MONOGRAPH



A revision of the fern genus Oleandra (Oleandraceae) in Asia

Peter H. Hovenkamp¹, Boon-Chuan Ho²

l Netherlands Centre for Biodiversity Naturalis (section NHN), Leiden University, PO Box 9517, 2300 RA Leiden, The Netherlands **2** Nees-Institut für Biodiversität der Pflanzen, Rheinische Friedrich-Wilhelms-Universität Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany

Corresponding author: Peter H. Hovenkamp (hovenkamp@nhn.leidenuniv.nl)

Academic editor: T. Ranker | Received 16 February 2011 | Accepted 29 March 2012 | Published 6 April 2012

Citation: Hovenkamp PH, Ho B-C (2012) A revision of the fern genus *Oleandra* (Oleandraceae) in Asia. PhytoKeys 11: 1–37. doi: 10.3897/phytokeys.11.2955

Abstract

The Asiatic species of *Oleandra* (Oleandraceae) are revised. We reduce a large number of species to *O. neriiformis* and *O. sibbaldii*, we provide a revised circumscription of *O. cumingii* and *O. undulata* and we establish the identity of *O. vulpina*. In total, we recognize 9 species, with full synonymy, descriptions and distribution maps. A list of identifications is appended.

Keywords

Oleandra, systematics

Introduction

Virtually all authors who have dealt with the genus *Oleandra* Cav. have commented on its distinctness or naturalness. The shrubby growth form, particularly distinct in *O. neriiformis* Cav., prompted Cavanilles (1799; 1802) not only to derive the genus name, but also the species name from *Nerium oleander* L. (Apocynaceae). From this it should be clear that he saw the aerial stems of *Oleandra neriiformis*, of which the forms with distinctly whorled fronds are indeed strongly reminiscent of branches of *Nerium oleander*. Subsequently, Swartz (1801; 1806) included *Oleandra* in *Aspidium* Sw., but Presl (1836) reinstated the genus, followed by Smith (1841; 1842), and the distinctness of the genus has not been questioned since, not even by Hooker (1862), and only one author has preferred to recognize *Oleandra* at subgeneric level, but not without some doubts (Splitgerber 1840, "An genus proprium? habitus distinctissimus!").

Two genera have been described that are now universally included in *Oleandra*. Reinwardt (1825) described *Ophiopteris* Reinw., with the only species *O. verticillata* Reinw., without distinguishing either from *Oleandra* or *O. neriiformis*. Don (1825) distinguished *Neuronia* D. Don, with *N. asplenioides* D.Don as only species.

The characters of *Oleandra* were summarized most recently by Smith et al. (2006) as "blades simple; leaves articulate, abscising cleanly upon senescence from pronounced phyllopodia; sori indusiate, indusia round-reniform; spores reniform, monolete", while Tryon (2001) stressed the parallel veins, the unusual roots ("rhizophores"), the peltate scales and the articulate phyllopodia.

There is as much unanimity on the distinctness of the genus as there is uncertainty on the distinctness of species in Oleandra, and many authors who have dealt with the genus have commented on the difficulties of species delimitation. Smith et al. (2006) estimated a total number of c. 40 species, in which they follow many earlier authors, where the estimated number varies between 40 ("many species are similar in appearance", Kramer 1990) to 50 ("closely related", Pichi Sermolli 1965). However, Tryon (1997; 2001) reduced the number of American species to 4 (with one species indicated as of doubtful validity: "it may well be a variety ...") and of the Asiatic to 6. In addition, Pichi Sermolli (1965: "the delimitation of the species is not always easy, since some of them show a high degree of polymorphism"), distinguished no more than 5 species in Africa, and as his distinctions are sometimes subtle and based on limited material, the number should perhaps be reduced. A reasonable estimate of the number of species in *Oleandra* should accordingly be between 15 and 20. In this taxonomic treatment, we deal with the Asiatic species of Oleandra, extending the rather summary treatment in Tryon (2001), which was based on specimens in only two herbaria, and should be considered, according to the author, as "a prodromus that may be amplified". After examining many more specimens in a much larger number of herbaria, we can only agree with Tryon and all others who have considered species delimitation in this group difficult.

Morphology

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 without field study. In the Asiatic species that we have seen, 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. Branches are often opposite each other, and then both branches grow in the same direction, either downwards (positively geotropic) or upwards (negatively geotropic). Negatively geotropic branches can also be found on parts of the main rhizome where this starts to curve upwards, forming props that support the main stem. This is the shrubby growth form that is most often associated with the genus, although it occurs only in a minority of the species.

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. When aerial parts develop, they tend to be more strongly sclerified.

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 they were identified as real roots by Wetter (1951). Branching and the formation of root hairs appears to be limited to the parts of the root that 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 subterraneous rhizome.

Fronds arise on the rhizome without any apparent regularity, sometimes clustered, sometimes more regularly spread over the length of a creeping rhizome. They do not appear to grow in regular rows, 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, with a plane of dehiscence that is perpendicular to the stipe. The part below the abscission point might be called a phyllopodium, the part above it the stipe, but the upper part of the phyllopodium is in all structural details similar to the stipe, while basally it shows a gradual transition to the rhizome. A stipe-like phyllopodium like this is restricted, in ferns, to Oleandra and Arthropteris J. Sm., but in the latter genus, the articulation is distinctly much more oblique. In other ferns where fronds are articulated to the rhizome (Polypodiaceae, Davalliaceae), the part below the articulation is more clearly rhizomatous in structure and indument. In the most inclusive phylogenetic analyses available (Schuettpelz and Pryer 2007; Tsutsumi and Kato 2006), the optimization of the articulation of the fronds for the common ancestor of Oleandra and Arthropteris is ambiguous, so the homology of this type of articulation in Oleandra and Arthropteris is uncertain. Presence of an articulation in general (including the articulation of pinnae to the rachis) could well be an apomorphy for the crown clade of Eupolypods (Schuettpelz and Pryer 2007), related to the development of a climbing or epiphytic habit with a full reversal in the terrestrial Tectariaceae and a weaker reversal in the similarly terrestrial Cyclopeltis J.Sm.

The lamina is uniformly simple in all species, and varies little in shape, except in *O. werneri* Rosenst., which is dimorphic, with the fertile fronds or parts of fronds strongly contracted. Sori are indusiate with a reniform indusium, and always separate. The indusia may be firm and persistent or shriveling and inconspicuous in older sori. The sori are borne dorsally and singly on the veins, at distances from the costa that 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.

Spores

Figs 1-10

The morphology of the spores of *Oleandra* as shown with SEM has been illustrated by Liew (1977) and Tryon and Lugardon (1991), who illustrate the whole range of variability in perispore morphology in *Oleandra*.

Two distinct types of perispore morphology can be distinguished. The first type occurs in all species studied except O. wallichii. It is highly variable but the variation can be described in terms of just three parameters describing the folds, the ornamentation of the surface and the degree of perforation. This type shows a surface with a pattern of coarse folds, a variable ornamentation and a variable degree of perforation ("lophate", Liew 1977). The folds may be broad (fig. 1), narrow (fig. 2), or replaced by fissures (fig. 3), the ornamentation ranges from warty (fig 1) to densely spinose (fig. 2, 4). This surface may be perforated (fig. 4) or fissured to varying degrees, exposing an inner structure of numerous narrow cylindrical pillars c. 0.5 µm thick (fig. 7). 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 (fig. 4). Within this range of variability, most species that could be studied with an adequate sample of specimens show variability in two or more of these parameters, and it is difficult either to subdivide this type or 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 second type occurs exclusively in *O. wallichii* (figs 5, 6, 8). Here the perispore is composed of a thicker basal layer and thicker, more conical spines (fig. 8) with a basal diameter of $1-2 \mu m$, which are, mainly in the specimens from Taiwan, partly fused in irregular ridges (fig. 7). In this type there never is an outer layer overlaying this pattern of conical spines, and thus the entire perispore is massive.

The exospore is smooth in all cases where it has been observed. Spore size variability was assessed based on SEM observations, with length of the spore measured including the perispore (Table 1, fig.9). The limited data available do not allow a full statistical analysis, but it is clear that several species and even several specimens show a large variability in spore size. A similar variability in *Oleandra* from Southern Africa was found by Harmata and Kornas (1978).



Figures 1–8. I Oleandra cumingii, perispore with broad folds, low warty ornamentation, not perforated. scale bar 10 μm. *Schmutz 6086* (L) **2** Oleandra cumingii, perispore with narrow wings, spiny ornamentation, few perforations. Scale bar 10 μm. *Ting & Shih 796* (L) **3** Oleandra musifolia, perispore with wings partly replaced by fissures, irregularly warty ornamentation, few perforations. Scale bar 10 μm. *Ting & Shih 796* (L) **3** Oleandra musifolia, perispore with wings partly replaced by fissures, irregularly warty ornamentation, few perforations. Scale bar 10 μm. *Brooks s.n.* (L 0317430) **4** Oleandra sibbaldii, perispore highly perforated. Scale bar 10 μm. *Brass 29706* (L) **5** Oleandra wallichii, perispore spiny. Scale bar 10 μm. *De Haas 2622* (L) **6** Oleandra wallichii, perispore spiny, spines confluent into ridges. Scale bar 10 μm. Van Steenis 20870 (L) **7** Oleandra sibbaldii. Perispore spines on a thin basal layer, exospore smooth. Scale bar 1 μm. *Elmer 11451* (L) **8** Oleandra wallichii, perispore with thick basal layer, exospore smooth. Scale bar 1 μm. De Haas 2622 (L).



Figure 9. Distribution of spore lengths in *Oleandra*, arranged by specimen.



Figure 10. Distribution of spore lengths in *Oleandra*, arranged by species. Horizontal: spore length in μ m, vertical: number of observed spores.

Specimen	Identification	number of spore
		measurements
Kato et al. B 9511	Oleandra coriacea	2
Geesink & Santisuk 5384	Oleandra cumingii	3
Schmutz 6086	Oleandra cumingii	3
Ting & Shih 796	Oleandra cumingii	1
Davidse & Sumithraarachchi 7965	Oleandra musifolia	5
Holstvoogd 472	Oleandra musifolia	6
Brooks	Oleandra musifolia	4
Kato, M. et al. C 4121	Oleandra neriiformis	2
Kato, M. et al. C 1365	Oleandra neriiformis	4
Clunie et al. LAE 63399	Oleandra neriiformis	4
Degener 14279	Oleandra neriiformis	3
Siew 125	Oleandra neriiformis	3
Gaerlan et al. PPI 13079	Oleandra neriiformis	5
Kato et al. B 7901	Oleandra neriiformis	4
Kato et al. 1160	Oleandra neriiformis	5
Croft 66	Oleandra neriiformis	4
Craven & Schodde 133	Oleandra neriiformis	4
Brass 29706	Oleandra sibbaldii	6
Elmer 11451	Oleandra sibbaldii	2
Hennipman 5430	Oleandra sibbaldii	2
Kato et al. C 7480	Oleandra sibbaldii	1
Sledge 1790	Oleandra sibbaldii	1
Hennipman 3334	Oleandra undulata	4
Maxwell 74/907	Oleandra undulata	2
Banoc 3	Oleandra undulata	3
Van Steenis 20870	Oleandra wallichii	4
De Haas 2622	Oleandra wallichii	4
Van Royen & Sleumer 5959	Oleandra werneri	5
Braithwaite RSS 4045	Oleandra werneri	2

Table 1. List of specimens (all L.) of which spores were studied (see figs. 9, 10).

Karyology

Data on chromosome numbers for species of *Oleandra* were summarized by Löve et al. (1977), who cite a basic number of x=41. Reports of n=40 (Kramer 1990) are based on a count that is acknowledged as uncertain by the authors (Manton and Sledge 1954) and that has not been confirmed by others.

Of the Asiatic species, *O. neriiformis* (1 count, source Himalayas), *O. musifolia* (Bl.) C. Presl (2 counts, Ceylon and Southern India) and *O. wallichii* (Hook.) C. Presl (2 counts, Northern India) have been reported. The report of a tetraploid taxon in *Oleandra* is based on a count for unsourced material growing in Kew (presumably from Africa), and is complemented by reports of n=41 for another plant from West Tropical Africa. The large variation in spore size in *Oleandra* from Southern Africa

was conjectured by Harmata and Kornas (1978) as due to the presence of different polyploidy levels, and this explanation would also fit well with the observed variability in morphology of *Oleandra* in Asia. However, actual confirmation of polyploidy in *O. neriiformis* or any other Asiatic species is needed.

Systematics

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* Schott and *Arthropteris* (Copeland 1947, Holttum 1959, Nayar and Bajpai 1978). More recent views exclude *Nephrolepis* from this alliance (Kramer 1990, Tryon and Lugardon 1991, Tryon and Tryon 1982), and phylogenetic molecular studies (Kuo et al. 2011, Schuettpelz and Pryer 2007) have shown that these three genera do not form a clade, but that they are associated with different clades in the crown leptosporangiates.

Taxonomic revision

This study is based on material from B, BISH, BM, BO, K, KEP, KLU, L, P, PE, PNH, MICH, SING, UC (abbreviations follow Index Herbariorum, Thiers 2011). All specimens cited were seen except where noted otherwise. Specimens seen only as on-line images (provided either directly through the database of the holding institute or via JSTOR, http://plants.jstor.org) are marked with *. The identification list (see Appendix 1) has been prepared with the help of BRAHMS (http://dps.plants.ox.ac.uk/bol/BRAHMS), and the distribution data with BRAHMS and DIVA-GIS (http://www.diva-gis.org/).

Oleandra

http://species-id.net/wiki/Oleandra

- Oleandra Cav., Anales Hist. Nat. 2: 115. 1799; Descr. Pl. (Cavanilles): 252. 1802. Lumbreras, Flora Montiber. 28: 19. 2004. Aspidium subg. Oleandra Splitg., Tijdschr. Natuurl. Gesch. Physiol. 7: 411. 1840. Type: Oleandra neriiformis Cav. (as "neriformis").
- *Ophiopteris* Reinw., Syll. Pl. Nov. 2: 3. 1825. Type: *Ophiopteris verticillata* Reinw., = *Oleandra neriiformis.*
- Neuronia D.Don, Prodr. Fl. Nepal.: 6. 1825. Type: Neuronia asplenioides D.Don, =Oleandra wallichii.

Description. 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. Fronds stipitate, lamina simple, margin entire, veins distinct, somewhat raised

on both sides, 1-2 ' 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 9 Asian species

1	Rhizome with stiff, erect to pendent rootless aerial branches2
_	Rhizome creeping
2	Fronds strongly dimorphic, scattered on the rhizome or somewhat clustered
	Erende menormerie en dichtly dimembie eften in yherle eff. 10 frende 2
2	Lamina thick corrigances costs with conicus contribution 2 (mm long
3	Lamina unick, conaceous, costa with copious, conspicuous, 5–4 min long
-	Lamina thin, papyraceous when dry, costa mostly with few or inconspicuous scales on the abaxial surface
4	Rhizome in older parts not entirely covered with scales; scales with squarrose
	acumen and entire or distinctly glandular margin
_	Rhizome entirely covered with overlapping scales; scales with appressed or
	spreading apex, usually with non-glandular cilia
5	Rhizome scales with gradually narrowed apex, stipes 0.5–4.5 cm long, costa and stipe often with distinct dark colouration on the abaxial surface
_	Rhizome scales with abruptly narrowed apex, stipe to 2-3 mm long, costa
	and stipe without dark colouration on the abaxial surface 7 O. vulpina
6	Phyllopodia, inconspicuous, 2-5 mm, rarely 1 cm long, much shorter than
	the stipe, sori mostly in a closely costal single row7
_	Phyllopodia, conspicuous, 2–10 cm long, often as long as or longer than the
	stipe, position of sori costal to medial
7	Rhizome scales squarrose, costa and stipe usually with dark colouration,
	frond apex distinctly apiculate
_	Rhizome scales appressed, costa and stipe without dark colouration, frond
	apex acute to acuminate
8	Rhizome scales spreading, long triangular with a wide acumen, brown, cen-
	tral part not conspicuously thickened, roots branching with root hairs over
	their entire length; lamina glabrous on upper surface and margin
_	Rhizome scales appressed to spreading, narrowly ovate-lanceolate with long
	narrow acumen, central part dark, thickened, roots often with glabrous, un-
	branched part ("rhizophore"), lamina hairy or glabrous 2 O. cumingii

1. Oleandra coriacea

http://species-id.net/wiki/Oleandra_coriacea Map 1, fig. 11 d–f

Oleandra coriacea Copel. J. Straits Branch Roy. Asiat. Soc. 63: 72. 1912. Type: MA-LAYSIA. Borneo: Moulton s.n. (SAR? not seen).

Description. *Rhizome* with creeping parts unknown, aerial stems unbranched and rootless, 2–3 mm thick (when dry), not white waxy, in cross-section with a distinct sclerified peripheral sheath and few, scattered sclerified strands, phyllopodia in weak to distinct clusters of 4–6, short, usually less than 5 mm long. *Scales* persistently covering the rhizome, peltate, $5-70 \times 0.5-1$ mm, appressed (sometimes spreading), dark, shining with pale to brown margin and acumen, margin ciliate especially when young. *Fronds* monomorphic; stipe 1–1.5 cm long, without dark colouration, with up to 1 mm long glandular hairs and often small, appressed scales; lamina 13–30 × 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 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,



Map I. Distribution of Oleandra coriacea (triangles), O. musifolia (circles).



Figure 11. Oleandra neriiformis (a-c, g-m), O. coriacea (d-f). a middle part of lamina, medial sori with indistinct indusia b entire lamina c lyrate lamina base with stipe articulation immediately below lamina base: Brass 23016 (New Guinea) d middle part of lamina, with conspicuous scales on midrib and sori with persistent indusia e entire lamina f lamina base with elongated stipe: Yahud et al SAR 88396 (Borneo) g entire lamina with costal sori h middle part of lamina, sori costal with persistent indusia i rounded lamina base with short stipe j whorl of short phyllopodia on aerial stem: Chew, Corner & Stainton 298 (Borneo) k middle part of lamina sori with inconspicuous indusium I rounded lamina base with short stipe m lamina: Copeland s.n. 29 jan 1933 (Philippines)., All views of lamina showing abaxial surface; all specimens L.

indusium distinct, c. 1.5 mm wide, most often 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. Brunei, Indonesia: Kalimantan Timur; Malaysia: Sarawak.

E**cology.** Terrestrial in montane forest, mainly on ridges and in summit vegetation, 1100–2200 m.

Discussion. Creeping and rooting parts of the rhizome are absent in all collections seen, but presumably present, as in *O. neriiformis*. The lamina of *O. coriacea* is indeed much more coriaceous than *O. neriiformis*, and has 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

http://species-id.net/wiki/Oleandra_cumingii Map 2

- Oleandra cumingii J.Sm., J. Bot. (Hooker) 4: 413. 1842. C.Presl, Epimel. Bot.: 41. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Hook., Sp. Fil.: 158. 1862. Baker, Syn. Fil. (Hooker & Baker): 303. 1868. Copel., Polypod. Phil. Isl.: 49. 1905. Copel., Fern Flora of the Philippines: 184. 1958. Ching, Fl. Reipubl. Popularis Sin. 2: 324. 1959. X.C.Zhang, Ching Mem. Vol.: 91. 1999. Type: PHILIP-PINES. Luzon: Cuming 60. (holotype: K; isotypes: B, BM, SING, US*),
- Oleandra macrocarpa C.Presl, Epimel. Bot.: 41. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Holttum, Novit. Bot. Inst. Horto Bot. Univ. Carol.: 43. Type: PHIL-IPPINES. Luzon: Cuming 60 p.p. (Holotype: PRC, teste Holttum; isotypes: B, BM, K, SING, US*).
- *Oleandra chinensis* Hance, Ann. Sci. Nat. (Paris) 18: 238. 1862. Type: CHINA. Guangdong: Si Chu Shan, Parry s.n., herb. Hance 9408 (holotype: K; isotype BM).
- *Oleandra scandens* Copel., Philipp. J. Sci. 46: 218. 1931., Fern Flora of the Philippines: 184. 1958. Type: PHILIPPINES. Baguio: Elmer 6513 (holotype: US*).
- Oleandra intermedia Ching, Bull. Fan Mem. Inst. Biol. 11: 187. 1931. Ching, Fl. Reipubl. Popularis Sin. 2: 323. 1959. X.C.Zhang, Ching Mem. Vol.: 92. 1999. Type: CHI-NA. Yunnan: Henry 9484c (holotype: K; isotypes: B, BM, MO*, PNH, US*).
- *Oleandra cumingii* var. *longipes* Hook., Sp. Fil.: 158. 1860. *Oleandra longipes* Ching, Lingnan Sci. J. 12: 158. 1933. Type: BIRMA. Mergui: Parish 59 (holotype: K).
- *Oleandra cantonensis* Ching, Fl. Reipubl. Popularis Sin. 2: 324, 378. 1959. Type: CHI-NA. Guangdong: Canton, Peiyinshan, Y. Liang 60252 (holotype: PE).
- *Oleandra yunnanensis* Ching, Fl. Reipubl. Popularis Sin. 2: 325. 1959. Type: CHINA. Yunnan: anon. s.n. (holotype: PE).
- *Oleandra guangxiensis* S.L. Mo & Y.C. Zhong, Guihaia 7: 289. 1987. Type: CHINA. Giangxi: Damingshan, Guangxi Forest ecology group 84422 (holotype: IBY, not seen; isotype: PE).



Map 2. Distribution of Oleandra cumingii (squares), O. undulata (triangles), O. wallichii (circles).

Description. Rhizome short- to long creeping, 3-8 mm thick, sometimes white waxy in the older parts, little branched and not forming extensive stands, in crosssection with or without scattered sclerified strands; roots scattered, sometimes with unbranched aerial parts; phyllopodia scattered or more or less tufted, (1-)3-10 cm long. Scales persistently covering the rhizome, peltate, $4-9 \times 0.5-1.5$ mm, appressed, acumen with dark center and lighter acumen and margin, margin ciliate especially when young. Fronds monomorphic, stipe 2–12 cm long, without dark colouration, glabrous or hairy with catenate to acicular up to 2 mm long hairs, lamina 12- 40 × 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 colouration, 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. China: Yunnan, Guangdong, Guangxi, Guizhou; Laos; Thailand (Peninsular); Malaysia: Peninsular Malaysia; Indonesia: Flores; Timor Leste; Philippines: Luzon.

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

Discussion. Contrary to Holttum (1968a), *Oleandra cumingii* J. Sm. is not a *nomen nudum*, but provided with an adequate diagnosis. *Cuming 60* is distributed in several herbaria with many duplicates, and it is impossible to tell which ones should be considered isotypes of *O. cumingii* and which ones of *O. macrocarpa*.

Oleandra cumingii is a variable assemblage of fairly widely scattered forms, in many characters intermediate between O. undulata and O. musifolia. From O. undulata it can be distinguished by the more narrowly elongated, appressed rhizome scales with a more or less thickened costa in the acumen, and by the often hairy upper surface of the lamina. From O. musifolia, O. cumingii differs in the elongated phyllopodia and the distinctly tomentose indusia and lower surface of the lamina. The differences with either species, however, are often slight and bridged by specimens with an intermediate character combination. This may indicate that Oleandra cumingii is a hybrid or a hybrid swarm between the two other species, but failing positive evidence for that interpretation, we prefer to regard it here as a separate species.

3. Oleandra musifolia

http://species-id.net/wiki/Oleandra_musifolia Map 1

- Oleandra musifolia Blume, Enum. Pl. Javae: 141. 1828. (as Oleandra musaefolium).
 Oleandra musaefolia C.Presl, Epimel. Bot.: 42. 1851. Fée, Mém. Foug., 5. Gen.
 Filic.: 304. 1852. Ching, Fl. Reipubl. Popularis Sin. 2: 321. 1959. Oleandra musifolia C.Chr., Index Filic.: 466. 1906. Backer & Posth., Varenfl. Jav.: 87. 1939.
 X.C.Zhang, Ching Mem. Vol.: 94. 1999. R.M.Tryon, Rhodora 102: 434, fig. 4. 2001. Type: INDONESIA. Java: Gedeh, Blume s.n. (holotype: L).
- Aspidium moritzii Kunze, Bot. Zeitung (Berlin) 6: 238. 1848., Kunze, Bot. Zeitung (Berlin) 9: 348. 1851. Oleandra moritzii C.Presl, Epimel. Bot.: 42. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Type: INDONESIA. Java: Zollinger 1306B (L, lectotype L 0317415, here selected).
- *Oleandra geniculata* Alderw., Bull. Jard. Bot. Buitenzorg Ser. 2: 23. 1914. Type: IN-DONESIA. Java: Docters van Leeuwen s.n. (holotype BO? not seen).
- *Oleandra benguetensis* Copel., Philipp. J. Sci. 46: 217. 1931. Fern Flora of the Philippines: 183. 1958. Type: PHILIPPINES. Baguio: Elmer 6286 (holotype: US*).
- Oleandra whangii Ching, Bull. Dept. Biol. Sun Yatsen Univ. 6: 23. 1933. Type: CHI-NA. Guangxi: Sin & Whang 300 (holotype: SYS, not seen; isotypes: NY, PE, BM).
- *Oleandra hainanensis* Ching, Acta Phytotax. Sin. 8: 141, pl. 20 fig. 17. 1959. 141; Ching, Fl. Reipubl. Popularis Sin. 2: 322. 1959. X.C.Zhang, Ching Mem. Vol.: 91. 1999. Type: CHINA. Hainan: S.K. Lau 27326 (holotype: PE).

