cm wide, stipe 36–80 cm long. Lamina base truncate, tapering over 20–40 cm, reduced basal pinnae 4–8 cm distant, middle pinnae slightly to distinctly falcate. Sterile pinnae 6–15 by 1.3–2.4 cm, herbaceous, thick, base strongly unequal, basiscopic base rounded, acroscopic base cuneate or truncate, not auricled, margin in basal part crenate, apex acuminate or caudate, cauda to 3 cm long. Fertile pinnae 7–17 by 0.9–2.1 cm, more strongly dentate between the sori and more gradually narrowed than the sterile pinnae to an acute apex without a distinct cauda. *Indument.* Basal scales peltate, appressed (rather sparse), 2.5 by 1 mm, central part dark brown, dull, hyaline margin wide, distinct, fimbriate in basal part, marginal glands absent. Transition to rhachis scales abrupt. Rhachis scales very sparse, without a distinctly protracted acumen, appressed and often very inconspicuous, hyaline. Scales on lamina absent. Hairs on lamina absent, costa absent. *Sori* marginal (often on teeth), 30–45 pairs on fully fertile pinnae, round. Indusium reniform, with narrow sinus or reniform, with open sinus, attached at sinus. — **Fig. 1e; Plate 2i.**

Distribution — East Malesia to Australia (Queensland) and the Pacific (Solomon Islands, Vanuatu, New Caledonia, Carolines). In *Malesia*: Moluccas, New Guinea, New Britain.

Habitat & Ecology — Usually at low elevations, from sea level to 150 m, occasionally to 1000 m. In various types of forests or plantations, in mangroves and swamp forest; often abundant in undergrowth, in clearings or on riverbanks and forest margins, also as low epiphyte on tree trunks or on fallen trees.

Notes — 1. The name *N. saligna* has been frequently applied to specimens of this species.

2. *Nephrolepis obliterated* is not easy to characterize. It usually has quite large pinnae, with nearly marginal sori. Characteristically, they are gradually narrowed from close to the base upwards, and gradually falcate from $\pm 1/2$, sometimes all the way from the base. The best distinguishing characters are in the indument. The indument of *N. obliterated* differs from that of *N. biserrata*, with which it has often been confused, in the scales at the base of stipe being closely appressed, with a rather sharp transition to sparse, appressed, very translucent and inconspicuous peltate scales upwards on the stipe and on the rhachis. The very sparse, inconspicuous rhachis scales and the absence of hairs on the costae also distinguish it from *N. brownii*, *N. davallioides* or *N. falciformis*. In addition, *N. brownii* has usually less distinctly falcate pinnae, and those of *N. falciformis* are usually smaller.

14. *Nephrolepis radicans* (Burm.) Kuhn

Nephrolepis radicans (Burm.) Kuhn, Ann. Mus. Bot. Lugduno-Batavi 4 (1869) 285; Backer & Posth., Varenfl. Jav. (1939) 93; Copel., Fern Fl. Philipp. (1958) 185; Holttum, Revis. Fl. Malaya 2, 2nd ed. (1968) 381; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 176; Hovenkamp & Miyam., Blumea 50 (2005) 308. — *Polypodium radicans* Burm.f., Fl. Ind. (1768) 233, pl. 66, f. 3. — Type: *Pryon s.n.* (n.v.), Java.

Nephrolepis clementis H.Christ, Philipp. J. Sci., Bot. 3 (1908) 272; Copel., Fern Fl. Philipp. (1958) 185. — Type: *Clemens 920* (P), Philippines.

Lepidonevron volubile Fée, Mém. Foug., 5. Gen. Fil. (1852) 301. — *Nephrolepis volubilis* (Fée) J.Sm., J. Bot. (Hooker) 3 (1841) 413; Kunze, Bot. Zeitung (Berlin) 6 (1848) 236; C.Presl, Epimel. Bot. (1851) 44. — Type: *Cuming 37* (holo P; iso BM), Philippines.