Aspidium lomatopus Kunze, Bot. Zeitung (Berlin) 6: 238. 1848. Oleandra lomatopus C.Presl, Epimel. Bot.: 43. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Type: INDONESIA. Java: Zollinger s.n. (lectotype: K, here selected).
Oleandra neriiformis auct. non Cav.:Bell, Flora of Australia 48: 446. 1998.

Description. *Rhizome* creeping, 5–8 mm thick, white waxy in the older parts, 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 short phyllopodia, usually less than 5 (-15) mm long, often hidden by the scales, rhizome often innovating 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, roots scattered, with long unbranched aerial parts. Scales persistently covering the rhizome, peltate, $5-10 \times 1-1.5$ mm, appressed, with dark center and lighter brown acumen and margin, margin ciliate especially when young and with sessile glands. Fronds monomorphic, stipe 0.5-4 cm long, without dark colouration, with short, glandular hairs; lamina to 60×4.2 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 colouration, 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. South China, Southern India, Sri Lanka, Thailand, Indonesia: Java, Lesser Sunda Islands, Sulawesi; Philippines: Luzon, Australia: Queensland.

Ecology. Mostly terrestrial or on rocks, less often as low trunk epiphyte, in various types of forests, often disturbed, sea level to c. 2000 m.

Discussion. ICN 60.8 specifies that the spelling of the original epithet "musaefolia" should be corrected to "musifolia".

Aspidium moritzii is one of the two species distinguished by Kunze (1848) among the collections under Zollinger 1306 (see also discussion under *Oleandra neriiformis*). The description conforms to *O. musifolia*, and the specimen selected as lectotype for *Aspidium moritzii* is conform to the original description, and bears a label "Aspidium moritzi 1306B". *Aspidium lomatopus* is based on a description and name in Kunze (1848) that was evidently considered preliminary by Kunze, as he did not refer to this species in his later account (Kunze 1851). A specimen in K is labeled "Zollinger 1306 b Aspidium moritzii Kze", with a separate label "Oleandra lomatopus" in what may be Kunze's hand. It is *O. musifolia*, and is here selected as lectotype. Oleandra musifolia is variable in the density of hairs is variable, and the distance of the sori to the costa. It can be distinguished from *O. cumingii* mainly by the short phyllopodia (longer in *O. cumingii*). Incomplete collections are easily confused also with *O. neriiformis* but can often be recognized by the flatter, softer rhizome without sclerenchyma strands (rhizome more rigid, rounded, with sclerenchyma strands in *O. neriiformis*) and by the catenate hairs with capitate or glandular apex (more acicular, not capitate in *O. neriiformis*). Distinguishing these two species on basis of juvenile material, however, is difficult, and often impossible.

4. Oleandra neriiformis

http://species-id.net/wiki/Oleandra_neriiformis Map 3, fig. 11 a–c, g–m, 12

- Oleandra neriiformis Cav., Anales Hist. Nat. 2: 115. 1799. (as "neriformis"); Descr. Pl. (Cavanilles): 252. 1802. C.Presl, Tent. Pterid.: 78. 1836. (as "neriifolia"); C.Presl, Epimel. Bot.: 42. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Hook., Sp. Fil.: 156. 1862. Copel., Polypod. Phil. Isl.: 49. 1905. Backer & Posth., Varenfl. Jav.: 87. 1939. Copel., Philipp. J. Sci. 73: 346. 1940. C.Chr., Bull. Bernice P. Bishop Mus. 177 45. 1943. Copel., Fern Flora of the Philippines: 182. 1958. Brownlie, The Pteridophyte Flora of Fiji: 156. 1977. M.Kato, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 240. 1989. R.M.Tryon, Rhodora 102: 430. 2001. Aspidium neriiforme Sw., Syn. Fil. (Swartz) 42. 1806. Willd., Sp. Pl., ed. 4 [Willdenow] 5: 212. 1810. Blume, Enum. Pl. Javae: 140. 1828. Gariletti, Fontqueria 38: 40. 1993. Type: PHILIP-PINES. Mauban: Née s.n. (holotype: MA 476029, teste Gariletti, not seen).
- Aspidium pistillare Sw., J. Bot. (Schrader) 1800: 30. 1801. Oleandra pistillaris C.Chr., Index Filic., Suppl. Tertium pro Annis 1917-1933: 132. 1934. Holttum, Rev. Fl. Mal. 2: 386. 1954. X.C.Zhang, Ching Mem. Vol.: 91. 1999. Type: INDONESIA. Java: Unknown s.n. (holotype S, not seen) (teste Sw. 1806).
- *Ophiopteris verticillata* Reinw., Syll. Pl. Nov. 2: 3. 1825. Type: INDONESIA. Java: Reinwardt (?) s.n. (L).
- Aspidium bantamense Blume, Enum. Pl. Javae: 141. 1828. Oleandra bantamense Kunze, Bot. Zeitung (Berlin) 9: 349. 1851. Type: INDONESIA. Java: Bantam, anon. (Kuhl & van Hasselt?) s.n. (Holotype: L).
- Aspidium micranthum Blume, Enum. Pl. Javae: 141. 1828. Oleandra micrantha Kunze, Bot. Zeitung (Berlin) 9: 349. 1851. Type: INDONESIA. Java, Salak.: anon. (Kuhl & van Hasselt?) s.n. (holotype: L).
- Aspidium salaccense Blume, Enum. Pl. Javae: 140. 1828. Aspidium neriiforme var. salaccense Blume, Enum. Pl. Javae: Add. et emend. 1828. Oleandra neriiformis var. salaccensis Kunze, Bot. Zeitung (Berlin) 9: 348. 1851. Type: INDONESIA. Java: Blume s.n. (holotype: L).
- Blechnum colubrinum Blanco, Fl. Filip. [F.M. Blanco]: 834. 1837. Oleandra colubrina Copel., Polypod. Phil. Isl.: 48. 1905. Copel., Fragm. Fl. Philipp. 3 179. 1905.

Merrill, Sp. Blancoan.: 43. 1918. Copel., Fern Flora of the Philippines: 181. 1958. M.Kato, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 240. 1989. Type: PHILIP-PINES. Unknown.

- Aspidium phyllarthron Kunze, Bot. Zeitung (Berlin) 6: 237. 1848. Oleandra phyllarthron C.Presl, Epimel. Bot.: 42. 1851. Kunze, Bot. Zeitung (Berlin) 9: 349. 1851.
 Type: INDONESIA. Java: Zollinger 1306 (lectotype: L 0317564, here selected) (see discussion).
- *Oleandra hirtella* Kunze, Farnkräuter: 70, pl. 129. 1847. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. *Oleandra neriiformis* var. *hirtella* Hook., Sp. Fil.: 156. 1862. Type : INDONESIA. Java : Miquel? s.n. (holotype L?, not found).
- Oleandra mollis C.Presl, Epimel. Bot.: 41. 1851. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Type: PHILIPPINES. Luzon: Cuming 94 p.p. (holotype: PRC, not seen; isotypes: BM, L, SING, US*).
- *Oleandra neriiformis* var. *brachypus* Hook., Sp. Fil.: 156. 1862. Type: UNKNOWN. Malay Archipelago: Norris s.n. (holotype: K, not seen).
- *Oleandra cumingii* var. *tahitense* Hook., Sp. Fil.: 159. 1862. Type: FRENCH POLY-NESIA. Tahiti: Greville s.n. (holotype: K, not seen).
- *Oleandra ciliata* Kuhn, Linnaea 36: 126. 1869. Type: VANUATU. Aneiteum: Cuming 48 (holotype: B).
- *Oleandra cuspidata* Baker in Becc., Malesia 3: 44. 1886. Copel., Philipp. J. Sci. 73: 346. 1940. M.Kato, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 239. 1989. Type: INDONESIA. New Guinea: Arfak, Beccari s.n. (holotype: K).
- Oleandra colubrina var. nitida Copel., Philipp. J. Sci., C 3: 33. 1908. Oleandra nitida Copel., Fern Flora of the Philippines: 181. 1958. Amoroso & Pava, Philipp. J. Sci. 120: 423, 437. 1991. Type: PHILIPPINES. Mindanao: Mt. Apo, Copeland 1474 (lectotype: US*, here selected).
- *Oleandra colubrina* var. *membranacea* Copel., Philipp. J. Sci., C 3: 32. 1908. Type: PHILIPPINES. Luzon: Mt. Maquiling, Copeland PPE57 (holotype MICH; isotypes K, PNH, UC).
- *Oleandra oblanceolata* Copel., Philipp. J. Sci., C 7: 64. 1912. Type: MALAYSIA. Sarawak: Bungo Range, Brooks 115 (holotype: MICH).
- Oleandra samoensis Gand., Bull. Soc. Bot. France 66: 306. 1919. Type. SAMOA. Upolu: Reinecke s.n. (not seen).
- Oleandra colubrina var. membranacea Brause, Bot. Jahrb. Syst. 56: 119. 1921. Type: PHILIPPINES. Luzon: Mt. Banajao, Whitford 999 (holotype: B, not seen).
- Oleandra parksii Copel., Bull. Bernice P. Bishop Mus. 59: 86. 1929. Type: FRENCH POLYNESIA. Fiji: Parks 20759 (holotype: BISH? not seen; isotypes: BM*, MICH, US*).
- Oleandra platybasis Copel., Bull. Bernice P. Bishop Mus. 59 86. 1929. Type: FRENCH POLYNESIA. Fiji: Gillespie 3249 (holotype: BISH? not seen; isotypes: MICH, NY*, UC*).
- *Oleandra angusta* Copel., J. Arnold Arbor. 12 48. 1931. Type: SOLOMON ISLANDS. Vanikoro: Kajewski 5371 (holotype: A? not seen; isotypes: US*; UC*).

- Oleandra maquilingensis Copel., Philipp. J. Sci. 46: 217. 1931. M.G.Price, Philipp. Agric. 57: 42. 1974. Zamora & Co, Guide to Philippine flora and fauna 2: 145. 1988. Amoroso & Pava, Philipp. J. Sci. 120: 423-437. 1991. Type. PHIL-IPPINES. Luzon: Matthew s.n. (lectotype: MICH 1210440, here selected, see discussion).
- *Oleandra archboldii* Copel., Philipp. J. Sci. 73: 346. 1940. Type: PAPUA NEW GUINEA. Brass 13002 (holotype: MICH*).
- Oleandra subdimorpha Copel., J. Arnold Arbor. 24: 441. 1943. Type: PAPUA NEW GUINEA. Brass 6886 (holotype: GH, not seen, isotypes: BM*, MICH*).
- Oleandra christopherseni C. Chr, Bull. Bernice P. Bishop Mus. 177 47. 1943. Type: SAMOA. Christophersen 126 (holotype: BISH; isotype: BO). Oleandra clemensiae Copel., Philipp. J. Sci. 81 12. 1952. Copel., Fern Flora of the Philippines: 182. 1958. Type: PHILIPPINES. Clemens 16494 (holotype: MICH; isotype: UC*).
- *Oleandra herrei* Copel., Philipp. J. Sci. 81 12. 1952. Copel., Fern Flora of the Philippines: 182. 1958. Type: PHILIPPINES. Herre s.n. (holotype UC*).
- Oleandra malasianum Ghosh, J. Bombay Nat. Hist. Soc. 80: 630. 1984. Type. MA-LAYSIA. Penang: : Cantor, Wallich 2235 (CAL, not seen, ill. in Ghosh 1984).

Description. Rhizome with main stems creeping or ascending, 3-8 mm thick, white waxy in the older parts, 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 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, phyllopodia on creeping parts few, scattered, on aerial parts in more or less dense, often whorled clusters and branches, short to 15 mm long. Scales persistently covering the rhizome, peltate, $4-6.5 \times 1-1.5$ mm, appressed to squarrose, with dark center and lighter margin and acumen, margin ciliate. Fronds monomorphic or weakly dimorphic, stipe short to 3.5 cm long, without dark colouration; fertile lamina $12-43 \times 0.5-4.5$ cm, base 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 × 5.5 cm; texture thin-chartaceous, costa and lamina on lower surface without dark colouration, 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.

Distribution. India (Himalayas), China (Xizang), Malesian archipelago to Australia, 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.



Map 3. Distribution of Oleandra neriiformis.

Discussion. The epithet *neriformis* published by Cavanilles has to be corrected to "*neriiformis*" (ICBN 60.8). The epithet *neriifolia* used by Presl is either a mistake to be corrected or a superfluous *nom. nov.* and should not be used.

Oleandra neriiformis does not occur in Australia. The reference in Bell (1998) to O. *neriiformis* refers indeed to O. *musifolia* as suggested.

Oleandra maquilingensis is based on two sterile specimens that are considered to represent juvenile plants by Price (1974). Price selected, but did not publish, a lecto-type from among the two, and we here follow that lectotypification. The identification of these sterile specimens with *O. neriiformis* rather than *O. cumingii* is somewhat conjectural, as is the identification of *Blechnum colubrinum* Blanco, for which no specimens at all are available.

Aspidium phyllarthron is one of the two species distinguished by Kunze (1848) among the specimens distributed as Zollinger 1306. In addition, Kunze cited Zollinger 1957. We have not found any specimens of Zollinger 1957, and from the several specimens that have been distributed as Zollinger 1306, we have selected one that fits the description of Aspidium phyllarthron and has a label "1306=1957". Another specimen, labeled "Zollinger 1306 a, Aspidium phyllarthron" (L 0317412), does not fit the description and is O. musifolia.

Variability. With its wide-creeping and persistent rhizome, *Oleandra neriiformis* may form extensive and probably long-lived stands, which, especially when it is collected a number of times over a long period, may give the impression of the presence of a locally abundant species with a highly constant and distinct combination of characters. We expect this is at least partly the basis for the multitude of local species that have been described, and that we all include in *O. neriiformis*. Another problem is posed by the occurrence 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*.



Figure 12. Oleandra neriiformis. **a** scattered phyllopodia on aerial stem **b** middle part of lamina with very closely costal sori and conspicuous indusia **c** lamina **d** lamina base with long stipe : *A.C. Smith 6104* (Fiji) **e** lamina **f** lyrate lamina base with long stipe **g** middle part of lamina, sori costal with conspicuous indusia: *Croft 66* (New Guinea) **h** middle part of lamina, sori costal with conspicuous indusia **i** lamina **j** cuncate lamina base with distinct stipe: *Van Balgooy 5223* (Java) **k** irregularly whorled phyllopodia on aerial stem **I** middle part of lamina with very closely costal sori and conspicuous indusia **m** narrowed lamina base with articulation close to the lamina base **n** lamina: *Chew W-L 942* (Peninsular Malaysia). All views of lamina showing abaxial surface; all specimens L.

The following characters or character complexes, some of which have been used to distinguish species, are variable in particular:

- 1 Place of the stipe articulation. The phyllopodium may be distinctly longer than the very short stipe (fig. 12 k, n), or a distinctly elongated stipe may be present equal to or longer than the phyllopodium (fig. 12 a, d)
- 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 (fig. 12 b, n), or in a more irregular zone at some distance from the costa (fig. 11 b, m).
- 4 Indusium. The presence of an indusium is rarely constant over an area. It may vary from distinct and often firm (fig. 11 h, 12 b) to inconspicuous (then often hairy) or absent (fig. 11 a, k).
- 5 Costal scales: Some forms have uniformly pale and flat costal scales, some have almost uniformly narrow, dark scales, and there are forms that vary in this character.

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 (fig. 12 k–m). This corresponds to the type of *O. neriiformis.* The other form is characterized by longer phyllopodia, stipes short or absent (thus the lamina appearing sessile with regard to the articulation, fig. 2 b), 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, fig. 2 c) that is clearly set off against the stipe, and sori in a more variable position, in some cases almost at the margin (fig. 2b). Other characters, such as indument, or indusium are independently variable and often vary in a similar way across the two forms where they co-occur, thus giving rise to different characteristic character combination in different parts of the distribution area.

Continental Asia. The few collections from continental Asia do not allow for an evaluation of the variability.

Java, Sumatra. On Java and Sumatra, there is no distinction between stipitate and sessile forms, as both stipe and phyllopodium lengths are strongly variable and extremes are not sharply separated. In Backer and Posthumus (1939), all are taken together as *O. neriiformis*. Description (see also fig. 12 h–j): Phyllopodia 2–6 mm, stipes 3–10 mm, lamina base narrowed, never lyrate, lamina variably hairy (mostly glabrous), costal scales usually few, medium dark; sori costal or at short distance from the costa, indusia distinct to firm, glabrous.

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. Holttum (1968b) also distinguishes these two forms, on basis of the same characters, but notes that that they are not sharply distinct, nor ecologically sharply separated, although he cites a difference in elevational specificity. The scant label data indicate no differences in specificity for epiphytism vs terrestrial, or for elevation. Stipitate form description: Phyllopodia very short, stipes elongated, c. 5–10 mm long, lamina glabrous, occasionally hairy, margin glabrous or very nearly so, sori subcostal in an irregular row. Sessile form description (see also fig. 12 k–n): Phyllopodia elongated, 1–6 mm long, stipes mostly very short, sometimes to 3 mm long, lamina hairy, sori strictly costal (rarely to 1 mm from costa).

Borneo. On Borneo, the two forms also differ in hairiness of lamina, but not in the position of the sori, which is 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. Stipitate form description: Phyllopodia up to 6 mm long, stipe 7–25 mm, lamina at base gradually narrowed, usually hairy with relatively long hairs (rarely glabrous), costal scales more or less frequent, mostly brown. Almost exclusively reported as epiphyte. Sessile form description (see also fig. 11 g–j): Phyllopodia 2–8 mm long, stipes at most 1 mm, lamina at base truncate, often ± lyrate, lamina mostly glabrous, sometimes short-hairy, costal scales not frequent, dark, narrow. Mostly reported as terrestrial.

Philippines. On the Philippines, distinctly stipitate forms represent a small minority of all collections (e.g., *Cuming 94, Soejarto 8874, PNH 3862, 8710*), but include the type of *Oleandra neriiformis* (Christensen 1937). 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 (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 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.

Stipitate form description: Phyllopodia to 2 mm, stipes to c. 7 mm, lamina and margin hairy with highly variable density, costa mostly with many pale scales, sori not closely costal to medial or submarginal, indusia glabrous, often small, indistinct. Sessile form description (fig. 11 k–m): Phyllopodia 5–15 mm, stipes short, up to 1 mm long, otherwise similar.

Celebes, Moluccas. In eastern Malesia south of the Philippines, two forms cooccur on Celebes and the Moluccas, while the stipitate form extends to the Solomon islands and Vanuatu. Both forms here have indusia that are frequently shortly setose.

Stipitate form description: Phyllopodia 1–5 mm, stipes 8–25 mm, lamina base gradually narrowed, costal scales pale except near base of lamina, lamina setose, lamina

hairs relatively long, margin often distinctly fimbriate with hairs shorter or equal to those on lamina, sori costal, indusia firm, with wide sinus, usually glabrous.

Sessile form description: Phyllopodia 5–15 mm, stipes very short to occasionally 3 mm long, lamina base narrowed to ultimately cuneate, not distinctly lyrate, lamina indument often long, conspicuous on all veins, margin often distinctly fimbriate with hairs similar to these on the lamina, costal scales few or absent, dark, sori narrowly costal, indusium distinct and persistent but not firm, often with narrow sinus, sometimes setose.

Kato (1989) distinguishes the specimens from Ceram with a very small, setose indusium as *O. cuspidata*, but this represents only the extreme state of variability.

Fiji, Samoa. More eastwards in the Pacific Islands, there is no variability in the location of the articulation. All specimens from this area have elongated stipes, and can collectively be distinguished from the forms in other areas by the distinctly more lax clusters of fronds on the aerial stems (fig. 12 a), with the fronds mostly hardly clustered at all (a character in which they resemble *O. pilosa* Hooker, from Tropical America). Regional differences show up mainly in the indument of the fronds. On Samoa, the lamina is less densely hairy than on Fiji, and the hairs on the lamina, when present, are distinctly shorter than those on the margin. Costa scales also differ, and are distinctly darker on Samoa than on Fiji, while sori are somewhat less strictly costal on Samoa.

Fiji form description (see also fig. 12 a–d): Phyllopodia 1–9 mm, stipes 5–35 mm, lamina base gradually narrowed, costal scales pale, lamina setose, lamina hairs 1–2 mm long, margin often distinctly fimbriate, hairs on margin shorter or at most equal to those on lamina, sori costal, indusia distinct, glabrous or setose,

Samoa form description: Phyllopodia 1–7 mm, stipes 2–28 mm, lamina base gradually narrowed, costal scales brown to dark, lamina glabrous or setose, with hairs to 0.5 mm long on the lamina, 1–2 mm long on the margin, sori costal or subcostal leaving a sterile zone of 0.5–3 mm wide, indusia distinct, glabrous or setose.

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.

Stipitate form description (see also fig. 12 e-g): Phyllopodia to 4 mm, stipes 5–25 mm, lamina base gradually narrowed, costal scales pale except near base of lamina, lamina setose, with hairs 0.5–1.5 mm long, margin glabrous, sori costal or subcostal leaving a sterile zone of 0.5–2.0 mm wide, indusia firm, with wide sinus, usually glabrous.

Sessile form description (see also fig. 11 a–c): Phyllopodia to 4 mm, stipes very short or absent, articulation directly below the base of the lamina, fronds slightly but usually distinctly dimorphic, lamina narrowed to a truncate or somewhat lyrate base, costal scales mostly brown to dark, lamina glabrous or sometimes short setose, with hairs to 0.5 mm long, margin usually with a few scattered pale, acicular hairs especially near the base, sori medial or submarginal leaving a sterile zone of 0.5–7 mm wide, indusia small and inconspicuous in older sori, occasionally more distinct, often fringed with pale acicular hairs.

5. Oleandra sibbaldii

http://species-id.net/wiki/Oleandra_sibbaldii Map 4

- Oleandra sibbaldii Grev., Ann.and Mag.Nat.Hist.Ser.2 1: 327. 1848. Copel., Bull. Bernice P. Bishop Mus. 93: 61. 1932. Philipp. J. Sci. 73: 346. 1940. C.Chr., Bull. Bernice P. Bishop Mus. 177 47. 1943. Copel., Fern Flora of the Philippines: 183. 1958. Brownlie, The Pteridophyte Flora of Fiji: 157. 1977. M.Kato, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 239. 1989. R.M.Tryon, Rhodora 102: 436, fig. 7. 2001. Oleandra cumingii var. sibbaldii Baker, Syn. Fil. (Hooker & Baker): 303. 1868. Type: FRENCH POLYNESIA. Tahiti: Sibbald s.n. (holotype: E, barcode E00417634, not seen).
- *Oleandra tricholepis* Kunze, Kunze, Bot. Zeitung (Berlin) 9: 349. 1851. Type. INDO-NESIA. Bornea: Hupe s.n. (holotype: LZ, probably destroyed).
- *Oleandra whitmeei* Baker, J. Bot. 5: 11. 1876. ("*whitmei*"). *Oleandra whitmeei* Copel., Polypod. Phil. Isl.: 49. 1905. Copel., Bull. Bernice P. Bishop Mus. 59 87. 1929. Type. SAMOA. Savai'i : Whitmee & Powell s.n. (holotype: K).
- *Oleandra gracilis* Copel., Univ. Calif. Publ. Bot. 12: 397, pl. 52b. 1931. Copel.Philipp. J. Sci. 73: 347. 1940. Type: PAPUA NEW GUINEA. New Guinea: Keysser 74 (holotype: UC).
- *Oleandra crassipes* Copel., Philipp. J. Sci. 73: 347, Pl. 2. 1940. Type: INDONESIA. New Guinea: Bernhard camp, Brass 12109 (holotype: UC; isotypes: BO, L).

Description. Rhizome long-creeping or pendulous, sparsely branching, 1.5-4.5 mm thick, very strongly white waxy, in cross-section without or with few scattered sclerified strands, phyllopodia scattered, (0.3–)0.8–4.0(–5.7) cm long, roots with distinct unbranched parts. Scales deciduous, exposing the rhizome in older parts, peltate, (3- $)5-15(-18) \times (0.3-)0.4-0.9(-1.2)$ 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; stipe (0.3-)0.5-3.5(-4.5) cm long, often with dark coloration on abaxial side; lamina to $(4.5-)15-40(-58) \times$ 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 $6(-11) \times 1(-1.2)$ 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 ca. $4 \times 1 \mu m$, perispore baculate, outer layer much perforated.



Map 4. Distribution of Oleandra sibbaldii.