Aspidium obtusifolium Willd., Sp. Pl. 5, 1 (1810) 231; Blume, Enum. Pl. Javae (1828) 145. — *Nephrodium obtusifolium* (Willd.) C.Presl, Reliq. Haenk. (1830) 32. — *Nephrolepis obtusifolia* (Willd.) C.Presl, Tent. Pterid. (1836) 80; Brack., U.S. Expl. Exped. 16. Filic. (1854) 210. — Type: *Klein s.n.* (B, Willdenow herb. 18756).

Habit, rhizome morphology. Plants terrestrial, forming tufts of 3–5 fronds. Runners tendril-like, proliferous or free, 1 mm thick, branching angle divaricate or straight. Scales on runners very sparse or sparse, appressed, spreading or (some) squarrose. Tubers absent. *Fronde* 94–102 by 7.5–10 cm, stipe 12–14 cm long. Lamina base strongly reduced, tapering over 20–35 cm, basal pinnae 0.5–1 cm long, 2.5–3 cm distant, middle pinnae straight or slightly falcate. Sterile pinnae 3.5–4 by 0.9–1 cm, herbaceous, thick, base slightly to strongly unequal, basicopic base rounded, acroscopic base truncate, slightly auricled, margin in basal part crenate, apex rounded or obtuse. Fertile pinnae 4.5–6 by 0.7–0.8 cm, otherwise similar to sterile ones. *Indument.* Basal scales peltate, appressed, 2 by 0.7 mm, central part dark brown or blackish, shining, margin in basal part hyaline, ciliate, in acumen pale brown (often abruptly distinct from the dark central part), entire or denticulate; strongly elongated, lightly coloured marginal glands present around the scale. Rhachis scales sparse or dense, without a distinctly protracted acumen, appressed (often somewhat bullate when dry), light brown. Scales on lamina sometimes present, very few, appressed, on lower surface. Hairs on lamina absent, on costa constantly present (also on lower surface, usually sparse). *Sori* submarginal,

20–23 pairs on fully fertile pinnae, round, not impressed. Indusium reniform, with open sinus, attached at sinus. — **Plate 2c.**

Distribution — India to Indochina; in *Malesia*: Throughout; New Caledonia.

Habitat & Ecology — At low elevations to 1000 m, terrestrial and scrambling over shrubs or trees, on waste ground, in *belukar*, often in swamps or on riverbanks.

Note — One of the most distinct and easily recognizable species of *Nephrolepis*, with a unique growth form. In *N. radicans* the runners are strongly differentiated and three distinct types can easily be distinguished on a single plant. Thick runners which, in contrast to normal runners, tend to grow upwards, form dense scrambling thickets, attached to supporting vegetation by tendril-like runners originating on the frond-bearing rhizomes. These frond-bearing rhizomes are short, densely scaly side branches, each apparently with a limited growth and with a limited number of fronds; typically only 3 or 4 well-developed ones present at the same time. In addition, they also bear long runners which bear roots wherever they come into contact with a suitable substrate. Apart from this distinct growth form, this species is easily recognizable by the obtuse or rounded pinnae and the scales on the rhachis of the fronds that are somewhat bullate when dry.

15. *Nephrolepis undulata* (Afzel.) J.Sm.

Nephrolepis undulata (Afzel.) J.Sm., Bot. Mag. 72 (1845) 35; Pic.Serm., Ann. Mus. Civico Storia Nat. Genova 77 (1969) 273; Hovenkamp & Miyam., Blumea 50 (2005) 310. — *Aspidium undulatum* Afzel. in Sw., J. Bot. (Schrader) 1800 (1801) 32; Sw., Syn. Fil. (1806) 45. — *Nephrolepis tuberosa* (Bory) C.Presl var. *undulata* (Afzel.) Kuhn, Filic. Afr. (1868) 156. — *Nephrolepis cordifolia* (L.) C.Presl var. *undulata* (Afzel.) C.Chr., Index Filic. (1906) 453, 455. — Type: *Anon. s.n.* (BM).

Nephrolepis delicatula M.J.Decne. in Jacquem., Voy. Inde 4 (1844) 178, t. 179; Pic.Serm., Ann. Mus. Civico Storia Nat. Genova 77 (1969) 275; Tagawa & K.Iwats., Fl. Thailand 3. Pteridophytes. 2 (1985) 174. — *Nephrolepis tuberosa* (Bory) C.Presl var. *delicatula* Hook., Sp. Fil. (1846) 151. — Type: *Jacquemont 598* (holo P; iso K), India.

Nephrolepis pluma T.Moore, Gard. Chron. n.s. 9 (1878a) 588, f. 108. — Type: *Anon. s.n.* (K), in cultivation.

Nephrolepis glabra Copel., Philipp. J. Sci. 1, Suppl. 2 (1906) 146; Fern Fl. Philipp. 1 (1958) 186. — Type: *Copeland 1819* (holo MICH; iso KYO, P, SING), Philippines.

Habit, rhizome morphology. Plants forming tufts of 2 or 3 fronds. Runners 0.5–1 mm thick (or thinner), branching angle divaricate. Scales on runners very sparse or sparse, spreading. Tubers present. *Fronde*s 50–90 cm long (or longer), 5–7 cm wide, stipe 6.5–15 cm long. Lamina base strongly reduced, tapering over 8–15 cm, basal pinnae 0.6 cm long, 2–4 cm distant, middle pinnae straight to distinctly falcate. Sterile pinnae 2.9–3.2 by 0.6–0.8 cm, herbaceous, thin, base slightly unequal, strongly unequal or fully 1-sided, basiscopic base cuneate or cordate, acroscopic base cordate, auricled (often dilated and crossing the rhachis), margin in basal part crenate or dentate, towards apex dentate or deeply dentate, apex acute. Fertile pinnae 2.1–3.5 by 0.5–0.7 cm, the base often more distinctly 1-sided and the margin more deeply dentate than the sterile pinnae. *Indument.* Basal scales peltate, spreading, 3.5 by 0.5 mm, straw-coloured or hyaline, dull, margin in basal part irregularly lacerate with a few protrusions, in acumen entire, marginal glands absent. Rhachis scales very sparse (persistent only around the

pinna-bases), with a well-developed spreading, ciliate acumen, or completely dissected into narrow filaments, with hyaline or dark glandular apical cells. Scales on lamina absent. Hairs on lamina frequently present (very inconspicuous), on costa absent. *Sori* submarginal or medial, 6–10 pairs on fully fertile pinnae, elongated, slightly impressed. Indusium lunulate or broad, attached at broad base.

Distribution — Worldwide. In Asia there is a distinct distributional centre from Indochina to Northern India; in *Malesia*: Philippines (Luzon).

Habitat & Ecology — Usually terrestrial, in grassland, brushwood or forest, or epilithic, on cliffs, lava flows or rocky outcrops, rarely indicated as epiphytic, altitude 300–2450 m. In *Malesia*: on rocks in pine forest, at 1500 m.

Notes — 1. The name *N. undulata* has been applied traditionally to the form occurring in Africa, which is relatively robust. The smaller forms from Asia have often been named *N. delicatula*, while the forms from the Americas were distinguished as *N. occidentalis*.

2. *Nephrolepis undulata* is distinct from *N. cordifolia* by the seasonal mode of growth, with new fronds sprouting each season from underground tubers. In most cases, no more than two well-developed fronds develop in a single season, and in many cases collections contain only plants with a single frond. Apart from this characteristic growth form, this species can usually also be distinguished from *N. cordifolia* by the more glabrous stipe and rhachis, the basal part of which is often conspicuously thicker than in *N. cordifolia*, and the, especially in comparison to the stipe, thin runners originating from the rhizome bud.

EXCLUDED SPECIES

Nephrolepis iridescens Alderw., Bull. Jard. Bot. Buitenzorg II, 20 (1915) 20. — Type:

Jaheri s.n. (BO), Key Islands = **Asplenium sp.**

Nephrolepis trichomanoides J.Sm. ex C.Presl, Epimel. Bot. (1851) 44. — Type: *Cuming*

101 (L, P), Philippines = **Arthropteris palisotii** (Desv.) Alston.