Distribution. Eastern Malesia to Pacific Islands. Malaysia: Sabah, Sarawak, Philippines: Mindanao; Indonesia: Sulawesi; Moluccas, Papua; Papua New Guinea; Solomon islands; Vanuatu; Tahiti and Marquesas: Hiva Oa, Nuku Hiva, Tahuata, Ua Huka and Ua Pou; Western Samoa: Savaii; Fiji.

Ecology. Epiphytic, epilithic, or less commonly terrestrial (most often at elevations over 1500m), commonly collected from mossy forests, climbing or sprawling among bryophytes and other epiphytes, or pendulous from mossy tree branches, to 600 m (Marquesas and Tahiti); or from 1000 to 3000 m (elsewhere).

Discussion. *Oleandra sibbaldii* is common on New Guinea, but appears to be much sparser towards the periphery of the distribution area.

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 undulata

http://species-id.net/wiki/Oleandra_undulata Map 2

- Oleandra undulata Ching, Lingnan Sci. J. 12: 565. 1933. Holttum, Rev. Fl. Mal. 2: 384. 1954. Ching, Fl. Reipubl. Popularis Sin. 2: 322. 1959. X.C.Zhang, Ching Mem. Vol.: 92. 1999. R.M.Tryon, Rhodora 102: 346, fig. 6. 2001. Polypodium undulatum Willd., Sp. Pl., ed. 4 [Willdenow] 5: 155. 1810. Type: INDIA. Tranquebar: Klein 887 (holotype: B - Willdenow 19616 -01 0).
- Oleandra pubescens Copel., Univ. Calif. Publ. Bot. 12: 397, Pl. 52A. 1931. Type: THAILAND. Eryl Smith 1072 (holotype: UC*).

Description. *Rhizome* short-creeping, little branching, 5–6 mm thick (3–5 when dry), not white waxy, in cross-section with many scattered sclerified strands; phyllopodia irregularly scattered, close together or distant, 2–8 cm long, roots scattered, without distinct unbranched parts. *Scales* persistently covering the rhizome, peltate, $3–5 \times 1-1.6$ mm, slightly spreading, acumen brown, with sparsely ciliate margin, apex short, wide. *Fronds* monomorphic; stipe 3–15 cm long, without dark coloration, articulation at

1/5-1/2 from base; lamina to $60 \times 1-5.5$ cm, widest in middle part, base truncate or cuneate to gradually narrowed, apex acute to narrow-acuminate, texture herbaceous, upper surface glabrous or sparsely, lower surface more densely set with usually acicular, sometimes slightly catenate hairs to c. 0.5-1.0 mm long; costa on lower surface without dark coloration, without scales. *Sori* close to costa or leaving a distinct 1-6 mm wide sterile zone between costa and soral zone, indusium firm, to 2 mm wide, hairy. Sporangial stalk without glands below the sporangium. Spores finely papillose and coarsely ridged, perispore baculate, outer layer not perforated.

Distribution. Burma, Laos, Thailand, China: Yunnan. Mostly below 1000 m.

Ecology. In open or deciduous forests, often disturbed; terrestrial or epilithic, rhizome subterraneous, on rocks or in crevices, mostly on granite.

Discussion. Oleandra undulata can be difficult to distinguish from O. cumingii. In addition to the differences listed under that species, subterraneous growth of the rhizome may be characteristic for O. undulata, but field observations are lacking for many specimens.

7. Oleandra vulpina

http://species-id.net/wiki/Oleandra_vulpina Map 5

Oleandra vulpina C.Chr., Dansk Bot. Ark. 9 68. 1937. Type. PAPUA NEW GUIN-EA. New Guinea: Ledermann 7652 (holotype: BM).

Description. Rhizome long-creeping, ca. 3 mm thick, not white waxy, sparsely branching, roots with unbranched parts; in cross-section with weakly developed sclerified shealth and few scattered sclerenchyma strands, phyllopodia scattered, 3-6 cm distant, 6–7 mm long. Scales scattered, not covering the rhizome, peltate, to 5×0.5 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; stipes with scales as the rhizome but less dense and with short fine glandular hairs; stipe 2–3 mm long, without dark coloration on abaxial side, bearing short fine glandular hairs; lamina linear-lanceolate, 17.5-20 × 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 absent.

Distribution. New Guinea, at 975 m.

Ecology. Scandent on trunk of Sago palm in garden, or in forest.

Vernacular name. Taingelem (Wapi language, Miwaute)



Map 5. Distribution of Oleandra vulpina (triangles), O. werneri (circles).

Discussion. Oleandra vulpina is distinct from O. sibbaldii in the rhizome and costa scales. Rhizome scales are darker in colour with pale-coloured margin, long subulate apices, and margin strongly ciliate with glandular hairs. A similar glandular scale indument is found in the American O. articulata (Sw). C. Presl, but not in the other Southeast Asian species. The costa scales beneath are small and inconspicuous, narrowly lanceolate. 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 and bear numerous setose hairs.

8. Oleandra wallichii

http://species-id.net/wiki/Oleandra_wallichii Map 2

- Oleandra wallichii C.Presl, Tent. Pterid.: 78. 1836. Fée, Mém. Foug., 5. Gen. Filic.: 304. 1852. Hook., Sp. Fil.: 158. 1862. Ching, Fl. Reipubl. Popularis Sin. 2: 321. 1959. Shieh, DeVol & Kuo in Huang, Fl. Taiwan, ed. 2.: 203, Pl. 83. 1994. X.C.Zhang, Ching Mem. Vol.: 94. 1999. R.M.Tryon, Rhodora 102: 434, fig. 5. 2001. Aspidium wallichii Hook., Exot. Fl.: Pl. 5. 1823. Pl. Neuronia asplenioides D.Don, Prodr. Fl. Nepal.: 7. 1825., nom. illeg. Type: NEPAL. Wallich s.n. (holotype K; isotypes: BM, PE).
- *Oleandra wallichii var. lepidota* Christ, Bull. Acad. Int. Geogr. Bot. 15: 140. 1906. Type: CHINA. Western China: Wilson 5246 (holotype P; isotype: K).

Description. *Rhizome* creeping, 3–4 mm thick (2–3 when dry), white waxy in the older parts, with long, leafless parts alternating with more or less dense clusters of very short phyllopodia, usually less than 2 (–5) mm high, of which usually only 1–2 bear fronds at the same time, branches usually in opposite pairs; in cross-section with weak sclerenchyma sheath and without sclerified strands, roots scattered, usually with long unbranched parts. Scales persistently covering the rhizome, peltate, $3–7 \times 1–1.3$ (–1.5) mm, base appressed, with dark center and lighter margin, acumen brown, usually recurved, with ciliate margin, apex twisted and with frizzly cilia. *Fronds* monomorphic; stipe 1–5 cm long, with dark coloration on abaxial side often distinctly bicolorous, with catenate hairs; lamina $13–45 \times 2–4.5$ cm, base truncate to rounded, apex often abruptly caudate, texture thin-herbaceous, translucent, both surfaces densely set with catenate hairs 0.5–1 mm long; costa on lower surface in basal half of lamina with dark coloration, with copious 2–4 mm long pale scales. *Sori* close to costa, indusium thin, to 1 mm wide, glabrous or hairy. Sporangial stalk without glands below the sporangium. Spores echinate and ridged, perispore solid.

Distribution. Himalayas to Northern Thailand, Yunnan and Taiwan, 1600 to 3600 m. India, Nepal, Bhutan, China (Yunnan, Taiwan), Thailand.

Ecology. Mostly epiphytic, on mossy trunks, also on cliff faces or boulders.

Discussion. Oleandra wallichii differs from O. undulata in the more wide-creeping rhizome that is often distinctly glaucous beneath and between the scales, without sclerenchyma strands; the often conspicuously bicolorous stipe, lamina with usually very distinctly apiculate apex and costa with frequent scales, sori constantly closely costal, with small indusia.

9. Oleandra werneri

http://species-id.net/wiki/Oleandra_werneri Map 5

- Oleandra werneri Rosenst., Repert. Spec. Nov. Regni Veg. 5: 40. 1908. Copel., Philipp. J. Sci. 73: 347. 1940. R.M.Tryon, Rhodora 102: 433, fig. 3. 2001. Type. INDO-NESIA. New Guinea: Werner 12 (lectotype: L, "Rosenstock 28", here selected; isotype: B).
- *Oleandra dimorpha* Copel., Philipp. J. Sci. 60: 111. 1936. M.Kato, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 239. 1989. Type. SOLOMON ISLANDS. San Christoval: Brass 2916 (holotype: MICH).

Description. *Rhizome* with main stems creeping, scrambling or pendent, 2–3 mm thick, white waxy in the older parts, sparsely rooting, mostly terete when dry, bearing scattered short, usually less than 5 mm long phyllopodia, phyllopodia on aerial parts more closely together but not densely clustered; all parts in cross section with a peripheral sclerified sheath and scattered sclerified strands. *Scales* covering the rhizome, peltate, $3-4 \times 0.5-1$ mm, somewhat squarrose, with dark center and lighter margin and acumen, margin

ciliate especially when young. *Fronds* strongly dimorphic, stipe 0.5-2.5 cm, without dark colouration, especially upwards with up to 2 mm long hairs; lamina chartaceous; fertile $27-56 \times 0.5-1$ (-1.7) cm, base and apex narrow, sterile $17-30 \times 2.2-5.7$ cm, base mostly cuneate, apex distinctly 2–3.5 cm caudate; costa and lamina on lower surface glabrous or with up to 2 mm long hairs, costa without dark colouration, 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. Indonesia (Maluku, Papua); Papua 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 forests, most frequently in montane or mossy forests, on ridges, up to c. 2000 m.

Discussion. As in *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.

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.

Acknowledgements

We are grateful for the directors of the herbaria of BISH, BM, MICH, PNH, SING, UC for the loan of material, and of B, BM, BO, K, KEP, KLU, P, PE for the permission to study their collections. The contributions of many staff members in L, but in particular Peter van Welzen and Niels Raes, to the georeferencing of collecting localities and thus to the maps presented here are gratefully acknowledged.

References

- Backer CA, Posthumus O (1939) Varenflora voor Java. `s Lands plantentuin, Buitenzorg, XLVII + 370 pp.
- Bell GH (1998) Oleandra. Flora of Australia. Australian Biological Resources Study/ CSIRO Publishing, Melbourne, xxii + 766 pp.
- Cavanilles AJ (1799) Nuevos caractéres genéricos de los Helechos por Smith. Anales de Historia Natural 2: 108–115.
- Cavanilles AJ (1802) Descripcion de las plantas. Imprenta real, Madrid, cxxxvi+625 pp.
- Christensen C (1937) Taxonomic fern studies III. Revision of the genera and species of ferns described by A.J. Cavanilles. Dansk Botanisk Arkiv Udgivet af Dansk Botanisk Forening Copenhagen 9: 3–32.

Copeland EB (1947) Genera Filicum. Chronica Botanica, Waltham, Mass, 247 pp.

- Don D (1825) Prodromus Florae Nepalensis. J. Gale, London, 256 pp.
- Harmata K, Kornás J (1978) Spore morphology in two varieties of Oleandra distenta Kunze (Davalliaceae, Filicopsida) from southern tropical Africa. Zeszyty Naukowe Uniwersitetu Jagiellónskiego; Prace Botaniczne Cracow 493: 8–14.
- Holttum RE (1959) Introductory matter. In: Van Steenis CGGJ (Ed) Flora Malesiana II. Martinus Nijhoff, Dr. W. Junk, The Hague, Boston, London, i-xxiii
- Holttum RE (1968a) A commentary on some type specimens of ferns in the Herbarium of K.B. Presl. Novitates Botanicae ex Instituto et Horto Botanico Universitatis Carolinae Pragensis Prague: 3–57.
- Holttum RE (1968b) A revised Flora of Malaya II. Ferns. Government Printing Office, Singapore, 653 pp.
- Hooker WJ (1862) Species Filicum. William Pamplin, London, 211–249.
- Kramer KU (1990) Oleandraceae. In: Kramer KU, Green PS (Eds) The Families and Genera of Vascular Plants. Springer, New York etc., 190–193.
- Kunze G (1848) In filices Javae Zollingerianas. Botanische Zeitung Berlin 6: 234–239.
- Kunze G (1851) Oleandra Botanische Zeitung Berlin 9: 345–349.
- Kuo L-Y, Li F-W, Chiou W-L, Wang C-N (2011) First insights into fern matK phylogeny. Molecular Phylogenetics and Evolution San Diego, CA 59: 556–566. doi: 10.1016/j. ympev.2011.03.010
- Liew FS (1977) Scanning electron microscopical studies on spores of Pteridophytes. 11. The family Oleandraceae (Oleandra, Nephrolepis and Arthropteris). Gardens' Bulletin Singapore 30: 101–110.
- Löve A, Löve D, Pichi Sermolli REG (1977) Cytotaxonomical atlas of the Pteridophyta. J. Cramer, Vaduz, 398 pp.
- Manton I, Sledge WA (1954) Observations on the cytology and taxonomy of the pteridophyte flora of Ceylon. Philosophical Transactions of the Royal Society of London Series B, containing papers of a Biological Character London 238: 127–185.
- Nayar BK, Bajpai N (1978) Morphology in relation to phylogeny of the Davallioid-Oleandroid group of ferns. Phytomorphology; an International Journal of Plant Morphology Delhi 26: 333–354.
- Pichi Sermolli REG (1965) Adumbratio Florae Aethiopicae. 11. Oleandraceae. Webbia; Raccolta de Scritti Botanici Florence 20: 745–769.
- Presl CB (1836) Tentamen Pteridographiae. Theophilus Haase, Prague.
- Price MG (1974) The Pteridophytes described from Mount Makiling, Luzon. Philippine Agriculturist Manila, Los Baños, Laguna 57: 37–48.
- Reinwardt CGC (1825) Sylloge plantarum novarum itemque minus cognitarum a praestantissimis botanicis adhuc viventibus collecta et a societate regia botanica Ratisbonensis edita. C.E. Brenck, Ratisbonae, 3–16.
- Schuettpelz E, Pryer KM (2007) Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon; Official News Bulletin of the International Society for Plant Taxonomy Utrecht 56: 1037–1050.

- Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PC (2006) A classification for extant ferns. Taxon; Official News Bulletin of the International Society for Plant Taxonomy Utrecht 55: 705–731.
- Smith J (1841) Enumeration Filicum Philippinarum. Journal of Botany, (Being a Second Series of the Botanical Miscellany), Containing Figures and Descriptions London III 393–422.
- Smith J (1842) An arrangement and definition of the genera of Ferns, with observations on the affinities of each genus. Journal of Botany, (Being a Second Series of the Botanical Miscellany), Containing Figures and Descriptions London 4: 38–70.
- Splitgerber FL (1840) Enumeratio Filicum et Lycopodiacearum quas in Surinamo legit F.L. Splitgerber. Tijdschrift voor Natuurlijke Geschiedenis en Physiologie Amsterdam 7: 411
- Swartz O (1801) Genera et species filicum ordine systematico redactarum. Journal für die Botanik [Edited by H A Schrader] Göttingen 1800.
- Swartz O (1806) Synopsis Filicum. Bibliopolii novi academici, Kiel, 44 pp.
- Index Herbariorum: A global directory of public herbaria and associated staff. http://sweetgum. nybg.org/ih/ [accessed 24 3 2011.2011]
- Tryon AF, Lugardon B (1991) Spores of the Pteridophyta. Springer, New York etc., x + 648 pp.
- Tryon RM (1997) Systematic notes on Oleandra. Rhodora; Journal of the New England Botanical Club Cambridge, MA 99: 335–343.
- Tryon RM (2001) Systematic notes on the Old World fern genus Oleandra. Rhodora; Journal of the New England Botanical Club Cambridge, MA 102: 428–438.
- Tryon RM, Tryon AF (1982) Ferns and allied plants, with special reference to tropical America. Springer, New York etc., 857 pp.
- Tsutsumi C, Kato M (2006) Evolution of epiphytes in Davalliaceae and related ferns. Botanical Journal of the Linnean Society 151: 495–510. doi: 10.1111/j.1095-8339.2006.00535.x
- Wetter C (1951) Über die Luftwurzeln von Oleandra. Planta Archiv für wissenschaftliche Botanik (Zeitschrift für wissenschaftliche Biologie Abt E) Berlin 39: 471–475.

Appendix I

Identification list

O. coriacea: 1

- O. cumingii: 2
- O. musifolia: 3
- O. neriiformis: 4
- O. sibbaldii: 5
- O. undulata: 6
- O. vulpina: 7
- O. wallichii: 8
- O. werneri: 9
- Abbe, L.B.; Abbe, E.C. 9650 : 4; 9805 : 4; Abdul Samat, A. 118 : 4; Adelbert, A.G.L.
 128 : 4; 252 : 4; 490 : 4; Aet; Idjan 324 : 4; Ajoeb 265 : 4; Allen, B.M. 1427 : 4;
 1779 : 4; Alston, A.H.G. 16962 : 4; Anderson, J.A.R. S 18570 : 4; Andrews, S.B.;
 Stocker, G. 283 : 3; Ashton, P.S. 242 : 4; 424 : 1.
- Backer, C.A. 12576 : 3; 23016 : 4; 25877 : 4; 36909 : 3; Bakhuizen v.d. Brink, R.C. 1539: 4; 2777: 4; 3208: 4; 4482: 4; 7677: 4; Balgoov, M.M.J. van 1887: 5; 5037 : 4; 5223 : 4; Balgooy, M.M.J. van; Wiriadinata, H. 2865 : 4; Bamler, G. 31 : 4; Bamler, M.G. ROS 132 : 4; Banoc, L.M. 3 : 6; 58 : 6; Banying ak Nyudong S 17211 : 4; S 19419 : 4; Barcelona, J.F. 2040 : 4; Barcelona, J.F.; Busemeyer, D.T. 717 : 4; Barcelona, J.F.; Busemeyer, D.T.; Ippoli, A. 575 : 4; 622 : 4; Bartlett, H.H. 15759 : 4; Beaman, J.H. 6957 : 4; 8027 : 4; 9605 : 4; 9921 : 4; 10332 : 4; Beusekom, C.F. van; Beusekom, R.J. van 1542 : 3; Beusekom, C.F. van; Charoenphol, C. 1690 : 3; Beusekom, C.F. van; et al. 4517 : 3; 4526 a: 3; 4813 : 6; Beusekom, C.F. van; Phengkhlai, C. 2431 : 8; Bor, S. 767 : 8; Borssum Waalkes, J. van 1290 : 4; 2824 : 4; Braithwaite, A.F. 4216 : 9; R.S.N.H. 2370 : 5; RSNH 2087 : 4; RSNH 2110 : 4; RSNH 2436 : 4; RSS 4045 : 9; RSS 4174 : 4; RSS 4471 : 9; RSS 4676 : 5; Brass, L.J. 2916 : 9; 3032 : 4; 3341 : 4; 3893 : 4; 7115 : 4; 11266 : 5; 11870 : 4; 12109 : 5; 12158 : 5; 12841 : 9; 12842 : 4; 13002 : 4; 13214 : 9; 13215 : 4; 13323 : 4; 23016 : 4; 23174 : 5; 24907 : 4; 25803 : 4; 25805 : 4; 26074 : 4; 26087 : 4; 29706 : 5; 31944 : 4; 32064 : 9; Britton, B.B. 326 : 4; Brooke, W.M.A. 8590 : 4; Brooks, C.J. 115 : 4; 263 s: 4; Brown, E.D.W. 980 A: 5; 980 B: 5; 980 C: 5; 980 D: 5; 980 E: 5; Brownlie, G. 1717 : 4; Bünnemeijer, H.A.B. 675 : 4; 3875 : 4; 4127 : 4; 4238 : 4; 5494 : 4; 8969 : 4; 11481 : 3; 12161 : 3; Burkill, I.H. 12904 : 4; SFN 8497 : 4; Buwalda, P. 3640 : 4; 5171 : 4; 6622 : 4; 8063 : 4.
- Caerlan; Sageed; Romero PPI 13079 : 4; Carr, C.E. 13428 : 4; 13552 : 5; 13981 : 9; 14419 : 5; 14831 : 9; Carrick, J. JC 102 : 4; Chai, P. S 37561 : 4; S 39456 : 4; Chao Yu Zhang 21441 : 8; Charoenphol, C. 4241 : 3; Cheesman, L.E. 128 : 4;

1199 : 9; Chen Nian-qu 40930 : 2; Cheng Shu-Zhi; Li Bosheng 1015 : 8; 5250 : 4 Chew, W.L. 942 : 4; 1273 : 4; Chew, W.L.; Corner, E.J.H.; Stainton, A. 298 : 4; 1461 : 4; Chin, S.W. 28 : 4; Ching, R.C. 25432 : 8; Christophersen, E. 15 : 4; 125 : 4; 520 : 4; 826 : 5; 866 : 4; 2138 : 5; 3095 : 5; Christophersen, E.; Hume, E.P. 2305 : 4; Chun, N. 40930 : 2; Cicuzza, D. 178 : 4; Clarke, C.B. 42231 A: 6; Clemens, J. 421 : 4; 4534 : 9; 32552 : 5; 32871 : 5; Clemens, J.; Clemens, M.S. 27210 : 4; 28337 : 4; 28763 : 4; 30705 : 4; 30902 : 4; Clemens, M.S. 9114 : 5; 11053 : 4; 16494 : 4; 41009 : 5; Clunie, N.M.U. LAE 63276 : 9; LAE 63380 : 9; LAE 63399 : 4; Co, L. 3197 : 4; Coert, J.H. 644 : 4; 1497 : 4; Collecteur de Darjeeling 109 : 8; Coode, M.J.E. 6498 : 4; NGF 32846 : 4; Coode, M.J.E.; et al. 7548 : 4; Copeland, E.B. 137 : 4; 1381 : 4; 1474 : 4; 1766 : 4; 1804 : 2; 2016 : 4; ppe 56 : 4; Cox, P.A. 224 : 4; 345 : 4; 838 : 4; Craven, L.A. 1123 : 5; 1269 : 5; Craven, L.A.; Schodde, R. 133 : 4; 287 : 9; Croft, J.R. 34 : 4; 66 : 4; 224 : 9; 817 : 4; 821 : 4; 1223 : 4; 1897 : 9; 1987 : 9; Croft 11 : 5; Croft 875 : 5; Croft 1508 : 5; LAE 65781 : 5; LAE 65822 : 5; LAE 68337 : 5; LAE 68911 : 4; LAE 71012 : 4; LAE 71112 : 4; Croft, J.R.; Katik, P. NGF 14933 : 4; Croft, J.R.; Lelean, Y. LAE 65642 : 4; Croxall, J.P. 6016 : 5; Cuming, H. 60 : 2; 94 : 4; Curry, P. 1644 : 4; Curtis, C. 160 : 4.

- Damas, K. LAE 58855 : 4; Danser, B.H. 5971 : 4; Darbyshire, P.J. 226 : 7; 325 : 9;
 Darnaedi, D. 1554 : 5; 2362 : 4; 2725 : 3; Davidse, G.; Sumithraarachchi, D.B. 7965 : 3; Davis, A.P. 464 : 4; 814 : 5; 814 : 5; Degener, O. 14279 : 4; Docters van Leeuwen, W.M. 10942 : 4; Dodd, J. E 10 : 9; Dransfield, S. 976 : 4.
- Ecology Highland Group 14053 : 8; Edaño, G.E. 26 : 4; 71 : 4; 303 : 4; 637 : 4; 647
 : 4; 796 : 4; 806 : 4; 1540 : 4; 2596 : 4; 5922 : 4; 6260 : 4; 8031 : 4; pnh 17267
 : 4; Edwards, P.J. 724 : 1; 1988 : 4; 2141 : 4; Elbert, J. 1650 : 3; Elmer, A.D.E.
 7940 : 4; 9069 : 4; 9959 : 4; 10908 : 4; 11451 : 5; 14140 : 4; 14149 : 4; 17694 :
 4; 17964 : 4; Endert, F.H. 3030 : 4; 4244 : 4; Evans, J.H.N.; Gordon, W. 998 : 2; Eyma, P.J. 1664 : 5; 4484 : 9; 4726 : 4.
- Fallen, M.E. 437 : 5; Faurie, U. 611 : 8; Florence, J. 3634 : 5; 4336 : 5; 6780 : 5; 7498
 : 5; 9623 : 5; 9770 : 5; Forbes, H.O. 662 : 3; 884 : 3; 3482 : 2; Foreman, D.B. LAE
 59150 : 9; NGF 45759 : 4; forest production group 84422 : 2; Forrest, G. 11799
 : 8; 18581 : 8; 24238 : 8; 26691 : 8; Fosberg, F.R. 62670 : 5; Foxworthy, F.W. 72
 : 4; 77 : 4; 359 : 4; Fu Guoxun 415 : 8; Fuchs, H.P.; Collenette, S.H. 21671 : 4.
- Gaerlan, F.J.M.; Sagcal, E.; Romero PPI 10874 : 4; PPI 13079 : 4; Gagné, B.H. 1113 : 5; 1580 : 5; BHG 2318 : 5; Garber, D.W. 724 : 4; 1046 : 4; Gawi, M. 11 : 5; Gebo, A. 1619 : 4; Geesink, R.; Santisuk, T. 5384 : 2; Ghose, G. 11 : 3; Gideon, O. LAE 57504 : 4; Gideon, O.; Silu, J. LAE 76918 : 4; Gillespie, J.W. 2748 : 4; 3249 : 4; 3815 : 4; 4110 : 5; Gillett, G.W. 2174 : 5; Gong Wu Su 479 : 8; Graeffe 1078 : 4; Grant, M.L. 3704 : 5; 4095 : 5; Gravendeel, B. 593 : 4;

Grey; Wilson, E.H.; Phillips 289 : 3; Gurung, V.L. 55 : 2; Gwynne Vaughan, D. 431 : 4.

- Haas, J.H. de 2622 : 8; Hallier, H. 418 : 4; 1699 : 4; 3297 : 4; Hansen, B.; Smitinand, T. 11846 : 2; Hansen, C. 1128 : 4; Hardeveld, C. van 318 : 3; Hartley, T.G. 11417 : 4; Harvey, H.D. 1668 : 4; Hassan Flora Project 579 : 3; 692 : 3; 887 : 3; Henderson, M.R. 11197 : 4; 17879 : 4; Hennipman, E. 3092 : 3; 3334 : 6; 3334 A: 2; 3334 B: 6; 3413 : 8; 3568 : 3; 3655 : 3; 5370 : 5; 5430 : 5; 5518 : 4; 6158 : 4; Henry, A. 9484C : 2; 9484 : 8; Hirano, M.; Hotta, M. 1522 : 4; Hirschland, J.G. 2 : 4; Hochreutiner, B.P.G. 1755 : 4; 3326 : 4; Hodel, D.R. 1373 : 5; Höft, R. 2260 : 5; 2733 : 5; 2953 : 5; 3659 : 5; Holstvoogd, C. 471 : 4; 472 : 3; 847 : 3; 848 : 3; Holttum, R.E. 1668 : 4; 20580 : 4; 31319 : 4; N.G.F 40181 : 5; SFN 10686 : 4; SFN 11403 : 4; SFN 14852 : 2; SFN 25723 : 4; SFN 39209 : 3; Hoover, W.S. 434 : 9; Hortus, Bogor 57 : 4; 177 : 4; Hosokawa, Takahide 8677 : 4; Hotta, M. 14797 : 1; Hou, D. 213 : 4; Hovenkamp, P.H. 527 : 4; 05 05 : 4; Huang, T.C.; Kao, M.T. 1730 : 8; Hume, H.L. 7174 : 4.
- Investigation team in western Yunnan 11416 : 8; Iwatsuki, K. 484 : 8; 531 : 3; B 1870 : 4; B 2495 : 4; B 2505 : 4; C 921 : 9; P 597 : 3; Iwatsuki, K.; Fukuoka, N. T 3424 : 6.
- Jaag, O. 1110 a: 3; 1170 : 3; 1960 : 4; Jacobs, M. 7948 : 4; Jacobson, E. 2549 : 4; Jermy, A.C. 3488 : 5; 13677 : 4; 14420 : 1; Jiang Xinglin 35239 : 8; John, H.; St 17025 : 5; Johns, R.J. 7369 : 4; 7986 : 5; 9023 : 5; 9091 : 5; 10303 : 4; 10329 : 5; Jones, W.B. 1798 : 5.
- Kadim bin Tassim K 491 : 2; Kajewski, S.F. 874 : 4; 2691 : 4; Kalkman, C. 4005 : 4; 4379 : 5; 4469 : 5; Kathmandu Expedition KE 1067 : 8; Katik, P. LAE 56318 : 4; Kato, M. 822 : 9; B 3674 : 4; B 6042 : 4; B 7667 : 4; B 7901 : 4; B 9511 : 1; B 9569 : 1; B 9813 : 1; B 10920 : 1; B 11131 : 4; C 1278 : 9; C 1365 : 4; C 1729 : 4; C 1945 : 4; C 2907 : 4; C 4121 : 4; C 5058 : 4; C 7412 : 9; C 7480 : 5; C 11656 : 4; C 12846 : 5; C 12965 : 4; C 13351 : 4; C 14279 : 4; C 14361 : 5; C 14446 : 4; Kato, M.; Setoguchi, H.; Darnaedi, D. 1160 : 4; Kato, M.; Wiriadinata, H. B 4749 : 4; B 4924 : 4; B 5283 : 4; B 5931 : 4; Kaudern, W. 86 : 4; Keenan 1386 : 6; Kerr, A.F.G. 9363 : 6; 9645 : 3; Kessler, P.J.A. 2857 : 4; Keysser, C. II 74 : 5; Kinbag, F. 013 : 5; King's collector 2424 : 4; Kog, P. 004 : 5; Koorders, S.H. 14942 B: 4; 19832 b: 3; 36678 B: 4; Koster, C. BW 13848 : 4; Kostermans, A.J.G.H. 2280 : 4; 5549 : 4; 6513 : 4; Kostermans, A.J.G.H.; Soegeng, W. 509 : 4; Kostermans, A.J.G.H.; Wirawan, N. 747 : 3; Kuhl, H.; Hasselt, J.C. van 7 : 4; Kurz, S. 203 : 3.
- Lace, J.H. 4227 : 6; LAE 65715 : 4; Lai, J.; Enjah S 64162 : 4; Lam, H.J. 537 : 4; 1449 : 4; 1856 : 5; 1943 : 5; 6897 : 4; Lang Kai-Yong; Zhang Yongtian 3360 : 8; Larsen, K. 44 : 3; 964 : 3; 2689 : 6; 8936 : 6; 10678 : 3; 31861 : 6; Larsen, K.; Larsen, S.S.

30713 : 3; Lau S.K. 1490 : 2; 3108 : 2; 27368 : 2; Lavarack, P. NGF 31446 : 5; Lavarack, P.; Ridsdale, C.E. NGF 31444 : 9; LeBronnec, G. 809 : 5; Ledermann 7652 : 7; Leeuwenberg, A.J.M. 3 : 4; Li Bosheng 14023 : 8; Li Hua Hou 1009 : 2; Li Yang Yi; Li Bosheng 13537 : 8; Liu Bingrong 5064 : 2; 5065 : 2; Lorence, D.H. 6094 : 5; Lörzing, J.A. 728 : 3; 5202 : 4; 6890 : 4; 14050 : 4; Luang Winit-Wanadorn 47 : 6; Luang, Winit 1003 : 3; Ludlow, F. 6496 : 8; 6685 : 8; Ludlow, F; Sherriff, G.; Hicks, J.H. 17008 : 8; 17416 : 8; 17499 : 8; 17536 : 8; 17540 : 8; 19563 : 8; 20909 : 8; Luerssen 3766 : 4; 9902 : 4.

- M. K. Li 450 : 2; MacDaniels, L.H. 1531 : 5; Main 261 : 4; Mamit, J.D. S 34391 : 4; Mangen, J.M. 2227 : 4; Manickam, V.S.; Matthew, K.M. RHT 34242 : 3; Manner; Street 346 : 4; 592 : 4; Manseima, J. 011 : 5; Martellino, A.; Edaño, G.E. BS 35643 : 4; Maxwell, J.F. 85-194 : 4; 74 777 : 3; 74 907 : 6; 76 571 : 3; 78 167 : 4; 85 495 : 4; 87 227 : 2; 87 641 : 6; 89 858 : 6; 91 495 : 6; 92 716 : 6; 93 774 : 3; 93 1359 : 6; 94 1030 : 8; 94 1303 : 6; 95 919 : 6; 96 1265 : 3; 97 720 : 6; 97 1082 : 6; 98 636 : 6; McClure, F.A. 20061 : 2; McGregor, R.C. BS 10316 : 4; McKee, H.S. 3054 : 5; Meebold 7512 : 6; Mei Fung 4879 : 8; Meijer, W. 69 : 3; 905 : 4; 9473 : 4; 10341 : 3; Mendoza, D.R.; Convocar, P. 712 : 4; 748 : 4; Merrill, E.D. 624 : 4; 3238 : 4; 5937 : 4; 6682 : 2; Sp. Blan 490 : 4; Middleton, D.J.; Meng Monyrak 617 : 4; Millar N.G.F. 15745 : 5; Mogea, J.P.: Wilde, W.J.J.O de 3715 : 4; Mohd Haniff SFN 8019 : 4; Mohd Nur SFN 34358 : 4; Mohd Shah MS 656 : 4; MS 2803 : 4; Molesworth Allen, B. 4574 : 2; Moulton, J.C. SFN 6764 : 4; Moysey, L. 31884 : 4; Mumford, E.P. 472 : 5; Murata, G. J 890 : 4; T 16057 : 8.
- Nakaike, K. 558 : 5; native collector 2222 : 4; SFN 4179 : 2; Neervoort, A.M. 253 : 4; Nitta, A. 15091 : 3; Normal School Students 12691 : 4; Norris, W. 856 : 4.

Oliver, R.L. 3109 : 5; Ooststroom, S.J. van 14090 : 3.

- Pacific Entomological Survey 474 : 5; Ex 472 : 5; Palmer, W. 512 : 4; Palmer, W.; Bryant, O. 254 : 3; Parks, H.E. 20759 : 4; 70904 : 4; Parris, B.S. 7913 : 5; 10550 : 4; 11252 : 4; 11331 : 4; Parris, B.S.; Croxall, J.P. 5968 : 4; Parris, B.S.; Edwards, P.J. 10479 : 2; Parry Hance 1998 : 2; Pearce, K.G.; Serukit, D. S 95467 : 1; Perlman, S. 10118 : 5; Petrmitr, O. 164 : 6; 397 : 6; Phengkhlai, C. 283 : 2; 305 : 6; Phoon, S.N. FRI 53265 : 4; Pierre, L. 5713 : 4; Piggott, A.G. 2187 : 4; Pleyte, D.R. 343 : 4; Poilane, E. 4219 : 3; 9540 : 6; 12673 : 8; 15805 : 2; 23031 : 4; Polak, A.M. 931 : 4; Polak, E. 2048 : 4; Pooma, R. 4830 : 6; Pooma, R.; et al. 4373 : 4; Posthumus, O. 2429 : 4; 4058 : 4; Price, M.G. 1157 : 4; 2691 : 4; Price, M.G.; Hernaez, B.F. 701 : 4; Pulle, A.A. 113 : 4; 484 : 4; 596 : 4; 722 : 5; 1086 : 5; Pullen, R. 7738 : 4; 8069 : 4.
- Qi Xinping Q 77 : 8; Qinghai-Tibet Team 4427 : 8; 4920 : 8; 8673 : 8; Qiu Yun 52907 : 8; Quayle, E.H. 61 : 5; 1145 : 5; 1258 : 5.

- Raap, H. 218 : 4; 227 : 4; Rachmat 496 : 4; Ramos, M. 14881 : 4; Raynal, J. 17073 : 4; Raynal, J.; Schmid, R. RSNH 16123 : 4; Reinecke, F. 108 : 4; Reinecke, F.? 94 : 4; Reynoso; Garcia; Sagcal, E. PPI 14300 : 4; Ridley, H.N. 571 : 2; 5171 : 2; 5172 : 2; 7832 : 4; Riswan, S.; Afriastini, J.J. J 075 : 4; Robinson, H.C. 6024 : 4; Rock, J. 2026 : 6; Römer, L.S.A.M. von 770 : 4; Royen, P. van 3644 : 4; 3842 : 4; 3870 : 5; 7373 : 5; Royen, P. van; Sleumer, H.O. 5959 : 9; 6344 : 4; 7485 : 4; 7651 : 4; Rutten 1567 : 4; 2047 : 9; 2198 : 9; 2244 : 4.
- S. Y. Dong 136 : 3; Sachet, M.-.H. 1021 : 5; Saigol, P. SAN 93067 : 4; Saldanha 17990 : 3; Sands, M.J.S. 6399 : 4; Sauveur; Sinke 2516 : 4; Schiffner, V. P 209 : 4; Schlechter, R. 16689 : 9; 18572 : 4; 19626 : 4; Schmutz, E. 59 : 3; 636 : 3; 2282 : 3; 6086 : 2; F 24 : 2; Schnell, R. 10176 : 3; Schwartz, A. 2448 : 4; 2795 : 3; 2822 : 4; Scortechini, B. 394 : 4; Seimund, E. 236 : 4; Setchell, W.A. 398 : 4; Shimizu, T. M 13244 : 4; T 8959 : 2; T 11457 : 3; T 22791 : 2; Shui Yumin 3730 : 8; Sidiyasa, K.; Arifin, Z. 1586 : 4; Siew Wei Hoe 125 : 4; Simpson, D.A. 2306 : 4; Sinclair, J. SFN 38688 : 4; Sino-Japanese expedition 9391 : 8; T 273 : 8; Sino-Soviet joint mission in Yunnan 2439 : 8; 3798 : 8; 4494 : 8; Sledge, W.A. 1106 : 3; 1790 : 5; Sleumer, H.O.; Vink, W. BW 14084 : 4; BW 14245 : 4; Smith, A.C. 283 : 4; 1870 : 4; 1975 : 4; 4695 : 4; 4811 : 4; 5162 : 4; 5163 : 5; 5423 : 4; 6104 : 4; 8369 : 4; 8502 : 4; 8678 : 4; Smith, E. 894 : 4; 1073 : 3; 1074 : 3; 1281 : 6; 1283 : 6; Smith, L.S. 4602 : 3; Soegeng, W. 433 : 4; Soejarto, J.J.; Fernando, O.; Sagcal, E. 8874 : 4; Soepadmo, E.; Mahmud 1091 : 4; Steenis, C.G.G.J. van 3688 : 4; 18293 : 3; 18504 : 2; 18505 : 4; 20870 : 8; Stevens, P.F. LAE 50373 : 4; LAE 58317 : 9; LAE 58759 : 9; Stevens, P.F.; Lelean, Y. LAE 58693 : 4; Stewart, R.R. 15949 : 8; Stone, B.C.; Price, M.G. 12190 : 4; Stone, B.C.; Reynoso; Sagcal, E. PPI 447 : 4; Streimann, H. N.G.F. 35860 : 5; NGF 28939 : 4; Streimann, H.; Kairo, A. NGF 39009 : 4; NGF 44042 : 9; Stresemann, E. 9 : 4; 12 : 9; 365 : 9; 405 : 9; 405 a: 5; Strugnell, E.J. 14611 : 4; Sulit, M.D. 1211 : 4; 5376 : 4; Sun Hong Fan Herb 9434 : 3; Surbeck, H. 152 : 4; 600 : 3; 1036 : 4; 1093 : 4; Survey team who collected herbs in Tibet 1102 : 8; 1102 : 8; 1139 : 8; Swart, J.W. 2448 : 4.
- Tagawa, M. 542: 8; T 634: 3; T 646: 2; T 1524: 3; T 9311: 3; Takeuchi, W. 5340: 9; 5390: 9; 6229: 4; 6317: 9; 6318: 4; 8920: 4; 9234: 4; 10703: 5; 10758: 4; 10775: 4; 10814: 9; 11714: 4; 12970: 4; Takeuchi, W.; Towati, A.; Ama, D. 19917: 5; Teck, L.S. S 68652: 4; Thwaites, G.H.K. CP 1378: 3; Ting, K.C. 796: 2; Topping, D.L. 450: 4; 850: 4; 1338: 4; 1856: 4; Tsiang, Y. 4731: 2; Tsoong, K.K. 1284: 2; Turnau, E.A. 846: 4.
- Ueda, K.; Darnaedi, D. B 8941 : 4; University of San Carlos 79 : 4; 120 : 4; Unknown 46-2 : 4; 56 : 8; 60 : 2; 4699 : 8; 13924 : 4; 15513 : 4; Utteridge, T.M.A. 381 : 5.
- Vaupel, F. 337 : 4; Vegetation team Qinghai-Tibet group 2503 : 8; Veldkamp, J.F. 8446 : 4; Versteeg, G.M. 1335 : 4; Versteegh, C. BW 10299 : 4; BW 10419 : 4;
BW 10420 : 5; BW 10424 : 9; BW 12561 : 4; Vink, W. 17596 : 5; Vogel, E.F. de 1939 : 4; Vogel, E.F. de; Vermeulen, J.J. 7310 : 4; 7561 : 4; Voogd, C.N.A. de 128 : 4; 2498 : 3; Vriese, W.H. de 6 : 3; 25 : 3; 26 : 4; 28 : 3; 35 : 4; 66 : 4; 342 : 3.

Wagner, W.L. 6225 : 5; Waitz, F.A.C. 27 : 4; Walker, T.G. 8042 : 9; 8265 : 9; T 7541
: 5; Wallich, N. 373 : 8; Wang, C.W. 39287 : 3; 39445 : 8; 74763 : 6; 78515 : 3; 87504 : 2; Wang, W.T. 10419 : 6; Wang, Z.R. C 621 : 2; Watthana, S. QBG 21791 : 3; Webster, G.L.; Hildreth, R. 14181 : 4; Werner, E. ROS 28 : 9; Western China Academy of Sciences 4699 : 8; Whistler, A. 3549 : 4; Whitford, H.N. 999 : 4; 2248 : 4; Whitmore, T.C. BSIP 997 : 9; BSIP 2133 : 9; Whitmore, T.C.; Womersley, J.S. BSIP 688 : 9; Widjaja, E.A. 4207 : 4; Wilde, A.G. de; Vervoort, W. 530 : 4; Wilde, W.J.J.O. de; Wilde-Duyfjes, B.E.E. de 12942 : 4; 13787 : 4; 15022 : 4; Williams, K. 1981 : 4; Wilson, E.H. 5246 : 8; Winckel, W.F. 967 B: 4; 1359 : 4; 1656 B: 4; Winkler, H. 467 : 4; 1078 : 4; Wiriadinata, H. 144 : 4; Womersley, J.S.; Millar, A. NGF 7775 : 4; NGF 8377 : 4; Wong, K.M. 459 : 4; 1122 : 4; 1444 : 4; FRI 32229 : 4;; Wood, K.R. 4442 : 5; 4583 : 5; 6387 : 5; Worthington, R.D. 12919 : 4; Wray, L. 585 : 4; 1601 : 4; 3729 : 4; 5357 : 4; Wuzhishan Fern Survey 217 : 3; Wyatt-Smith, J. KEP 78837 : 4.

Xinggong Xia Xia 5419 : 8; 5520 : 8; Xu 4 : 8.

- Y. Tsiang 11574 : 8; Yahud; Mahmud; S 88396 : 1; Yates, H.S. 2899 : 4; Yii Puan Ching SAR 48495 : 4; Yoshida, S. 1552 : 4; Yan Yue-Hong 3101 : 2; 12943 : 2; Yu, T.T. 16648 : 8; 17303 : 8; 17305 : 8.
- Zhang Xian-Chun 106 : 2; 2355 : 3; Zhang Xian-Chun; Chen Zhen Chuan 3781 : 2; Zhang Xian-Chun; Dong Shiyong 1404 : 6; 1423 : 6; Zhongshan University 23749 : 8; Zhu Taiping 189 : 6; 476 : 6; Zhu Weiming 2705 : 8; Zollinger, H. 507 : 3; 1306 : 4; 1306 ?: 4; 1306 a: 3; 1306 B: 4; 1993 : 3.

RESEARCH ARTICLE



Revision of the Maddenia clade of Prunus (Rosaceae)

Jun Wen¹, Wenting Shi¹

Lepartment of Botany, National Museum of Natural History, MRC 166, Smithsonian Institution, Washington, D.C. 20013-7012, USA

Corresponding author: Jun Wen (wenj@si.edu)

Academic editor: Hanno Schaefer | Received 2 February 2012 | Accepted 11 April 2012 | Published 17 April 2012

Citation: Wen J, Shi W (2012) Revision of the *Maddenia* clade of *Prunus* (Rosaceae). PhytoKeys 11: 39–59. doi: 10.3897/phytokeys.11.2825

Abstract

The *Maddenia* clade of *Prunus* L. is monographed based on herbarium and field studies. Four species are currently accepted in this group: *Prunus himalayana* J.Wen, *P. hypoleuca* (Koehne) J.Wen, *P. hypoxantha* (Koehne) J.Wen, and *P. gongshanensis* J.Wen, with the last described herein as a new species. *Maddenia fujianensis* Y.T.Chang and *M. incisoserrata* T.T.Yü & T.C.Ku are treated as synonyms of *Prunus hypoleuca*.

Keywords

Maddenia, Prunus, Prunus gongshanensis, revision, Rosaceae

Introduction

The *Maddenia* group has been shown recently to be nested within *Prunus* L., a genus with many economically important fruit crops and ornamental plants, such as almond and cherry blossom (Wen et al. 2008). Chin et al. (2010) showed *Maddenia* Hook.f. & Thomson as a monophyletic group closely allied with the temperate members in subgenera *Laurocerasus* and *Padus* of *Prunus*, and they transferred species of *Maddenia* to *Prunus*. The *Maddenia* clade contains a small group of trees distributed in temperate regions of the Himalaya and eastern to western China (Rehder 1940; Yü et al. 1986; Chin et al. 2010).

Hooker and Thomson (1854) described the genus *Maddenia* in honor of Major E. Madden for his contribution to the botany of the Himalayan regions. *Maddenia* was

Copyright Jun Wen, Wenting Shi. This is an open access article distributed under the terms of the Creative Commons Attribution License 3.0 (CC-BY), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

distinguished from *Prunus* based on its flowers with ten tepaloid perianth segments, i.e., petals not differentiated from sepals (Rehder 1940). The variable number of indistinguishable perianth segments was used as a diagnostic character for the approximately 40 paleotropical species of *Pygeum* Gaertn. (Backer and Bakhuizen van den Brink 1963). Nonetheless, Kalkman (1965) considered this undifferentiated perianth in *Pygeum* as an overlapping character with *Prunus*, which prompted him to transfer *Pygeum* species into *Prunus* subgenus *Laurocerasus* (Duhamel) Rehder (specifically to section *Mesopygeum* (Koehne) Kalkman).

Maddenia himalaica Hook.f. & Thomson was the first species described in this group. Hooker and Thomson (1854) pointed out that this plant had dimorphic flowers with 10 perianth segments and one or two pistils. The authors noted that this species of their new genus resembled Pygeum in its flowers and Cerasus in its foliage and drupe (Hooker and Thomson 1854). Maddenia pedicellata Hook.f. was the second described species, which differed from *M. himalaica* in its much longer pedicels (Hooker 1879). Three more species, M. hypoleuca Koehne, M. hypoxantha Koehne and M. wilsonii Koehne were added to the group by Koehne in 1911, while he was treating the collections by E. H. Wilson collected from central and western China. Hara (1976) published M. himalaica var. glabrifolia H.Hara, which was distinguished from var. himalaica in its glabrous leaves except on the axis of veins. Chang (1985) described M. fujianenesis Y.T.Chang, which differed from M. hypoleuca in M. fujianensis' looser raceme and its rusty tomentose inflorescence axis, pedicels and bracts. Maddenia incisoerrata T.T.Yü & T.C.Ku was described by Yü et al. (1985) as being similar to M. hypoxantha and M. wilsonii except that M. incisoserrata had abaxially glabrous leaves with deeply serrate margins and shorter and denser racemes.

The morphological differences among the species mostly concern pubescence and color on the abaxial leaf surface, teeth on the leaf margin, and the raceme length and density (Koehne 1911; Lu et al. 2003). However, species delimitations in Maddeina have been controversial and identifications of the Maddenia group of species are often extremely difficult in the field or in the herbarium, especially concerning *M. hypoleuca* and M. incisoserrata, and M. hypoxantha and M. wilsonii (J. Wen, pers. observ.). Koehne (1911) emphasized leaf pubescence and Lu et al. (2003) used size of bud scales, stipule shape and bract shape to separate *M. hypoxantha* and *M. wilsonii*. Hara (1976) stated that Maddenia himalaica var. glabrifolia was similar to M. hypoleuca in leaf pubescence, and suggested treating *M. hypoleuca* possibly as a variety of *M. himalaica*. In addition, Hara (1976) pointed out that a part of the holotype of *M. pedicellata* was not Maddenia, but belonged to the Cerasus subgroup of Prunus. Chang (1985) used flower density of the raceme to separate *M. fujianensis* from *M. hypoleuca*; and Yü et al. (1985) used leaf pubescence, leaf margin, and raceme length to differentiate M. incisoserrata from M. hypoxantha and M. wilsonii. Lu et al. (2003) separated M. hypolecua, M. incisoserrata and M. fujianensis based on their leaf color and size, number of veins, and teeth on margin.

Methodology

About 350 herbarium specimens from A, BM, CAS, CDB, E, GH, IBSC, K, KUN, L, MO, NY, PE and US were examined. We also conducted field studies in Fujian, Gansu, Hubei, Sichuan, Xizang and Zhejiang provinces of China. We herein provide a description of the *Maddenia* clade of *Prunus*, a key to all four species of the clade we recognized, and descriptions of each species.

Systematics

Description of the Maddenia clade

Trees or shrubs, deciduous. Winter buds ovoid, with several scales. Stipules caduceus, margin glandular at least on the lower part. Branchlet of first year's growth pubescent. Leaves alternate, simple; leaf blade abaxially glabrous to tomentose; leaf margin toothed, lower part with a few to many glandular teeth, teeth simple, irregularly doubly serrate or incised-serrate. Inflorescence a terminal raceme, 8–20 flowered. Hypanthium pubescent. Perianth segments usually 10, narrowly triangular, caduceus, pubescent, not differentiated into sepals and petals. Stamens 20–45. Style slender, glabrous. Ovary 1- to rarely 2-locular, glabrous. Drupe ovoid, glabrous, dark purple to black.

Four species distributed in temperate regions of the Himalaya and eastern to western China. The morphology-based species delimitation will be tested by molecular data in our future work. At present, our available molecular data are congruent with our delimitation (Chin et al. 2010; Liu et al. in press).

Key to species of the Maddenia clade

1a	Leaf blade pubescent to villous on the abaxial surface, or at least pubescent on
	veins
2a	Leaf blade abaxially densely pubescent to rusty tomentose, lower part of mar-
	gin densely with glandular teeth, bract and stipule margin glandular
	P. himalayana
2b	Leaf blade abaxially pubescent or sometimes only pubescent on the veins,
	lower part of leaf margin only with a few glandular teeth near the base
	P. hypoxantha
1b	Leaf blade glabrous on abaxial surface or with tufts of pubescence on lateral
	vein axils
3a	Leaf margin with fewer (fewer than 15) glandular teeth near the base, pubes-
	cence on abaxial vein axils usually not conspicuous, leaf base acute to rarely
	subcordate

3b Leaf margin with many (more than 20) glandular teeth at the lower 1/3 of the margin near the base, conspicuously with tufts of hairs on abaxial vein axils, leaf base subcordate to cordate*P. gongshanensis*

1. Prunus himalayana J.Wen (Bot. J. Linn. Soc. 164: 243. 2010). http://species-id.net/wiki/Prunus_himalayana Fig 1

Synonym. *Maddenia himalaica* Hook.f. & Thomson (Hooker's J. Bot. Kew Gard. Misc. 6: 381. 1854); non *Prunus himalaica* Kitam.

Type. India. Sikkim: temperate, 8–10000 ft, bearing flowers and fruits, J. D. Hooker s.n. (lectotype: K!, here designated; isolectotype: K!).

Description. Trees (2–) 3.5–10 m tall. Branches purple, slightly puberscent; branchlets of first year's growth densely pubescent. Winter buds purplish brown, ovoid; scales to $3-23 \times 3-12$ mm, broadly to narrowly ovate, outside brown pubescent. Stipules lanceolate, $12-25 \times 2-5.5$ mm, membranaceous, caduceus, margin with glandular and fine teeth, glandular teeth at the lower 1/3-1/2, apex acuminate to acute, base rounded. Petiole 2-4.5 mm, densely brownish pubescent. Leaves ovate-oblong, elliptic to ovate, $5.5-13.5 \times 2.7-6$ cm, abaxially light green, densely pubescent, adaxially dull green and pubescent along the veins; margin doubly irregularly serrate to serrulate at the upper 2/3, glandularly serrulate at the lower 1/3, teeth at the margin sharp; apex acuminate, base subcordate to broadly cuneate; secondary veins 13–15 on either side of midvein. Racemes 3.5-6.5 cm, axis densely pubescent, (8-) 10–18-flowered; bracts broadly lanceolate, narrowly ovate, $6-14 \times 2-5$ mm, membranaceous, caduceus, pubescent on both surfaces, margin sparsely with glandular teeth. Pedicel 2.5–5 mm at anthesis, densely pubescent. Hypanthium campanulate, $3-4 \times 5-7$ mm, densely brownish pubescent outside, glabrous inside. Perianth segments 10, narrowly triangular, $1.5-2 \times 1-1.3$ mm, caduceus, pubescent. Stamens 30-40, 4-7.5 mm long; filament cream white, 3.5-7 mm; anthers oblong, pale yellow, $0.5-0.6 \times 0.4-0.5$ mm. Ovary glabrous, 1- or occasionally 2-locular, sometimes developing into twin fruits as shown in Fig. 1. Style slender, 5-11 mm long. Drupe ovoid, $8-10 \times 5-5.5$ mm, glabrous, dark purple to black.

Distribution. Bhutan, Nepal, N India, N Myanmar and W China

Ecology. Forest. Fl Apr-May; fr May-Aug; 2000–3500 m.

Specimens examined. Bhutan. Wangdu Phodrung Ada, 10500 ft, 20 ft tree, 24 May 1966, S.Bower Lyon 3220 (BM). E Rudo La, tree 10–15 ft, flowers white, in rhododendron forest, 18 May 1940, Ludlow et al 18883 (BM, E). Tashiling (2100 m) – Neylong (2200) – Charikhachor (2250 m), 20 Apr 1967, fl, H.Kanai et al. 8284 (BM, E). West Donga La, 10000 ft, shrub 12–15 ft, flowers cream, calyx reddish brown, growing on edge of clearing in dense rain forest, 23 Apr 1949, fl, F.Ludlow et al. 20524 (E). Pangkar, near Lhuntse Dzong, Kuru Chu, 9000 ft, 25 Apr 1949 fl, tree 15 ft, filaments cream, anthers pale yellow, bracts and leaves dull dark red brown, F.

42



Figure 1. Prunus himalayana J.Wen A Habit, flowering branch B Flower C Flower laid open showing the inside of hypanthium and the gynoecium D Perianth segment E Fruit F Vertical section of ripe fruit G Front view of young fruit H Lateral view of young fruit I Ovary cut open J, K Ovules L Seed M Embryo N Inner face of cotyledon and plumule O Double ovaries P Vertical section of an imperfect double ovary Q Ripe fruits on infructescence. Figure source: from Hooker & Thomson (1854, p. 381).

Ludlow et al. 18756 (BM, E, PE). NE of Bhutan, Lao (Lao Chu), 9000 ft, 12 May 1949, fl, small tree, 20 ft, perianth insignificant, reddish green, stamens prominent, cream, an occasional (terminal) flower is observed with two carpels, F.Ludlow et al. 20265 (BM, PE). Tongsa, west slope below Yuto La, E of Tongsa 27°31'N, 90°34'E, margin of mossy Tsuga/Rhododendron forest, shrub 2-4 m, fr dark crimson, fleshy, 3100 m, 9 Jul 1979, A.J.C.Grierson & D.G.Long 2623 (E). West slope of Yuto La, Tongsa 27°31'N, 90°34'E, on bank in Abies densal Rhododendron forest, shrub 1-3 m, fls green tinged crimson, 3270 m, 19 May 1979, A.J.C.Grierson & D.G.Long 1166 (E). 4.6 km NW of Pele La on the road between Wangdu Phodrang and Tongsa, mixed Rhododendron-coniferous forest, 3200 m, small tree ca 3 m tall, flowers white, 5 May 1984, fl, B.Bartholomew 1552 (CAS, E, PE, US). Gyelsia: 9800 ft, 27 Jun 1938, B.J.Gould 603 (K). China. Sichuan: Jingtang, 1933, T.D.Tu 4524 (IBSC). Xizang: S Tibet, Migyikum, Tsari Clus, 10000 ft, tree 10-15 ft, anthers brownish yellow, 23 May 1936, F.Ludlow & G.Sherriff 1672 (BM). SE Tibet, between Kumang & Nyubsang (Tsangpo Gorge), Kongbo, 9000 ft, calyx reddish brown, corolla greenish brown, filaments white, anthers brown, tree 10 ft high, growing in deciduous forest, 28 Apr 1947, Ludlow et al 13560 (E). Bomi Xian, from Bomi to Ga Wa Long alpine lake, 3453 m, 29°49.378'N, 95°42.546'E, tree ca. 7–10 m tall, 22 Jun 2009, fr, Tibet-MacArther (J. Wen et al.) 2612 (US); Bomi Xian, Tree Farm, in cut-down Picea forest, 3100 m, tree 3 m tall, leaves with gray lower surface, 8 Jun 1973, Qing Zang Team 73-94 (PE). Yadong Xian, A-Sang-Chun, in forest, 2840 m, tree 3-5 m, 1 Jun 1975, Qing Zang Supplement Team 750141 (PE, 4 sheets). A-Sang-Qiao, 2750 m, tree 7-8 m, fruit purplish red, 3 Jun 1975, fr, Qing Zang Supplement Team 750177 (PE). S Tibet, Trimo, Nyam Sang Chu, 11500 ft, tree 30–40 ft, perianth dark reddish green, in dense mixed forest, 23 May 1947, fl, F. Ludlow et al. 12522 (BM, E, PE). Lower Cama River, deciduous broadleaf forest, tree 7-8 m tall, leaf margin with light reddish glands, 18 Jun 1959, fr, Collector unknown 355 (PE). SE Tibet, Trulung, Po-Tsangpo Valley, Pome, tree 15–20 ft, perianth green, filaments white, anthers golden, in wet mixed forest, 3 Apr 1947, fl, Ludlow et al. 12274 (E, BM, PE). Yunnan: Tengchong, Houqiao, Danzha Cun, in the vicinity of Zhaobitan forest farm, ca. 26.5 direct km NW of Houqiao (Guyong), 2600 m, N facing 0-10° slope, 25°32'42.4"N, 98°13'9.4"E, subtropical evergreen broadleaf forest disturbed by agriculture and felling, shrub ca. 2 m tall, flowers green, anthers yellow, occasional, growing in forest in shade, in loam on granite, 29 May 2006, Gaoligong Shan Biodiversity Survey 30758 (CAS). India. Sikkim: Lachung East Slope, 9500 ft, 20 ft, shrub, flower purplish green, 4 May 1971, fl, S.Bower Lyon 6022 (BM). Superior, 9000 ft, May 1885, L.Pantling 46334A (K); temperate, May 1885, C.B.Clarke 46514B (K); Superior, May 1885, L.Pantling 46514C (BM); temperate, 8–10000 ft, J.D.Hooker s.n. (GH). Nepal. Mewa Khola: Tamur Valley, Mewa Khola, SE of Topke Gola, 9000 ft, shrub, 12 ft, 16 May 1956, J.D.A.Stainton 310 (BM). E, Nepal, Mewa Khola, 27°30'N, 87°38'E, 8000 ft, shrub 20 ft, 19 May 1974, J.D.A.Stainton 7038 (BM); E Nepal, Tamur Valley, 27°25'N, 87°35'E, 9500 ft, shrubs 15 ft, filaments white, sepals and bracts red, 26 Apr 1967, J.D.A.Stainton 5888 (BM).

Basionym. Maddenia hypoxantha Koehne (in C. S. Sargent, Pl. Wilson. 1: 57. 1911).

Type. China. Sichuan: western Sichuan, southeast of Tachien-lu, 6–9000 ft, May 1908, E.H. Wilson 909 (holotype: A!, specimen barcode 00026559; isotypes: A!, 2 sheets, E!, K!, US!).

Maddenia wilsonii Koehne (in C. S. Sargent, Pl. Wilson. 1: 58. 1911). non *Pru-nus wilsonii* (C.K.Schneid.) Koehne. Type: China. Hubei: western Hupeh, Apr 1907, E.H.Wilson 63 (lectotype: A!, specimen barcode 00026560, here designated; isolecto-types: A!, BM!, 2 sheets, E!, K!, 2 sheets, US!).

Description. Shrubs to trees 1.5–10 (–15) m tall. Branches purple to dark purple, slightly pubescent; branchlets of first year's growth densely pubescent. Winter buds purple brown, ovoid; scales to $3-20 \times 3-12$ mm, broadly to narrowly ovate, pubescent to slightly so on the outside surface, margin entire to slightly glandular on the upper scales. Stipules lanceolate, $12-22 \times 2-6$ mm, membranaceous or herbacious, caduceus, margin often with glandular teeth, especially on the lower part of the margin, apex acuminate to acute, base rounded or truncate. Petioles 2-4 mm, densely pubescent. Leaves elliptic to ovate, $4.5-14 \times 2.5-6$ cm, abaxially light green, pubescent or densely so especially on veins, adaxially dull green, sparsely pubescent with scattered short hairs and/or along the veins; margin mainly doubly irregularly serrate to doubly serrullate, glandularly serrulate at the lower part of the base with 2–15 glandular fine teeth; apex acute, attenuate or acuminate, base broadly cuneate to occasionally subcordate; secondary veins 16-20 on each side of midvein. Racemes 2.5-5 cm, 10-18-flowered; bracts broadly lanceolate to narrowly ovate, $5-12 \times 1.5-4.5$ mm, membranaceous, often caduceus, margin sparsely with glandular teeth, more or less pubescent on both surfaces. Pedicel 2-4 mm at anthesis, pubescent to densely so. Hypanthium campanulate, 3-4.5 \times 3–6 mm, densely brownish pubescent outside, glabrous inside. Perianth segments 10, narrowly triangular to oblong-lanceolate, 1.8-2.4 × 0.8-1.1 mm, caduceus, densely pubescent. Stamens 25-35, 5-7.5 mm long; filaments 5-7 mm; anthers oblong, light yellow, 0.5–0.6 × 0.4–0.5 mm. Ovary glabrous, 1- or rarely 2-locular. Style slender, 7–9 mm long. Drupe ovoid, $7-10 \times 4-5.5$ mm, glabrous, dark purple to black.

Distribution. Western to central China.

Ecology. Forests. Fl Apr-May; fr Jun-Sep; 1800–3800 m.

Specimens examined. China. Locality & Date unknown, Collector unknown s.n. (E, speciemen barcode # E00419991). Gansu: Yongdeng Xian, Tulugou, Liancheng Forest Farm, Qilian Mountain, 2300 m, in clefts of rocks along stream, fruits black, 8 Jul 1991, fr, T.-N.Ho 1841 (CAS). Zhang Xian, Hedi, mountain slope, 4 Jun 1956, fr, Huanghe Team 4663 (PE). Hubei: Patung, Oct 1887, A.Henry 3759 (A, BM, K). Sichuan: Kam pars orientalis [probably in Sichuan], 1893, G.N.Potanin s.n. (A). Feb 1890, A.Henry 8952 (K); Sichuan, 26 Apr 1982, Collector unknown 41699 (CDB, 3 sheets). Ta-hsiang-ling, 2200–2500 m, 22 May 1028, H.Smith 2151 (A). Erjishan,



Figure 2. *Prunus hypoxantha* (Koehne) J.Wen **A** Habit, fruiting branch **B** Fallen fruit branch **C** End of flowering branch **D**, **E** Branch in full flower **F**, **G** Abaxial leaf surface **H** Flower **I** Stipule **J** Flower **K** Gynoecium **L** Fruit **M** Stipule **N–P** Bract **A**, **L** based on A.Henry 3759 (K) **B**, **F**, **H**, **J**, **K** E.H.Wilson 63 (E) **E**, **G**, **M**, **N**, **O** E.H.Wilson 909 (K) **D** E.H.Wilson 63 (K) & E.H.Wilson 3520 (K) **P** H.Smith 2151 (A) **C**, **I** A.Henry 3759 (A).

Maliuqiao, shrub 2.5 m, fruit green, 7 Jun 1957, Forestry Team of Sichuan Agric. Colleage 5064 (CDB). Lianghokow, slope 7500 ft, tree, fruit a berry, Aug 1938, T.K. Wang & T.S.Wen 0670 (A). West Szechuen and Tibetan Frontier, chiefly near Tachienlu, 9000-13500 ft, Dec 1890, A.E.Pratt 837 (A, BM, E); Szechuen and Tibetan Frontier, chiefly near Tachienlu, 9000-13500 ft, Dec 1890, A.E.Pratt 313 (BM). Jinyangbo, Luoliangzi, 3100 m, 16 May 1959, Sichuan Economic Plant Expedition 3014 (CDB, 2 sheets). Pao-Hsin-hsien, former Mupin, Apr-Aug, 1954, T.P.Soong 38472 (IBSC); Pao-hsin-hsien, former Mupin, 1954, T.P.Soong 38226 (IBSC); Baoxing, 1933, T.T.Yü 1908 (IBSC, PE); Pao-hsin-hsien, formerly Mupin, 1954, T.P.Soong 38543 (PE); Szechuan, Mupin, May 1908, E.H.Wilson 2851 (A, E, K); Baoxing Xian, 2500 m, 29 Apr 1959, H.Y.Chuan 0237 (CDB); Baoxing Xian, 2700 m, tree, 5 m, leaves adaxially dark green, abaxially light green, fruit black, 16 Jun 1958, Collector unknown 5611 (CDB 3 sheets); Baoxing Xian, Denglonggou, 2300 m, tree 4 m, 12 Jun 1958, Collector unknown 5353 (CDB, 2 sheets); Baoxing Xian, 3100 m, leaves ovate, abaxially white and pubescent, stipule with needle-like hairs, 15 Jun 1958, Collector unknown 5404 (CDB 2 sheets). Peiping, China, Mt. Omei, Jul 1931, F.T.Wang 23489 (IBSC, 2 sheets); Emei Shi: Mt. Omei, Y.H.Tau 50455 (IBSC); Mt. Omei, 27 Jun 1940, W.P.Fang 14599 (A); Mt. Omei, 2700–3000 m, in thicket, shrub, 5–10 ft, Jul-Aug 1931, F.T.Wang 23489 (A); Mt. Omei, Y.S.Shiao 48551 (IBSC); Mt. Omei, Y.S.Shiao 48677 (IBSC); Mt. Omei, Y.S.Shiao 48712 (IBSC); Mt. Emei, Leidongping, 29°32'37.3"N, 103°19'43.3"E, 2410 m, 17 Jul 2011, fr, J. Wen 12077 (US); Mt. Emei, on the way from Jingding to Taizhiping, tree 3 m, 29°31'38.7"N, 103°19'53.7"E, 2981 m, 17 Jul 2011, fr, J. Wen 12087 (US); Mt. Emei, Taizhiping, 17 Jul 2011, J. Wen 12089 (US); Mt. Emei, Luohanpo, on the way from Chudian to Zhanglaoping, 29°34'34.6"N, 103°21'46.8"E, 1499 m, 18 Jul 2011, J. Wen 12140 (US); Mt. Omei, Leidongping, tree 4 m, 12 Aug 1957, G.H.Yang 56615 (IBSC); Mt. Omei, 2800 m, slope, tree 3 m, flower green, stinky, 9 May 1964, K.J.Guan et al. 427 (CDB, IBSC); Mt. Omei, Xixiangchi, tree 5 ft, 26 Apr 1952, J.H.Hsiung et al. 30189 (IBSC); Mt. Omei, Qixing Po, 2600 m, in forest, tree 10 m, 24 Jun 1995, H.G.Xu 2140 (MO); Mt. Omei, Tai-tzu-ning, fl white, scented, 9 Jun 1939, S. C. Sun & K. Chang 115 (A); Mt. Omei, Chiu-Lao Tung, moist shady rock, shrub, fruit black, 14 Jun 1939, S.C.Sun & K.Chang 224 (A); Mt. Omei, in thickets, shrub 3 m high, common, 10 May 1941, W.P.Fang 16540 (A); Mt. Omei, Paiyunssu, on hill slope, 28 Jul 1938, H.C.Chow 7895 (A); Mt. Omei, Taiziping, 2916 m, shrub 2 m high, flower over, 18 Jun 1942, W.P.Fang 18985 (CAS); Omei, Taiziping, 2900 m, tree 4 m, flower yellow, H.G.Xu 1993122 (MO); Omei, 26 Jun 1960, H.Y.Yi 12555 (CDB); Omei Hsien, Mt. Omei, 16 Jul 1940, T.C.Lee 2891 (US); Mt. Omei, Leidongze, 2500 m, small shrub 1.5 m, high, flowers over, 16 May 1931, W.P.Fang 18811 (A); Mt. Omei, Jun 1904, E.H.Wilson 4857 (A, BM, K); W. Szechuan, Mt. Omei, Chinting, on hill slope, 3035 m, shrub 2 m, 1938, H.C.Chow 7662 (A); Emei Shi, Emei Shan, Jingding, 25 Jun 1955, fr, China - Soviet Expedition 2356 (IBSC, PE). Hanyuan Hsien, 1400 m, 17 Apr 1930, fl, W.C.Cheng 659 (BM, IBSC, PE, 2 sheets, US); Hanyuan-hsien, 20 Apr 1930, W.C.Cheng 705 (BM, IBSC, US). Hongya Xian, 1950 m, 27 Aug 1994, Bao et al. 2524 (CDB, 2 sheets); Hongya Xian, Huangshi Gou, tree 1.5–2 m, 1770 m, 4 Jun 1994, Zi et al. 1899 (CDB, 2 sheets); Hungya Hsien, Wa-wu-shan, shrub 5 ft, 16 Jul 1931, immature fr, T.T.Yü 289 (PE). Kangding Xian, Hebinxiang, 3300 m, tree 3 ft, 2 Jun 1953, Tsiang & Hgiung 35832 (IBSC); Kangding Xian, Zheduo Shan, Zheduotang, 3160 m, tree 2 m tall, 25 Jun 1953, fr, W.P.Fang et al. 36084 (PE); Kangding Xian, 2880 m, 14 May 1981, Z.Y.Chen, 112044 (A, E); Kangding Xian, 3000 m, 8 May 1981, Z.J.Zhao 113923 (A, CDB, E, K); Kangding Xian, Kangdingqu, Sheduoshan, 2800 m, Collector unknown 15013 (CDB, 4 sheets); Kangding Xian, Zheduoshan, 3100 m, Q.S.Zhao & Z.Z.Tan 119196 (CDB); Kangding Guzan Dapingshan, 2950 m, 3 Jun 1974, Kao & Wu 111489 (CDB); Kangding Xian, Ganhaizi, 3600 m, shrub 1.5 m, 29 May 1974, B.S.Qin 06136 (CDB, 3 sheets); Kangding Xian, Kongyuqu, 3300 m, 31 May 1974, Collector unknown 05344 (CDB, 3 sheets); Kangding Xian, May 1904, E.H.Wilson 3520 (A, BM, K); Kangding, Kongyuqu, 3500 m, 2 May 1974, Chao & Wu 110869 (CDB); Kangding, 2900 m, 19 May 1974, Y.T.Wu & Q. S. Zhao 111033 (CDB); Kangding, Xianglinxiang, 3000 m, tree 3 ft, 13 Jun 1953, H.L.Tsiang 35954 (IBSC). West of Kuan Hsien, 2230 m, on slope, shrub 10 ft, branchlets brown, fruit ovate-elliptic, 15 May 1930, F.T.Wang 20842 (A, IBSC); west of Kuan Hsien, ridge of thicket, 2600 m, 16 May 1930, F.T.Wang 20882 (A, IBSC). Leibo Xian, 2200 m, by Highway 284, tree 10-15 m, leaf green, stem brown, flower light yellow, filament light green, 8 May 1983, fl, Q.-S. Zhao et al. 118401 (CDB); Leibo Xian, mountain of Gudui Shan, 2300 m, 12 May 1965, K.T.Xiang & F.Y.Wang 11521 (CDB, 2 sheets); Leibo Xian, Huangmaogeng, 19 Jun 1959, fr, 2800 m, tree 3 m, Sichuan Economic Plants Expedition 0782 (PE). Li Xian, Miyaluo, north of the town of Miyaluo on highway 213, 31°43'32"N, 100°44'39"E, 3000-3200 m, mixed deciduous broad leaved-coniferous forest with Tilia, Acer, Prunus, Betula, Tsuga, Picea, Abies, Pinus and Larix, along stream, small tree ca. 5 m tall, fruit black, 8 Sep 1997, Boufford et al. 27976 (A); NW Sichuan, Mao Xian & Li Xian, former Lifan Xian, 1952, T.He & Z.L.Zhou 12553 (IBSC); Li-hsien (Li-fan-hsien), tree 6 ft, branchlet green and pubescent, 10 May 1952, C.Ho & T.L.Cho 12315 (IBSC). Luding Xian, 2800 m, tree 3.5 m, G.H.Xu 25514 (CDB); Luding Xian, top of Erlang Mountain, 2900 m, 29 May 1974, fl, Sichuan Luding Team 6863 (CDB, 3 sheets); Luding Xian, 2300 m, shrub 2-3 m, 21 Apr 1984, Cao et al. 045 (CDB, 3 sheets); Luding Xian, 3800 m, in forest, 13 Sep 1980, Collector unknown 23510 (CDB 2 sheets); Luding Xian, shrub 2 m, Zhibei Team 41616 (CDB, 3 sheets); Luding Xian, Moxigongshe, 2900 m, shrub 3-4 m, 10 Jun 1980, Q.C.Wang & Z.A.Liu 22250 (CDB, 2 sheets, IBSC); Luding Xian, Hongxigongshe, 2200 m, tree 6 m, G.H.Xu 25372 (CDB, 2 sheets); Luding Xian, Yaoxigongshe, tree 2 m, 4 Aug 1982, Zhibei Team 42068 (CDB, 3 sheets); Luding Xian, Hongxi, 26 Apr 1982, Zhibei Team 41698 (CDB 4 sheets); Luding Xian, 2300 m, X.H.Hu & Q.C.Wang 22078 (CDB, 2 sheets); Luding Xian, Hongxigongshe, 2300 m, tree 5 m, 22 Apr 1981, Collector unknown 225112 (CDB, 3 sheets). Mapien Hsien, 3200 m, in thickets, small tree to shrub, 10-20 ft, bark blackish to dark brown, 26 May 1931, fl, F.T.Wang 22942 (A, PE). Meigu Xian, Huangmaogeng, 2450 m, 14 May 1983, J.Y.He & Q.S.Zhao 116772 (CDB). Mao

Wen, Wolong Boshan, 2400 m, small tree 3–4 m, Dec 1963, H.C.Lee 2126 (CDB, 3 sheets). Baiyangxiang (Songpan), Baiziyawo, 1800 m, shrub 2.5–3 m, branchlet green and pubescent, abaxially pubescent on mid-vein, 7 May 1962, Yuan 0558 (CDB). Shih-mien-hsien, 1955, C.C.Hsieh 40278 (IBSC); Shih-mien-hsien, 1955, C.C.Hsieh 41335 (IBSC); Shih-mien-hsine, 1955, C.C.Hsieh 40287 (IBSC); Shih-mien-hsien, 1955, C.C.Hsieh 41145 (IBSC). Tianquan Xian, Niudingtou, 2890 m, 5 Aug 1982, Collector unknown 46017 (CDB); Tianquan Xian, Erlangshan, tree 3–5 m, 23 Jun 1951, W.P.Fang et al. 10078 (PE); Tianquan Xian, Erlangshan, 2300 m, 30 Apr 1980, Z.G.Liu & Y.B.Yang 21701 (CDB, 3 sheets, IBSC); Tianquan Xian, Erlangshan, 3300 ft, 19 May 1953, H.L.Tsiang 34169 (IBSC); Tianquan Xian, 2600 m, 5 May 1980, fl, Collector unknown 21795 (CDB, 3 sheets); Tien-chuan Hsien, 3500 m, 14 Jun 1936, K.L.Chu 2801 (E, IBSC). Xichang Xian, Luojishan, 2600 m, evergreen forest, shrub 5 m, Y.J.Li 730 (CDB, 2 sheets).

Cultivated plants. U.K. England. Cultivated at the Royal Botanic Gardens, Kew, source from E.H.Wilson 909, May 1924, J.C.Williams s.n. (K).

Discussion. Koehne (1911) described both *Maddenia hypothanxa* and *M. wilsonii. Maddenia wilsonii* was described to be densely pubescent on the lower leaf surface whereas *M. hypxantha* was pubescent only on veins. We have found a wide range of variation on the lower leaf pubescence. Furthermore, the lectotype E.H.Wilson 63 of *M. wilsonii* collected from western Hubei bears very small bracts, small stipules and tomentose lower leaves. Yet the syntype E.H. Wilson 2851 (A, E, K) collected from Mupin, Sichuan has larger bracts, bigger stipules and pilose lower leaves. The holotype of *M. hypoxantha* (E.H. Wilson 909) has bigger bracts, bigger stipules and hirsutulous lower leaf only on veins. Koehne (1911) indicated that the holotype of *M. hypoxantha* (E.H. Wilson 909, A) was a mixed collection of *M. hypoxantha* and *M. wilsonii*. We examined the specimen and found that the differences between the two branches on the same sheet seem to be extremely indistinguishable. Lu et al. (2003) used size of bud scales, stipule shape, stipule appearance and bract shape, to separate the two "species". We found that it is difficult to use these characters to consistently separate the two "species". We herein treat *Maddenia wilsonii* as a synonym of *Prunus hypoxantha*.

3. *Prunus hypoleuca* (Koehne) J.Wen (Bot. J. Linn. Soc. 164: 243. 2010). http://species-id.net/wiki/Prunus_hypoleuca Fig 3

Basionym. Maddenia hypoleuca Koehne (in C. S. Sargent, Pl. Wilson. 56: 59. 1911).

Type. China. Hubei: western Hubei, Hsing-Shan Hsien, bush 6–20 ft, woods, 4–6000 ft, flower greenish, May 1907, fl, E.H.Wilson 2850 (lectotype: A!, here designated, specimen barcode 00026557; isolectotypes: E!, K!, US!).

Maddenia fujianensis Y.T.Chang (Guihaia 5: 25. 1985). Prunus fujianensis (Y.T.Chang) J.Wen (Bot. J. Linn. Soc. 164: 243. 2010). Type: China. Fujian: Chong An Xian, Xing Chun, Shan Gang, Huang-Gang-Shan, in sparse forest, 1700 m, shrub



Figure 3. *Prunus hypoleuca* (Koehne) J.Wen **A** Habit, inflorescence branch **B** Fruiting branch **C** Abaxial leaf surface **D** Flower **E** Stipule **F** Flower **G** Gynoecium **H** Fruit. **A**, **D**, **E**, **F**, **G** based on E.H.Wilson 2850 (A) **B**, **H** J.F.Rock 12577 (A) **C** E.H.Wilson 2848 (K).

4 m, flowers yellowish green, 30 Apr 1981, fl, Wuyishan Expedition s.n. (holotype: FJSI, herbarium accession # 016600, 2 photos at PE!); synonym nov.

Maddenia incisoserrata T.T.Yü & T.C.Ku (Acta Phytotax. Sin. 23: 214. 1985). Prunus incisoserrata (T.T.Yü & T.C.Ku) J.Wen (Bot. J. Linn. Soc. 164: 244. 2010). Type: China. Sichuan: Heishui, Ma-He-Ba, 2880 m, tree 4 m tall, 16 Jul 1957, fr, X.Li 73195 (holotype: PE!); synonym nov.

Description. Shrubs to trees 1.5–6 m tall. Branches dark purple, glabrous; branchlets of first year's growth sparsely pubescent at the very young part, then glabrescent. Winter buds ovoid to narrowly or broadly so, scales $3-15 \times 3-8$ mm, several, imbricate, pubescent on the outer scales, but glabrous or nearly so on the inner scales, margin more or less ciliate. Stipules linear to lanceolate, 7–17 x 1–4.5 mm, membranaceous, slightly pubescent to glabrous, margin glandularly ciliate at least on the lower part. Petiole to 2-6 mm, slightly pubescent, glabrescent. Leaves ovate, elliptic to broadly so, $3.5-16 \times 1.3-7.5$ cm, abaxially pale green, glabrous or often pubescent in lateral vein axils, adaxially glabrous; margin doubly irregularly serrate, with 1-5 glandularly serrulate teeth at the base; apex acute, attenuate or acuminate, base acute to rounded; lateral veins 14-16 on each side of midvein. Racemes 1.5-5.5 cm, with 8-15 flowers; bracts lanceolate to narrowly triangular, $4-5 \times 1-2$ mm, nearly glabrous, with glandular teeth at margin. Pedicel 1.5-4 (-6) mm long, pubescent. Hypanthium campanulate, 2.5-6 \times 4–7 (–9) mm, slightly pubescent to glabrescent on the outer surface, glabrous on the inner surface. Perianth segments 10, slightly unequal, narrowly triangular to lanceolate, $1.5-3 \times 0.9-1.2$ mm, slightly pubescent to glabrescent. Stamens 20-30, 4-7 mm long; filaments 3.5–6.5 mm; anthers oblong, 0.25–0.35 × 0.2–0.25 mm. Ovary glabrous, 1- or rarely 2-locular (see E.J.Palmer 130, CAS). Style slender, 4-8 mm long. Drupe $6-8 \times 5-6$ mm, glabrous, dark purple to black.

Distribution. Eastern, central to western China.

Ecology. Forests. Fl Apr – Jun; fr late May–Jul; 1300–3700 m.

Specimens examined. China. W. China, Vallee de Ou-ma-hai, 2400 m, shrub, fl yellow, E.E.Maire 189/1914 (E). W. China, Avril, graud arbuste-feuil, exdugues, blauehes, brousse de Ou-ma-hai, 2000 m, E.E.Maire 916/1914 (E). Jon-sian-fu, N central China, 1897, Rev. Fr. Hugh (A, BM). Huan-tou-san, N Centrial China, Jul 1899, Rev. Fr. Hugh s.n. (A, BM). Anhui: 29 Apr 1925, R.C.Ching 2727 (IBSC). Ping-Tien-Kan, Huangshan, Anhui, in thickets, 1700 m, shrub, 2 m, high, base of the petals purplish-red, fr green, 12 May 1979, fl & young fr, Deng & Yao 79170 (NY). Bai Ma Zhai, Tian Tang Zhai, Jinzhai, at the mountain top in the bushy woods, 1650 m, tree, fr green, 21 May 1984, K. Yao 9047 (A, CAS, K, MO, NY). S Anhui, summer 1925, fl, R.C.Ching 2727 (A, K, PE). Chongching: Nanchuan, Jinfoshan, in forest 1860 m, tree 3-5 m, flower light red, S.Y.Yi 972823 (MO). Gansu: Min Xian, shaddy slope, 2700 m, tree 1-1.5 m, flower light yellow, 23 May 1957, Tao He Team 3106 (MO). Pinchow District, near Kansu, W.Purdom s.n. (A). SE Kansu, 6 Apr 1919, E.Licent 4980 (BM). Tiecheliang Pass (= Lazikou Pass), hillside, east-facing, scattered scrub, 2940 m, 34°14'59"N, 103°54'59"E, deciduous shrub to 2 m, leaf mid-green and matt above, paler below, veins below noticeably raised and indented above, fruit in short

racemes, green, broadly ovoid, 6-7 cm, turning red, 18 Jun 2000, Sino-British Qinghai Alpine Garden Society Expedition (SAQE) 242 (CAS; other associated material noted on the CAS specimen including DNA sample at E), herbarium specimen in fruit at HNWP, GB, and WSY). SE Kansu, Koan Kia ho et Lao Ling, 17 Apr 1919, A.E.Licent 5047 (BM, K). Qingshuishan, Menxiangdaji, 1750 m, slope, 24 Jun 1986, J.X.Yang 6838 (MO). T'ao River basin, mountains of Choni, W of Taoho, outskirts of Picea forest, 10000 ft, shrub 8-10 ft, May 1925, fl, J.F.Rock 12148 (A, E, K). SW Gansu, Upper Tebbu country, spruce forest among boulders, southern slopes of Minshan, 9600 ft, small tree or shrub 8-10 ft, Jun 1925, fl, J.F.Rock 12531 (A, US). Hsia Mo K'ou, near Lichen, 2000–2300 m, shrub up to 13 ft, woods, 8 Jul 1923, R.C.Ching 391 (A 2 sheets, E, NY, US). SW Kansu, T'ao River basin, in forest among spruces, Choni, 9000-10000 ft, small tree, 15 ft, Jul 1925, J.F.Rock 12577 (A, E, K). Baiyanglin, Huanghe Expedition 395 (PE). Baiyanglin, Huanghe Expedition 408 (PE). Min Xian, Wutaishan, on the top of mountain, moist area, slope, shrubby area, 2400 m, shrub 2 m tall, 26 May 1957, fl, Huanghe Expedition 3241 (PE). Yuzhong, 2450 m, in sparst forest, tree, 30 May 1983, Z.Y.Zhang 19178 (MO); Yuzhong Xian, Xinglongshan, 2600 m, 9 Jun 1990, X.Pu 558 (MO). Tulugou, Yongdeng Xian, in shrub forest, 2500 m, 10 Jul 1990, G.H.Wang 886016 (MO); Gansu, Lianhuashan, Kangle Xian, in shrub forest, 2700 m, 21 Jun 1991, G.H.Wang 91056 (MO). Guizhou: Zhengyi Shi, Shanpeng Dist., Xianrenshan, roadside, in sparse forest, 1950 m, tree 3-4 m tall, sepals green with reddish tint, 9 Apr 1959, fl, North Guizhou Team 0086 (PE, 3 sheets). Henan: Lushi Xian, Dayandi, on the way to Yuhuangfu, in dense forest, valley, 1760 m, 10 Jul 1959, fruits black, L.-Z. Chen & S-H.Dong 34526 (PE). Hubei: Changyang, 4 Apr 1900, E.H.Wilson 429 (A, E). Patung, W. China, 26 Apr 1900, E.H.Wilson 429 (US). Western Hubei, Jul 1907, fr, E.H.Wilson 2848 (A, BM, E, K), May 1907, fl, E.H.Wilson 2849 (A, BM, E, K). Shennongjia, Laojunshan, 2150 m, in dense forest, fruits black, 9 Jul 1976, fr, Hubei Shennongjia Expedition 31020 (PE); Shennongjia, Yanziya, 2000 m, slope, tree 4 m, Jun 1986. S.-H.Yang 18 (IBSC). Laojunshan, near Medicinal Herb Garden, in dense forest, tree 5–7 m tall, 31 May 1957, fr, Y.Liu 00626 (PE, 3 sheets). Xingshan Xian, Laojunshan, in dense forest, tree 6–8 m, fruits purple, 27 May 1957, fr, Y.Liu 496 (PE, 3 sheets); Xingshan, in dense forest, 1400-1450 m, tree 5-7 m, 31 May 1957, fr, H.J.Li 2298 (PE); Xingshan Xian, 1600 m, in dense forest, tree 6-8 m, fruit reddish purple, 27 May 1957, L.Ying 496 (IBSC, 2 sheets). Jiangsu: C.W.Yao 2748 (IBSC). Jiangxi: Qianshan Xian, Huanggangshan, in dwarf montane forest, 27°51.605'N, 117°47.003'E, 2070 m, 15 Jul 2011, juvenile plant about 1 m tall, J. Wen 12069 (US); Qianshan Xian, Huanggangshan, in dwarf montane forest, 27°51.605'N, 117°47.003'E, 2070 m, 15 Jul 2011, tree ca. 3.5 m tall, growing in rock crevice, fruit blackish purple, J. Wen 12071 (US); Qianshan Xian, Wuyishan, Huang-gang-shan, 2070 m, shrubs 1.5 m tall, old branches purple, new branches green, 7 May 1984, fl, Z.X.Yu 840010 (PE). Shaanxi: Huayin Xian, Huayang Commute, 1300 m, tree 3-4 m, petal deciduous, 24 Apr 1978, Zh.-Y.Zhang & Ch.-Sh.Liu 17587 (IBSC). Ningxia Xian, Juyangbei, 1360 m, small tree 1360 m, flower yellowish green, 24 Apr 1993, G.H.Tian & L.Tian T934014 (MO). Baoji, Weibin

District, 1700 m, in slope forest, tree 4 m, leaves adaxially green abaxially light green, voung fruit purplish green, 26 May 1977, Z.X.Hu & Y.H.Guo 210 (IBSC). Taibaishan, slope, 2850 m, 1 Jun 1965, C.L.Tang 1447 (IBSC). Feng Xian, Zhoujiazhuang, slope forest, 1530 m, fruit black, 2 Aug 1996, Y.S.Lian et al. 96181 (MO). Yang Xian, Huayang, Daping, forests, 2400-2700 m, 4 Jun 1999, G.H.Zhu et al. 1748 (MO). Ningxia Xian, Caiziping, 1850 m, tree 3 m, 20 Jul 1990, P.H.Yang 90336 (MO); Ningxia Xian, Caiziping, 1600 m, tree 2.5 m, 21 Jul 1990, P.H.Yang 90390 (MO). Western Shen-si, Lungchow, Kuan Shan, 2000 m, 3 Jul 1922, Native collectors 2352 (A). Tai-pei Shan, fruit black, 8000 ft, 8 Jul 1910, W.Purdom 436 (CAS, E, K, US). Taipaishan, near Haopingszu, 1500 m, in valley, tree with unpleasant odor, to 5 m, bark chestnut brown, 18 Apr 1937, fl, T.P.Wang 6526 (PE). Taipaishan, near Haopingszu, 1500 m, in valley, tree with unpleasant odor, to 5 m, bark chestnut brown, 18 Apr 1937, fl, T.P.Wang 6551 (PE). Sichuan: W. China, 2400 m, Su-tchuen oriental, Tchen-Kéou-Tin, R.P.Farges s.n. (K, H2010101913). Lian Ying Zhai, Baiguo forest Farm, Wuxi Co., damp valley, 1480-1630 m, shrub 3-5 m, gruit green, 30 May 1996, C.Z.Gu 960732 (MO). Tchen-Kéou-Tin, R.P.Farges s.n. (E, E00419987). Maowenfengyi Keyaozhai, Zhongshan, SW shaddy slope, 2200-2500 m, tree 2-3 m, stem black brown, branchlet light brown, abaxially light green, vein conspicuous, pubescent at vein axis, adaxial leaf dark green, fr purplish black, 21 Jun 1959, Mao Wen Team 2832 (CDB 2 sheets). Wanyuan Xian, Hua'E'Shan, top of the mountain, 2200 m, small tree 2-2.5 m, stem green, branchlet vellow and pubescent, leaf adaxially dark green and abaxially whitish green, fruit green, B.L.Li 2035 (CDB). Sichuan, Nanjiang Xian, Zhongshangu, shaddy slope, 1600 m, tree 2 m, stem purplish red, leaves simple and alternate, pubescent, abaxially whitish, adaxially green, fruit small, reddish green, 9 Jun 1959, B.W.Zuo 2850 (CDB). Sichuan, Heishui, Ma-He-Ba, 2880 m, 16 Jul 1957, fr, tree 4 m tall, X.Li 73195 (CDB); Heishui, Shidiaolu Xiang, Kuguazhai, mountain slope, 2900 m, uncommon, shrub 2-4 m tall, 28 May 1959, fl, Sichuan Economic Plant Expedition 1251 (CDB, 3 sheets, PE, 2 sheets). Sichuan, Dongrergo, in silva mixta primcera, ca. 3700 m, 8 Aug 1922, H.Smith 3499 (A, MO). Pingwu Xian, H. L. Tsiang 10054 (PE). Wushan Xian, Chaoyang Ping, Wenjia Chao, 2000 m, in forest at riverside, tree 2 m, 4 May 1958, fl, G.H.Yang 57953 (PE); Chaoyang Ping, mountain slope, 2100 m, shrub 2 m tall, 6 May 1958, fl, G.H.Yang 57979 (PE, 2 sheets). Nizhi Ping, 1800 m, streamside, tree 3 m tall, young leaves purple, sepals 5, green, with reddish tint, triangular, petals 5, lanceolate, smaller than sepals, 13 Apr 1958, fl, G.H.Yang 57684 (PE, 2 sheets). Sichuan, Pingwu, Xutang Commune, tree 1.5 m, mountain top, shady slope, Dec 1961, X.N.Tang 42 (CDB 2 sheets). Wushan Xian, Liziping, 1800 m, tree 3 m, young leaves purplish red, 13 Apr 1858, G.-H. Yang 57684 (IBSC). Zhejiang: Anji Xian, Baofu Township, Tianmushan area, 30°23.976'N, 119°26.441'E, 1336 m, tree 4-6 m tall, in wet area, 28 Apr 2010, fl, J.Wen 11291 (US, 2 sheets); Anji Xian, Longwangshan, 950 m, small tree 4.5 m, perianth segment green, anther yellow, petal absent, 30 Mar 1997, L.P.Yu & M.B.Deng 97099 B (MO).

Cultivated plants. U.K. England: Cultivated at the Royal Botanic Gardens, Kew, Arboretum South, 19 March 1969, Kew Accession Number 47–61 (K); cultivated at

the Royal Botanic Gardens, Kew, England, Arboretum South, 22 Apr 1969, Kew Accession Number 47–61 (K). **U.S.A.** Seed from E. H. Wilson material, originally from Suungpan, W Sichuan, 1910, cultivated in the Arnold Arboretum, #6120, 21 Apr 1938, E.J.Palmer 130 (CAS); cultivated in Arnold Arboretum, #6120, Bussey Hill, originally from W. China, E.H.Wilson 4008, 21 Apr 1931, Kobuski & Roush s.n. (K). Seed from Wilson 4008, Sungpan, W. Sichuan, China, 1910, cultivated in the Arnold Arboretum #6120, 25 Apr 1941, R.B.Clark 126 (MO).

Discussion. Yü et al. (1985) stated that *Prunus incisoserrata* was similar to *P. hypoxantha* and *M. wilsonii* except that the leaves of *P. incisoserrata* are abaxially glabrous; the margin is deeply serrated; and inflorescence is shorter and denser. The character of glabrous abaxial leaf blade is similar to that of *P. hypoleuca*. We also observed variations in the depth of the leaf teeth and inflorescence length of specimens of *Maddenia incisoserrata* and *Prunus hypoleuca*. In fact the type specimen of *P. hypoleuca* bears leaves with deeply serrated teeth at the margin. Chang (1985) compared *Maddenia fujianensis* with *P. hypoleuca*. Prunus hypoleuca was said to have a pubescent and dense inflorescence. Nonetheless, the inflorescence of *M. fujianensis* is also pubescent and dense. The differentiating characters among *Prunus hypoleuca*, *Maddenia incisoserrata* and *M. fujianensis* seem continuous. We thus treated *M. incisoserrata* and *M. fujianensis* as synonyms of *Prunus hypoleuca*, which has the nomenclatural priority.

4. Prunus gongshanensis J.Wen, sp. nov.

urn:lsid:ipni.org:names:77118671-1 http://species-id.net/wiki/Prunus_gongshanensis Fig 4

Type. China. Yunnan: Gongshan Xian, Gongshan, on the way from Qingnatong to Anwalong, 3100 m, small tree 4 m tall, in the valley in shrublands, 31 May 1979, fl, flowers white, common, Lujiang Expedition 790292 (holotype: KUN!; isotype: KUN!).

Maddenia himalaica var. *glabrifolia* H.Hara, J. Jap. Bot. 51(1): 8. 1976. Type: Bhutan. Rukubi: Chendebi, 2600 m, 14 Apr 1967, H. Kanai, G. Murata, H. Ohashi, O. Tanaka & T. Yamazaki 4191 (holotype: TI; isotype: E!).

Description. Small trees 4–8 m tall. Branches purple, shiny glabrous; branchlets of first year's growth pubescent. Winter buds purplish brown, ovoid; scales to 4–20 \times 3–15 mm, ovate, outside brown pubescent but glabrescent. Stipules lanceolate to broadly so, 12–25 \times 2–8 mm, membranaceous, margin with glandular teeth, apex acuminate to acute. Petiole 2.5–5 mm, brownish pubescent. Leaves oblong, elliptic to ovate, 5–13 \times 2–6 cm, abaxially light green, nearly glabrous, only pubescent on lateral vein axils, adaxially dull green and glabrous, margin doubly irregularly serrate at the upper 2/3, glandularly serrulate at the lower 1/3, teeth at the margin sharp, apex acuminate, base subcordate to broadly cuneate; secondary veins 20–24 on either side of midvein. Racemes 4–6 cm, brown pubescent, 12–16 flowered; bracts lanceo-



Figure 4. *Prunus gongshanensis* J.Wen **A** Habit, inflorescence branch **B** Fruit **C** Leaf branch **D** Abaxial leaf surface **E** Bud scale **F**, **G** Flower **H** Stipule **I** Gynoecium **J** Fruit **A**, **C**, **D**, **F**, **G**, **H**, **I** based on Gaoligong Shan Biodiversity Survey 20474 (CAS) **E** Gaoligong Shan Biodiversity Survey 20059 (CAS) **B**, **J** Nan Shui Bei Diao Team 8992 (KUN).

late to ovate, $4.5-6 \times 2.5-3.4$ mm, membranaceous, margin entire to serrate. Pedicel 2.5-4 mm at anthesis, densely brown-pubescent. Hypanthium campanulate, $4-6 \times 4-9$ mm, brownish pubescent outside, glabrous inside. Perianth segments 10, narrowly triangular to lanceolate, $1.5-3.2 \times 0.7-1$ mm, caduceus, pubescent. Stamens 25-45, 5.5-7 mm long; filaments 5-7 mm; anthers oblong, $0.3-0.35 \times 0.25-0.3$ mm. Ovary glabrous, 1-locular. Style slender, 7-9 mm long. Drupe ovoid, glabrous, $8-9 \times 5-6.5$ mm, dark purple to black.

Distribution. Western China, Bhutan, Myanmar, Nepal, and northern India.

Ecology. Shady valleys and forests. Fl. Mar–Jul; fr. Jun–Jul; 2100–3500 m.

Etymology. This species is named after the mountain range, the Gaoligong mountains or known as Gongshan, where this species was first recognized.

Specimens examined. Bhutan. Griffith 2057 (GH, K); Gasa (2600) - Pari La (3550) – Chamsa (3500), 14 May 1967, Kanai et al.12806 (E). Gasa (2600 m) – Pari La (3550) – Chamsa (3500 m), 14 May 1967, Kanai et al.12895 (BM). Buhtan, Mishina (1300 m) - Dochu La (3950 m) - Thimphu (2250 m), 28 Apr 1967, Hara et al. 10319 (BM); Punakha district, forest slopes between Dochong La and Menchunang 27°30', 89°45', evergreen oak forest, large shrubs or small tree 8 m, deciduous young leaves dark red, stamens creamy, sepals and petals crimson, 2750 m, 19 Apr 1982, A.J.C.Grierson & D.G.Long 4481 (E, K). China. Yunnan: Fugong Xian, Yaping Xiang. Between the Shibali logging station and Yaping pass,ca. 8.5 km W of Shibali, on the road from the Nujiang to Yaping pass, E side of Gaoligong Shan, 3106 m, 27°11'6"N, 98°43'12"E, moist forests with thickets, tree, 6-7 m tall, fl white, growing in forest, 8 May 2004, Gaoligong Shan Biodiversity Survey 20474 (CAS). Fugong Xian, Yaping Xiang, in the vicinity of Yaping near the Myanmar border, E side of Gaoligong Shan, 3500 m, 27°12'37"N, 98°42'33"E, Rhododendron-bamboo thicket, tree, 5 m tall, in moist area, along road, evergreen forest. 2 May 2004, Gaoligong Shan Biodiversity Survey 20059 (CAS). Gongshan Xian, Cikai Zheng, E side of Gaoligongshan, W of Gongshan, along the Pula He on the trail from Qiqi to Dongshao Fang and the Dulong Jiang Valley, 2770-3050 m, 27°42'28"N, 98°29'49"E, conifer-deciduous forest with mostly conifers at the upper elevation, deciduous tree ca. 7 m tall, young fruit green, growing along trail in sun, 15 July 2000, H.Li 12626 (CAS); Gongshan Xian, Dulongjiang, Dongshanpian, mixed forest, alt 2100m tree 8m tall, leaf purplish green, flower raceme, fruit green, 15 Apr 1991, Dulongjiang Expedition 5876 (CAS); Gongshan Xian, Cikai Zheng, E side of Gaoligongshan, W of Gongshan, along the Pula He on the trail from No. 12 bridge to Dongshaofang and Dulong Jiang Valley, 3000 m, 27°41'42.5"N, 98°29'5.8"E, primary evergreen broad-leaved forest, growing on the roadside, tree ca. 2 m tall, bud green, 1 May 2002, H.Li 14796 (CAS); Gongshan Xian, Mt. Kenicunpo, eastern and western slopes, Salwin and Irrawady divide, tree 10-12 ft tall, flowers yellow, middle slopes in forest, 10000 ft, May-July 1932, J.F.Rock 22026 (A, BM, E, K, NY); Gongshan Drungzu Nuza Zizhixian, Cikai Zheng. E side of Gaoligong Shan, W of Gongshan, along the Pula He on the trail from No. 12 bridge to Dongshaofang and Dulong Jiang valley, 3000 m, 27°42'54"N, 98°30' 8"E, primary evergreen broad-leaved forest, tree ca. 6 m tall, calyx green, stamens light

yellow, growing on the roadside, 1 May 2002, H.Li 14808 (CAS); Gongshan Xian, Dulongjiang, Dizhenggang, Dongshanan mixed forest, 2100 m, deciduous tree 8 m tall, 15 Apr 1991, fl, Dulongjiang Expedition 5876 (KUN); Gongshan, at the divide of Chang River and Lu River, Doyon - Lumba, 3000-3200 m, frequent, tree, 25 Aug 1940, sterile, K.M.Feng 6922 (KUN); Gongshan, Bingzhongle, Songta, slope, in Tsuga forest, 2900 m, tree, 25 Jun 1982, late fl & young fr, Qing Zang Team 7537 (KUN, PE, 3 sheets); Gongshan, Songta Snow Mountain, 3200 m, 17 Jun 1960, fr, Nan Shui Bei Diao Team 8992 (KUN, PE); on the way from Gongshan to Dulong, Jidu to Dongshaofang, in Tsuga forest, 2800 m, tree 5-8 m tall, 22 Jul 1982, fr, lower leaf surface gravish green, fruits green, turning red, Qing Zang Team 8425 (PE, 3 sheets). Weixi Xian, Anyi, Shimian Chang, Ershui Tang, 3170 m, tree, 7 m, 3 May 1960, slope, in Betula forest, Nan Shui Bai Diao Team 8421 (KUN). Xizang: Tibet, Burma-Tibet Frontier, flowers white, practically over, a small soft wooded tree in thickets, rare, leaves glabrous, except petiole which is pubescent, teeth at the base of leaf with glandular hairs, inflorescence & shoots also pubescent, stamens indefinite, style 1 simple, ovary 1-celled, 1-seeded, first noticed, just in flower, on 12 March and not seen again, 1950, F.Kingdon-Ward 9340 (E); Tsarong, SE Tibet, in thickets by streams in side valleys on the Salwin-Kiu Chiang divide, N.W. of Si-chi-to, 28°24'N, long. 98°24'E, 10000 ft. May 1922, fl, G.Forrest 21598 (A, BM, E, US); Tsarong, SE Tibet, foliage only, Oct 1922, G.Forrest 22836 (A, E). Medog Xian, Lage to Hanmi, tree 8 m tall, 3000 m, in Abies forest, fruit purple, 26 Jun 1980, fr, W.-N.Chen 10630 (PE); Lage to Hanmi, 2800-2400 m, in Tsuga forest, 26 Jun 1980, fr, W.-N.Chen 10616 (PE, 3 sheets). Tibet, Rong To Valley, 6000–9000 ft, flower white, appearing with the leaves, a shrub, abundant in the temperate forest, particularly in damp places at lower levels, 25 May 1933, fl, F.Kingdon-Ward 10366 (BM, PE). India. Assam: Manda La, Balipara frontier, 9000 ft, in the drier forest, a small tree with white flowers, 2 Aug 1933, F.Kingdon-Ward 11471 (BM). Sikkim: S Dentam, 27°12'N, 88°8'E, 9500 ft, filaments white, calyx reddish, 25 Apr 1966, J.D.A.Stainton 5358 (BM). Myanmar. Tibet-Burma frontier, northern Myanmar, Advance Base, Seinghku Wang, 10000 ft, flower white, very fragrant, small shrub in thickets or in the open steef faces, 1 Jun 1926, F.Kingdon-Ward 6811 (K). Nepal. Ilam, NW Ilam, 9000 ft, tree 20 ft, 4 May 1981, J.D.A.Stainton 8264 (BM).

Discussion. Prunus gongshanensis is similar to P. hypoleuca in its glabrous leaf abaxial surface and the pubescent axils on vein joints. It also resembles Prunus himalayana in the many glandular teeth at the lower part of leaf margin (c 1/3 of the leaf base). Prunus gongshanensis' relatively large bud scales, stipules and bracts are similar to those of P. hypoxantha. Prunus gongshanensis seems to share a close relationship with the other three species. However, P. gongshanensis stands out from the rest of the group by its subcordate to cordate leaf bases. It differs from P. himalayana and P. hypoxantha in its almost glabrous lower leaf surfaces (except on vein axils). It is also distinguishable from P. hypoxantha and P. hypoleuca by its highly glandular lower part of the leaf margin. Furthermore, the leaves of P. gongshanensis are much more mature than those of P. hypoleuca at anthesis.

Excluded name

Maddenia pedicellata Hook.f. (Fl. Brit. India 2: 318. 1878).

Type: India. Mishmi Hills, Griffith s.n. (holotype: K!, K000396854).

Note: As noted by Hooker (1878), *Maddenia pedicellata* was described based on a fragmentary specimen collected by Griffith from the Mishmi Hills. It was stated to be characterized by subcorymbose flowers on long slender pedicels on a short peduncle in unripe fruits (Hooker 1878, p. 318). The type was mounted on a sheet with *Prunus gongshanensis* collected from Bhutan (Griffith 2057, K) in flower condition, although Hara (1976) said it was a collection of *M. himalaica*, which should bear highly pubescent leaves. This specimen has glabrous lower leaf surfaces with only traces of hairs at the axils of veins on the lower leaves. Our examination of the type material confirms Hara's treatment of *Maddenia pedicellata* as a synonym of *Prunus cerasoides* Buchanan-Hamilton ex D. Don (Hara 1976; also see Lu et al. 2003).

Acknowledgments

This study was supported by NSF Award number 0515431, the Smithsonian Endowment Grant Program, and the Small Grants Program of the National Museum of Natural History of the Smithsonian Institution. Field assistance was provided by C.-X. Fu, Z.-L. Nie, Y.-X. Qiu, T.-S. Yi and S.-L. Zhou. We thank A, BM, CAS, CDB, E, GH, IBSC, K, KUN, L, MO, NY, PE and US for permission to examine their specimens, either through loans or during visits. We thank Kai Wen for providing the illustrations, Sue Lutz for herbarium assistance, and Larry Dorr for discussions on nomenclature and historical references.

References

- Backer CA, Bakhuizen van den Brink RC (1963) Flora of Java, vol. 1. N.V.P. Noordhoff, Groningen, the Netherlands, 1–648.
- Chang Y-T (1985) A new species of Maddenia (Rosaceae) from Fujian. Guihaia 5(1): 25-26.
- Chin S-W, Wen J, Johnson G, Potter D (2010) Merging *Maddenia* with the morphologically diverse *Prunus* (Roseaceae). Botanical Journal of the Linnean Society 163: 236–245. doi: 10.1111/j.1095-8339.2010.01083.x
- Hara H (1976) New or noteworthy flowering plants from Eastern Himalaya (17). Journal of Japanese Botany 51(1): 7–11.
- Hooker JD, Thomson T (1854) On *Maddenia* and *Diplarche*, new genera of Himalayan plants. Hooker's Journal of Botany and Kew Garden Miscellany 6: 380–384.
- Hooker JD (1878) Rosaceae. In: Hooker JD (Ed) Flora of British India, vol. 2. L. Reeve & Co., London, 307–388.

- Kalkman C (1965) The Old World species of *Prunus* subgenus *Laurocerasus* including those formerly referred to *Pygeum*. Blumea 13: 1–115.
- Koehne E (1911) Maddenia. In: Sargent CS (Ed), Plantae Wilsonianae: an Enumeration of the Woody Plants Collected in Western China for the Arnold Arboretum of Harvard University during the Years 1907, 1908, and 1910 by E. H. Wilson, vol. 1. The University Press, Cambridge, 56–59.
- Liu X, Wen J, Johnson G, Nie Z, Liang Z, Chang Z (in press) Polyphyly of the *Padus* group of *Prunus* (Rosaceae) and the evolution of biogeographic disjunctions between eastern Asia and eastern North America. Journal of Plant Research.
- Lu L, Gu C, Li C, Alexander C, Bartholomew B, Brach A, Boufford DE, Ikeda H, Ohba H, Robertson KR, Spongberg SA (2003) Rosaceae. In: Wu ZY, Raven PH (Eds), Flora of China, vol. 9. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis, 46–434.
- Rehder A (1940) Manual of Cultivated Trees and Shrubs Hardy in North America Exclusive of the Subtropical and Warmer Temperate Regions, 2nd ed. MacMillan, New York.
- Wen J, Berggren ST, Lee C-H, Ickert-Bond S, Yi T-S, Yoo K-O, Xie L, Shaw J, Potter D (2008) Phylogenetic inferences in *Prunus* (Rosaceae) using chloroplast *ndhF* and ribosomal ITS sequences. Journal of Systematics and Evolution 46(3): 322–332.
- Yü TT, Lu LT, Ku TC (1985) Taxa nova Rosacearum Sinicarum (V). Acta Phytotaxonomica Sinica 23: 209–215.
- Yü T-T, Lu L-T, Ku T-C, Li C-L, Chen S-X (1986) Rosaceae (3) Prunoideae. In: Flora Reipublicae Popularis Sinicae, vol. 38. Science Press, Beijing, 1–133.

· ·

RESEARCH ARTICLE



Two new mountainous species of *Lactuca* (Cichorieae, Asteraceae) from Iran, one presenting a new, possibly myrmecochorous achene variant

Norbert Kilian¹, Seyyedeh Bahereh Djavadi², Majid Eskandari²

l Botanic Garden and Botanical Museum Berlin-Dahlem, Dahlem Center of Plant Sciences, Free University Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany **2** Department of Botany, Iranian Research Institute of Plant Protection, P.O. Box 1454, Tehran 19395, Iran

Corresponding author: Norbert Kilian (n.kilian@bgbm.org)

Academic editor: V. Funk | Received 19 December 2011 | Accepted 26 March 2012 | Published 18 April 2012

Citation: Kilian N, Djavadi SB, Eskandari M (2012) Two new mountainous species of *Lactuca* (Cichorieae, Asteraceae) from Iran, one presenting a new, possibly myrmecochorous achene variant. PhytoKeys 11: 61–77. doi: 10.3897/ phytokeys.11.2563

Abstract

It is shown that the concept of the Iranian endemic *Lactuca polyclada* in the sense of both its original author Boissier and its current use actually admixes two entirely different species, as was first noted by Beauverd a hundred years ago but has been neglected by later workers. One is a putative relative of L. rosularis, the other was recognised by Beauverd as a member of the genus Cicerbita. The name L. polyclada Boiss. is lectotypified here, maintaining its use as established by Beauverd for the Cicerbita species. Both species are morphologically delimited and mature achenes of Cicerbita polyclada are illustrated for the first time. The putative relative of Lactuca rosularis, a rare local endemic of the summit area of Kuh e-Dena, which has remained without a valid name by now, is described as a new species, Lactuca denaensis N. Kilian & Djavadi, and illustrated. A third member of the Lactuca rosularis group, L. hazaranensis Djavadi & N. Kilian, discovered among a recent collection and apparently being a rare chasmophyte of the Hazaran mountain massif in the province of Kerman, Iran, is described as a species new to science, illustrated and delimited from the other two species. This new species has peculiar achenes representing a hitherto unknown variant: the body of the beaked achenes is divided into two segments by a transversal constriction in the distal third. The proximal segment contains the embryo, the distal segment is solid with a lipid-containing yellow tissue. The easily detachable pappus and the equally easily detachable beak potentially obstruct dispersal by wind. Since detachment of the beak also exposes the lipid-containing tissue of the distal segment, its potential as an elaiosome and myrmecochory as a possible mode of dispersal are discussed.

Copyright Norbert Kilian et al. This is an open access article distributed under the terms of the Creative Commons Attribution License 3.0 (CC-BY), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords

Compositae, Asteraceae, Cichorieae, *Lactuca rosularis* group, *Lactuca denaensis*, *Lactuca hazaranensis*, taxonomy, Iran, Kerman, Hazaran Mts, Zagros Mts, carpology, dissemination, elaiosome, myrmecochory

Introduction

Identification of a collection of a Cichorieae species, made by the third author together with A. Torabi in August 2010, in Kerman Province in the vicinity of the famous waterfalls near the city of Rayen on the eastern foot of Mt Hezar, revealed that it apparently represents a hitherto unknown lactucoid species. The species has strikingly unusual achenes, which show a transversal constriction in the distal third. Morphological comparison and evaluation of its affinities led to the discovery of another still unnamed species among the putatively related species.

The lactucoid genera, which form the subtribe Lactucinae, have a worldwide distribution in the northern hemisphere but extend also into the southern hemisphere in Africa and comprise about 230 species (Kilian et al. 2009). Iran belongs to the regions with a higher diversity of Lactucinae species. In the Flora Iranica area, seven lactucoid genera (*Cephalorrhynchus, Cicerbita, Lactuca, Mulgedium, Prenanthes, Scariola, Steptorhamphus*) with altogether c. 36 species, are known to science (Tuisl 1977), of which 22 occur in Iran itself. Relationships and delimitation of the lactucoid genera have been disputed since the time of Linnaeus and their circumscription is not yet settled. Ongoing morphological-molecular studies (Kilian et al. in prep.) reveal a considerable extent of homoplasy in morphological features, explaining the tremendous difficulties which all morphological attempts aiming at a natural classification of the lactucoid taxa have faced.

This paper (a) gives the description and delimitation of hitherto unknown or neglected plants, respectively, as two species new to science, (b) clarifies their morphological affinities among the lactucoid species, and (c) considers the peculiar achene morphology found in one of the two species with respect to its possible function for fruit dispersal.

Material and methods

The study is based on herbarium material of the Herbarium of the Iranian Research Institute of Plant Protection (IRAN) and of the Herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B) as well as on digitised type material from the herbaria of G, M, MO, P, WAG (herbarium abbreviations according to Thiers 2008+). Digitised specimens were received upon request from the herbaria, viewed via the online herbarium catalogues of the herbaria or via JSTOR (2012), respectively.

The authors observed all morphological data presented and used in the description and comparison of the new species on the herbarium material cited in the text under the new species or in the Appendix, respectively. Micromorphological features were examined under a WILD M5 optical reflected-light microscope. Documentation of morphological features was done with an Olympus DP72 digital camera mounted on an Olympus SZX16 stereo zoom optical reflected-light microscope equipped with the Olympus analySIS docu software.

Light microscopic histochemical analysis of the achene tissue to test the presence of lipids was performed using Sudan III staining following Wanner (2004: 21, 24).

Results and discussion

Lactuca denaensis N. Kilian & Djavadi, sp. nov.

urn:lsid:ipni.org:names:77118676-1 http://species-id.net/wiki/Lactuca_denaensis Fig. 1, 3C; Tuisl 1968: t. 2, fig. 12–13 = Tuisl 1977: t. 201, fig. 9–10 under *Lactuca polyclada* (achene, aspect and cross section)

Lactuca polyclada sensu Boissier (1846: 10, 1875: 812) p.p. et Tuisl (1968: 606, 1977: 190–191) p.p., non sensu lectotypi.

Diagnosis. Habitually similar to *Lactuca rosularis* but clearly distinguished by the rosette leaves being undivided (instead of lyrately to irregularly pinnatifid to pinnatisect), the involucre being 10-12 mm (instead of 6-9(-10) mm) long, the achenes having a 4–5 mm (instead of 2.2-3 mm) long corpus, a 0.4-0.9(-2) mm (instead of (1.1-)3-5.3 mm) long beak and a 5–6 mm (instead of 2.5-3 mm) long pappus.

Holotype. [Iran, Kogiluyeh & Boyer Ahmad], in glareosis alpis Kuh-Daëna, fl. lutescens, 14 Jul 1842, Kotschy Pl. Pers. autral. 662 (G-BOIS G00330211, specimen annotated by Beauverd in 1910, see CHG 2012); selected isotypes: B 100426936, M 0030847 [p.p., two rosulate plants on the left], G [3 sheets], MO 6264530 [p.p., rosulate plants on the left and right], P 00750254 [p.p., left plant], P 00750251 [p.p., second bottom right rosulate plant], P 00750252 [p.p., first bottom right rosulate plant], P 00750253 [p.p., three rosulate plants at the bottom], WAG 0004075 [p.p., sterile leaf rosette on the left].

Description. Perennial rosulate herb, with a woody subterranean caudex, rosette shoots often on vertical subterranean axes vested with cataphylls below the sometimes somewhat elongate rosette, acaulescent to usually very shortly caulescent and less than 5 cm tall (Fig. 1A), rarely to c. 15 cm. Stem one per leaf rosette, usually not or little projecting above the leaf rosette. Rosette leaves (Fig. 1A) obovate to spatulate, tapering towards base, $2-7 \times (1-)1.5-3.2$ cm, somewhat glaucous; base semiamplexicaul, margin ± densely dentate and denticulate, apex rounded to, more rarely, subacute. Synflorescence corymbosely paniculiform, condensed through conspicuously short axes, of c. 6–20 capitula (Fig. 1A, G); peduncles 0.4–0.7 cm long. Capitula with c. 10–14 flowers. Involucre (Fig. 1B–F) narrowly cylindric at anthesis, 10–12 mm long, not



Figure 1. *Lactuca denaensis* – **A** habit, acaulescent form **B–F** capitula, all to the same scale, before flowering (**B–D**), with faded flowers (**E**), after flowering (**F**); **G** details of synflorescence, one capitulum at fruiting. – All from Remaudière, 5252E (IRAN 10625)

elongating during maturation; outer phyllaries imbricate, outermost \pm narrowly ovate, c. 2 mm long, following ones gradually longer, lanceolate, the longest up to c. 1/2 as long as inner ones; inner phyllaries linear-lanceolate, 7–8, \pm in one row, subequal in length, with \pm narrow scarious margin. Receptacle flat to slightly convex, naked. Flowers with corolla yellow, ligule 6.7–7.5 mm, tube 5–5.5 mm long; anther tube without appendages 3.2–3.5 mm, basal appendages c. 0.4–0.6 mm, apical appendages 0.3–0.4 mm long; style arms 2.8–3.2 mm long. Achenes (Fig. 1G, 3C) homomorphic, including beak 4.8–5.7 mm long; corpus 4–5 mm long, up to 1.1–1.3 mm in diam., slender-obovoid, compressed, apex contracted into a stout, easily detachable beak c. 0.4–0.9(–2) mm long; achene body apart from the two lateral ribs with 1 similarly strong median rib on either side, rarely dorsally with 2 equally strong ribs, secondary ribs missing; achene surface \pm smooth, brown. Pappus simple, without an outer series of minute hairs, setae thin, white, 5–6 mm long, persistent. – Flowering and fruiting: July to September.

Notes. Boissier (1846) described a new species, Lactuca polyclada, based on two collections (no. 603 and 662) made by T. Kotschy in the Zagros mountains, in the first half of July 1842. Coming from the village Dozdkurd (Edmondson and Lack 2006), Kotschy collected the material on the upper slopes of the "Kuh Daena" [= Kuh e-Dena, c. 30°56'N, 51°28'E; summit c. 4448 m, see Wikipedia (2012), situated in the presentday province Kogiluyeh & Boyer Ahmad of Iran]. According to Kotschy's original labels present on the sheets in the Boissier herbarium in Genève (G-BOIS), the collection Kotschy 603 was collected on 10 July and Kotschy 662 on 14 July 1842. The entire material of Kotschy's gatherings from S Iran was revised by Boissier and subsequently edited and distributed by R. Hohenacker in his series of exsiccatae "Plantarum Persiae australis siccatarum species 440, collectae a Th. Kotschy, determinatae a Dre E. Boissier, editae a R. F. Hohenacker" (Triebel and Scholz 2001+; Edmondson and Lack 2006). Duplicates are present today in many herbaria. The material of Lactuca polyclada was distributed as a single item under the united numbers "603. 662." and with a single collecting date cited as "14 Jul 1842" on the printed label. The syntypes in Boissier's herbarium as well as the duplicates distributed by Hohenacker in this series of exsiccatae as no. "603. 622." contain two morphologically distinct elements: (a) small leaf rosettes with usually very short, branched, slender to capillaceous flowering axes; (b) almost leafless, from base on divaricately and intricately branched, conspicuously inflated flowering axes. Apparently it has been taken as evident by Boissier and later workers that both elements represent different forms or stages of development of the same species. This assumption is backed by the leaves, which are fairly similar in colour, size, shape and denticulation of the margin in both elements, as well as by the existence of a plant with exceptionally well developed flowering shoots, approaching those of Kotschy 603, among the material of Kotschy 662 (on G00330211, the holotype sheet of L. denaensis). Boissier (1846: 10) expressed this hypothesis in the following way: "panicula corymbosa intra folia subsessili ... Post anthesin saepe panicula valde augetur, ramosissima fit semipedalis ramis elongatis intricatis dichotomis spongiose incrassatis,

sed haec forma monstrosa est, nam in ea nunquam achenia perfecta observavi." ["with a corymbose panicle subsessile among the leaves ... after anthesis panicle often strongly enlarged, very much branched, becomes half a foot long, with elongate, intricate, dichotomous, softly inflated branches, but this is a monstrous form, because I never have observed a perfect achene in it."]. Tuisl (1977: 191) considered the two elements as different developmental stages: "caulis florifer abbreviatus, fructifer 10–30 cm longus" ["stems at anthesis very short, in fruit 10–30 cm long"].

Beauverd (1910: 131–132), in contrast, came to the conclusion that the syntypes of *Lactuca polycalda* in the herbarium of Boissier (G-BOIS) represent two entirely different species and correctly distinguished them. Beauverd (1910: 131) consequently restricted the name *Lactuca polyclada* to "K[otsch]y 603 solum! excl. No. 662 et descr. achen.," and formed the new combination *Cicerbita polyclada* (Boiss.) Beauverd for the taxon with divaricately branched inflated stems, smaller involucres, bluish flowers and a pappus with an outer row of minute hairs. Mature fruits of *Cicerbita polyclada*, missing in Kotschy 603, are known through a collection of T. Strauss (at B, see Appendix). They are illustrated here for the first time and show further differences between the two species, in particular with respect to the prominence of the ribs and shape and structure of the body apex (compare Fig. 2C and D–E). For a summary of the differences see Table 1.

According to Art. 7.11 of the Vienna Code, Beauverd's restriction of the name to Kotschy 603 does not, however, constitute a lectotypification, because he did not use "the term 'type' (typus) or an equivalent" (McNeill et al. 2006). Later authors apparently neglected Beauverd's rectification and we are also not aware of any lectotypification of Boissier's name. In accordance with Art. 9.12 (McNeill et al. 2006) and in this way maintaining the only unequivocal use of the name as established by Beauverd (1910: 131) for the species placed by him in *Cicerbita*, we formally lectotypify *Lactuca polyclada* Boiss. following his restriction: *Cicerbita polyclada* (Boiss.) Beauverd in Bull. Soc. Bot. Genève 2: 131. 1910 \equiv *Lactuca polyclada* Boiss., Diagn. Pl. Orient., ser. 1, 7: 10. 1846. – Lectotype (designated here): [Iran, Kogiluyeh & Boyer Ahmad], in glareosis ad latera septentr. m. Kuh-Daëna, flos caeruleus, 10 Jul 1842, Kotschy Pl. Pers. autral. 603 (G-BOIS G00330212 [2 sheets annotated by Beauverd in 1910], see CHG 2012).

The second species admixed by Boissier under the name *Lactuca polyclada* with a usually very short or almost missing flowering stem, yellow flowers, a pappus without an outer row of minute hairs and the achene anatomy as illustrated by Tuisl (1968: t. 2, fig. 12-13 = 1977: t. 201, fig. 9-10) was left by Beauverd without a legitimate name. We have named and described it therefore here as *Lactuca denaensis*, the name being typified with the syntype "Kotschy 662" of *L. polyclada* Boiss. in Boissier's herbarium. Since Kotschy's both collections no. 603 and 662 were combined by Hohenacker in his series of exsiccatae into a single unit of which each set usually contains both elements, isotypes are present in numerous herbaria. The corresponding exsiccatae sheets with the admixed material of *Cicerbita polyclada* and *Lactuca denaensis* carry the printed label "Th. Kotschy, Pl. Pers. austr. Ed. R. F. Hohenacker. 1845 // 603. 662. *Lactuca poly-*

Table 1. Morphological differences between *Lactuca hazaranensis* and its relatives *L. rosularis* and *L. denaensis*, as well as between the latter and *Cicerbita polyclada*. Based on the material studied. – The investigated material is listed in the Appendix.

Features	Lactuca hazaranensis	L. rosularis	L. denaensis	Cicerbita polyclada
Rosette leaves: division	undivided	lyrately to irregularly pinnatifid to pinnatisect with large terminal lobe	undivided	undivided, towards base sometimes shallowly pinnately divided
Rosette leaves: margin	coarsely and ± irregularly dentate and denticulate	irregularly dentate and denticulate	± densely dentate and denticulate	subentire to dentate and denticulate
Branching of stem	with dominating main axis, corymbosely paniculiform	with dominating main axis, paniculiform to corymbosely paniculiform	subacaulescent, with dominating main stem only few cm long or branched from base, corymbosely paniculiform	± without dominating main axis, repeatedly divaricately branched from base
Branches	slender to capillaceous	± slender (to capillaceous)	slender to capillaceous	conspicuously inflated
Penduncles, length [cm], shape	c. 0.3–0.7(–1), capillaceous	0–0.2, capillaceous if developed	0.4–0.7, capillaceous	1–3.5, inflated if well developed
Cauline leaves	usually present, gradually reduced to bracts	basally present, soon reduced to bracts	usually absent, reduced to bracts	absent
Involucre, length [mm]	6–7	6–9(–10)	10-12	7–9
Corolla, colour	yellow	yellow	yellow	blue
Achene, length [mm]	3.2–3.6	(3.8–)6–8	4.8–5.7	3.4–5.2
Achene: corpus, length [mm]	2.9–3.2	2.2–3	4–5	3-4.2
Achene: ribs	4(–5), strongly prominent	4, strongly prominent	4(–5), strongly prominent	5, subprominent to subdistinct
Achene: beak, length [mm]	0.3–0.5	(1.1–)3–5.3	0.4–0.9(–2)	0.5–1
Achene: transversal constriction	present	absent	absent	absent
Pappus, length [mm]	3–3.5	2.5–3	5–6	3-4
Pappus: outer ring of minute hairs	absent	absent	absent	present

clada / Boiss. n. sp. // In glareosis alpis Kuh-Daëna. D. 14. Jul. 1842. / Pl. lactescens." They are usually filed under *Lactuca* or *Cicerbita polyclada*, respectively, or, sometimes erroneously under *Cephalorrhynchus polycladus* (Boiss.) Kirp. The latter name is not a further homotypic synonym of *Lactuca polyclada*, but actually based on *Zollikoferia*

polyclada Boiss., which represents a different mountainous species distributed from E Iran and Afghanistan to Central Asia, also with intricately and divaricately branched stems. Habitually, the latter species can readily be distinguished by its indurate and never inflated stems and branches; also it is not present in the Zagros mountains.

Distribution and habitat. As far as we know, *Lactuca denaensis* is restricted to the higher elevations, probably above 3000 m, of Kuh e-Dena in the Zagros mountains of SW Iran (Fig. 4). From the rare material with subterranean parts preserved (e.g. on the sheets MO 6264530 and P 00750252 with isotypes), showing a subterranean caudex producing several cm long shoots vested with cataphylls below the leaf rosettes, it can be concluded that the species is a scree plant.

Additional specimen seen: Iran. Kogiluyeh & Boyer Ahmad: Dena [c. 30°56'N, 51°28'E], 3300 m, Sep 1955, Remaudière 5252E (IRAN 10625).

Etymology. *Lactuca denaensis* is named after the Kuh e-Dena massif of the Zagros mountains, where the only two collections known to us come from.

Morphological affinities and delimitation. Morphological comparison shows that *Lactuca denaensis* is most similar to *L. rosularis.* Both share the rosulate habit with a woody caudex, glaucous leaves and small yellow-flowered capitula but also the compressed, beaked achenes (compare Fig. 3B and C), characterised by 4 (only exceptionally 5) similar and strongly prominent main ribs (two lateral and one median on either side, exceptionally dorsally 2) and a simple pappus without an outer series of minute hairs (see also Table 1).

Preliminary conservation status. *Lactuca denaensis* is known only from the higher elevations of the Kuh e-Dena massif, which is part of a Protected Area, possibly also including the populations of the species. The species seems to be rare, since only two collections are known to us, but it has to be taken into account that it is rather inconspicuous. *Lactuca denaensis* must currently be assessed as Data Deficient (IUCN 2001) and an assessment of its populations in the field is strongly desirable.

Lactuca hazaranensis Djavadi & N. Kilian, sp. nov.

urn:lsid:ipni.org:names:77118677-1 http://species-id.net/wiki/Lactuca_hazaranensis Fig. 2, 3A, F–I

Diagnosis. Habitually similar to *Lactuca rosularis* but clearly distinguished from it by the rosette leaves being undivided (instead of lyrately to irregularly pinnatifid to pinnatisect), the peduncles being distinct, c. 0.3–0.7(–1) cm long (instead of indistinct, 0–0.2 cm long), the achenes having a 0.3–0.5 mm (instead of (1.1–)3–5.3 mm) long beak and the achene body being transversally constricted and sectioned in the distal quarter into an embryo-containing proximal and a solid distal segment (instead of being unconstricted and unsectioned).

Holotype. Iran. Kerman: Rayen, near Rayen falls [c. 29°33'N, 57°18'E], 2850 m, 10 Aug 2010, M. Eskandari & A. Torabi (IRAN 55199; photo at B).



Figure 2. *Lactuca hazaranensis* – **A** habit, left plant of holotype sheet **B–G** capitula, all to the same scale, before flowering (**B–C**), at fruiting (**D–E**), after fruiting (**F–G**); **H** plant in natural habitat **A–G** from the holotype **H** plant in the natural habitat at the type locality; photograph by M. Eskandari, 10 Aug 2010.



Figure 3. Achenes of the *Lactuca rosularis* group and *Cicerbita polyclada* – **A**, **F–I** *L. hazaranensis*; complete achene (**A**); achene after loss of easily detachable beak, dorsal view (**F**); ventral view (**G**); longitudinal section of achene showing two segments, proximal large segment with embry, distal small segment solid with yellow tissue (**H**); embryo (**I**); **B** *L. rosularis* **C** *L. denaensis* **D–E** *Cicerbita polyclada*, complete achene (**D**) and longitudinal section of distal portion showing apical cavity (**E**). – **A–D** and **F–H** each to the same scale **A**, **F–I** from the holotype at IRAN **B** from Rechinger 55980 **B**, **C** from Kotschy 662 (B 100426936) **D–E** from Strauss 14091 (B 100312952)

Description. Perennial rosulate herb (Fig 2A), with a taproot(?) and a woody caudex covered by the marcescent remains of old leaf bases. Stem one or a few per leaf rosette, erect, (2-)10-18 cm tall, branched already in lower half. Rosette leaves obovate to spatulate, $(2-)5-11 \times (1-)2-5$ cm, somewhat glaucous; base semiamplexicaul, margin densely, coarsely and ± irregularly dentate-denticulate, apex subacute to acute. Lower

71

and middle stem leaves spatulate to lanceolate, with auriculately clasping base, smaller, otherwise similar to rosette leaves; upper stem leaves distinctly smaller than lower and middle ones, lanceolate to ovate, with conspicuously auriculately clasping base, margin usually entire, apex acute to acuminate; uppermost stem leaves bractlike. Synflorescence (Fig. 2A) of a stem corymbosely paniculiform, with some to many capitula, axes wiry; peduncles c. 0.3-0.7(-1) cm long, capillaceous. Capitula with 7-14 flowers. Involucre (Fig. 2B-G) narrowly cylindric at anthesis, 6-7 mm long, not elongating during maturation; outer phyllaries imbricate, outermost ovate to narrowly ovate, 1.5-3 mm long, similar to the bracts on the peduncle, following ones gradually longer and ovatelanceolate to lanceolate, the longest up to c. 1/2 as long as inner ones; inner phyllaries linear-lanceolate, 6–9, ± in one row, somewhat unequal in length, with ± narrow scarious margin. Receptacle flat to slightly convex, naked. Flowers with corolla yellow, ligule 5.5–6.5 mm long, tube shorter than ligule; anther tube without appendages 1.6–2 mm, basal appendages c. 0.4 mm, apical appendages 0.4 mm long; style arms 1.6-1.8 mm long. Achenes (Fig. 3A) homomorphic, including beak 3.2-3.6 mm long, corpus 2.9-3.2 mm long, up to 0.8-1.1 mm in diam., ellipsoidal, compressed, with a transversal constriction of 0.4–0.8 mm diam. in the distal 1/3-1/4, distal segment c. 1.5×1.5 mm, contracted into a stout, easily detachable beak c. 0.3-0.5 mm long; achene body (Fig. 3F-I) apart from the two lateral ribs with 1 similarly strong median rib on either side, rarely dorsally with 2 equally strong ribs, secondary ribs missing or rarely 1-2 per side; achene surface faintly transversally wrinkled, proximal segment brown, distal segment and beak yellowish, ribs straw-coloured to yellowish in distal segment; proximal segment containing the whitish embryo (Fig. 3H–I), distal segment containing yellowish tissue (Fig. 3H). Pappus simple, without an outer series of minute hairs, setae thin, white, 3-3.5 mm long, easily detachable. - Flowering and fruiting: June to August.

Distribution and habitat. The type collection of *Lactuca hazaranensis* comes from the northeastern foot of Mt Hezar, which rises to 4465 m elevation, and has been collected in the vicinity of the Rayen falls, at an altitude of 2850 m, in rock crevices. A second collection, with mature achenes of the precisely the same variant, was traced in the Berlin herbarium and had been made by J. Bornmüller in 1892 some 50 km further NW on rocks at an altitude of 3700 m on Mt Jupar (c. 29°55.8'N, 57°11.5'E; spelled "Khu-i-Dschupar" by Bornmüller, see also Freitag and Kuhle 1980), which is also situated in the Hazaran or Hezar-Lalezar mountain range (Fig. 4). Bornmüller (1939: 224), who determined this collection as *Lactuca rosularis*, characterised it as very rare on Mt Jupar, having only traced three tiny individuals (all preserved on the single sheet at B). The Hazaran or Hezar-Lalezar mountain range, which is mainly composed of limestone, is the highest mountain range in southeastern Iran and known as a local centre of endemism (Noroozi et al. 2010).

Additional specimen seen: Iran. Kerman: in rupibus summi jugii m. Kuh-i-Dschupar [Kuh-i-Jupar, c. 29°55.8'N, 57°11.5'E], 3700 m, 13 Jun 1892, J. Bornmüller 4119 (B).

Etymology. *Lactuca hazaranensis* is named after its provenance, the Hazaran mountain massif in the Iranian province of Kerman, which is a southeastern outlier of the Zagros mountain range and reaches a maximum elevation of about 4500 m in the peak Kuh-e Hazar.



Figure 4. Distribution of *Lactuca hazaranensis* (circles) and the related species *L. rosularis* (squares) and *L. denaensis* (rhomb, actucal position as indicated by arrow), as well as of *Cicerbita polyclada* (triangles). – Georeferenced map based on the known collections (see Appendix and supplemented by collection cited in Kirpicznikov 1964 and Tuisl 1977) and generated with DIVA-GIS (Hijmans 2011) using an adaptation of the SRTM 90 m digital elevation data (CGIAR-CSI 2004).

Morphological affinities and delimitation. Morphological comparison revealed that the new species is most similar to both *Lactuca rosularis* and *L. denaensis*. The three species are perennial rosette herbs of montane to high-montane environments, which are most likely closely related to each other, and considered here as the *L. rosularis* group. They are all rare, being known from few collections only, and are endemic or almost so to the Iranian Highlands (Fig. 4). They share the rosulate habit with a woody caudex, the glaucous leaves, small yellow-flowered capitula and the principally same achene morphology. The differences between these three species are summarised in Table 1.

Preliminary conservation status. *Lactuca hazaranensis* is known only from two localities c. 50 km apart, which are not in protected areas. The species seems to be rare, but it has to be taken into account that it is rather inconspicuous in its rocky environment. Members of the tribe are among the most favoured food of livestock, grazed wherever in reach and are therefore particularly threatened by overgrazing. *Lactuca hazaranensis* must currently be assessed as Data Deficient (IUCN 2001), but since the status Endangered seems not unlikely, an assessment of its populations in the field would be desirable.
Transversally constricted achenes of Lactuca hazaranensis aiding myrmecochory? The shape of the achenes of *Lactuca hazaranensis* with the transversal constriction in the distal third (Fig. 3A, F–H) is curious. The fact that all achenes of all fruiting heads in two collections from different localities and centuries invariably show the same morphology, rules out the possibility that this achene variant represents a teratogenic manifestation.

Conspicuous transversal constrictions are, as far as we know, a very rare phenomenon in Asteraceae fruits. The present case is parallelled, however, by a few *Pulicaria* species of the Horn of Africa and southern Yemen (Wagenitz and Gamal-Eldin 1983 under *Sclerostephane*; Kilian 1999), which are likely not all closely related to each other (Englund et al. 2009) in contrast to what was thought initially. The possible function of these constrictions in the *Pulicaria* species is unknown.

In contrast to the cases in *Pulicaria*, where the constrictions chiefly affect the pericarp (Kilian 1999: fig. 2c, 3a, 4a, 5c), the constriction in *Lactuca hazaranensis* incompletely divides the achene into two segments (Fig. 3H). The large proximal segment contains the whitish embryo (Fig. 3I), the small distal segment is solid and of a yellowish tissue, which is partly identical partly contiguous with and therefore apparently derived from the intercostal yellowish pericarp tissue. The tissue of the embryo and the tissues of the distal segments are somewhat spatially separated from each other (Fig. 3H).

Conspicuous segmentation of the achene, although not precisely by a transversal constriction, is otherwise known from the probably unique case of the bispecific genus *Urospermum* (Cichorieae, Hypochaeridinae): the achenes of this genus consist of a proximal, compressed segment, which contains the embryo, and a larger, inflated distal segment tapering into the beak (for images, see *U. picroides* in ICN 2011). In contrast to our case, in *Urospermum* both segments are separated from each other by a transversal wall and the distal segment is hollow (Lack and Leuenberger 1979).

A morphological transition towards a segmentation might perhaps be an achene with a cavity below the beak as it can be observed, e.g. in *Cicerbita polyclada* (Fig. 3D–E). Within subtribe Lactucinae, the achenes of *Cephalorrhynchus polycladus* (Boiss.) Kirp., not to be confused with the habitually similar *Cicerbita polyclada*, might represent an even stronger morphological transition (pers. com. A. Sennikov, Feb 2012); the presumably empty apical achene portion below the beak is, as stated by Kirpicznikov (1964: 351 + t. 20, fig. 8), somewhat narrower and separated by a very slight (non-waisted) constriction proximally.

Being shortly beaked and provided with a pappus, the achenes of *Lactuca hazaranensis* appear principally suited for wind dispersal (anemochory). The entire beak is, however, detachable at its base from the distal segment of the achene by slightest pressure and also the pappus setae are very easily detachable and are thus not functional for dispersal by wind. Finally, the solid distal segment brings additional weight and thus impedes wind dispersal.

Light microscopic histochemical analysis, using Sudan staining, of the yellow tissue of the distal segment of *Lactuca hazaranensis* revealed abundant presence of lipid drops, which were similarly found also in the embryo. Lipids are well known in the embryo of

Lactuca as a major component of the reserves for the germination, accounting for 33 % dry weight of the achene in lettuce (*Lactuca sativa*) (Paulson and Srivastava 1968; Srivastava and Paulson 1968; Halmer et al. 1978), and for 35 % in the oilseed lettuce cultivar of *L. sativa* with particularly large fruits grown in Egypt as a source for cooking oil (Křístková et al. 2008).

Their spatial separation from the embryo makes it unlikely that the lipid reserves of the distal segment are related to the germination. A potential function for the dispersal of the achene seems more probable, in particular in connection with the easy detachment of the achene beak. The detachment of the beak has not only a potentially atelechorous effect but the rupture also exposes the lipid reserves of the distal segment. The distal segment could thus perhaps be an "elaiosome", a structure developing from seed or fruit tissue and aiding diaspore dispersal by ants (myrmecochory) in that it both attracts and rewards them (Bresinsky 1963; Lengyel et al. 2010). Usually, ants carry the diaspores into their nest, consume the lipid-rich tissue or feed it to their larvae and finally dump the diaspore in or outside their nest. Elaiosomes have convergently developed in seed plants many times, being known from 77 families and 334 genera (Lengyel et al. 2010). They are also long known from the Asteraceae (Sernander 1906; Nesom 1981), having been reported from many Cardueae species and also from five other tribes (Anthemideae, Arctotideae, Calenduleae, Heliantheae, Senecioneae), but not so far from the Cichorieae (Lengyel et al. 2010).

Usually, elaiosomes develop in Asteraceae at the base of the achenes from tissue separating the achene from the receptacle. In this way, the elaiosome is separated from the embryo by the indurate pericarp, which hinders the ants to get access to the embryo in the interior. The development of an elaiosome at the apex of the achenes and inside the pericarp appears in this context much less favourable. Apart from the presumably higher cost of this solution, the constriction only incompletely locks off the lipid reserves from the embryo, with the risk of its damage. In case the hypothesis of the myrmecochorous property of the distal achene segment of *Lactuca hazaranensis* is confirmed, e.g. by an experimental approach such as exemplified by Nesom (1981), it certainly would make an interesting case, considering both the chasmophytic growth of the plants and their apparent rarity.

The unparallelled and, so far as we know, transition-free occurrence of the transversally constricted achenes in the *Lactuca rosularis* group, is, independently of its potential function, a particularly striking evidence for a considerable developmental plasticity in achene features in the Lactucinae.

Acknowledgements

We are most grateful to Dr Laurent Gautier (Conservatoire et Jardin botaniques de la Ville de Genève) for his instantaneous invaluable help with the material in G-BOIS and G, to Dr Julia Lazar-Schurreit (Dahlem Center of Plant Sciences, Institute of Pharmacy, Pharmaceutical Biology, Freie Universität Berlin) for guiding the histochemical analysis, to Monika Lüchow for her assistance with the photographic documentation, Michael Rodewald for the preparation of the photographic plates, Prof. H. Walter Lack for reading a previous version of the manuscript, Prof. Werner Greuter for nomenclatural advice (all Dahlem Center of Plant Sciences, Botanic Garden and Botanical Museum, Freie Universität Berlin) and to Alexander Sennikov and an anonymous reviewer for their constructive comments on a previous version of the manuscript.

References

- Beauverd G (1910) Contribution à l'étude des Composées, 3. Le genre Cicerbita. Bulletin de la Société Botanique de Genève, ser. 2, 2: 99–145. http://biodiversitylibrary.org/page/5521285
- Boissier E (1846) Diagnoses plantarum orientalium novarum, Ser. 1, 7. Leipzig, Herrmann.

Boissier E (1875) Flora orientalis 3. Basel & Genève, Georg.

- Bornmüller J (1939) Iter Persico-turcicum 1892–1893. Beiträge zur Flora von Persien, Babylonien, Assyrien, Arabien. Fortsetzung III. Beihefte Botanisches Centralblatt, B, 60: 181–228.
- Bresinsky A (1963) Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. Studien zur myrmekochoren Verbreitung von Samen und Früchten. Bibliotheca Botanica 126: 1–54.
- CGIAR-CSI [Consortium of Spatial Information] (2004) NASA Shuttle Radar Topographic Mission (SRTM) 90 m digital elevation data (DEMs). http://srtm.sci.cgiar.org/
- CHG (2012) Catalogue des herbiers de Genève (CHG). Conservatoire & Jardin botaniques de la Ville de Genève. http://www.ville-ge.ch/musinfo/bd/cjb/chg
- Edmondson JR, Lack HW (2006) Karl Georg Theodor Kotschy's itinerary in southern Iran, 1841–42. Willdenowia 36: 579–588. doi: 10.3372/wi.36.36154
- Englund M, Pornpongrungrueng P, Gustafsson MHG, Anderberg AA (2009) Phylogenetic relationships and generic delimitation in Inuleae subtribe Inulinae (Asteraceae) based on ITS and cpDNA sequence data. Cladistics 25: 319–352. doi: 10.1111/j.1096-0031.2009.00256.x
- Freitag H, Kuhle M (1980) A plant list from the Kuh-e-Jupar (S. E. Iran), with some ecological remarks. Willdenowia 10: 161–169. http://www.jstor.org/stable/3996141
- Halmer P, Bewley JD, Thope TA (1978): Degradation of the endosperm cell walls of *Lactuca sativa* L., cv. Grand Rapids. Timing of mobilisation of soluble sugars, lipid and phytate. Planta 129: 1–8. doi: 10.1007/BF00390802

Hijmans R (2011) DIVA-GIS, ver. 7.4. http://diva-gis.org/

- ICN (2009+) Hand R, Kilian N, Raab-Straube E (Eds) *Urospermum picroides*. In: International Cichorieae Network: Cichorieae Portal. http://wp6-cichorieae.e-taxonomy.eu/ portal/?q=cdm_dataportal/taxon/da1ef992-e589-48cb-9670-fd76ef8cf4fd/images
- IUCN Species Survival Commision (2001) IUCN Red List Categories: Version 3.1. IUCN, Gland and Cambridge.
- JSTOR (2012) JSTOR Plant Science. http://plants.jstor.org/.
- Kilian N (1999) Studies in the Compositae of the Arabian Peninsula and Socotra 1. Pulicaria gamaleldinae sp. nova (Inuleae) bridges the gap between Pulicaria and former Sclerostephane

(now *P.* sect. *Sclerostephane*). Willdenowia 29: 167–185. http://www.ingentaconnect.com/ content/bgbm/will/1999/00000029/F0020001/art00016

- Kilian N, Gemeinholzer B, Lack HW (2009) Tribe *Cichorieae*. In: Funk VA, Susanna A, Stuessy T, Bayer R (Eds), Systematics, evolution, and biogeography of the *Compositae*. Vienna, IAPT, 343–383.
- Kirpicznikov ME (1964) Subtribe 5. Lactucinae [p.p.]. In: Bobrov EG, Tzvelev NN (Eds), Flora SSSR 29. Moskva et Leningrad, Nauka, 237–375.
- Křístková E, Doležalová I, Lebeda A, Vinter V, Novotná A (2008) Description of morphological characters of lettuce (*Lactuca sativa* L.) genetic resources. Horticultural Science (Prague) 35: 113–129. http://www.agriculturejournals.cz/web/hortsci.htm?volume=35&firstPage=113&type=publishedArticle
- Lack HW, Leuenberger B (1979) Pollen and taxonomy of *Urospermum* (Asteraceae, Lactuceae). Pollen and Spores 21: 415–425.
- Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR (2010) Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. Perspectectives in Plant Ecolology, Evolution and Systematics 12: 43–55. doi: 10.1016/j. ppees.2009.08.001
- McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersema JH, Turland NJ (Eds & Compilers) (2006) International Code of Botanical Nomenclature (Vienna Code), adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005. Regnum Vegetabile 146. http:// www.ibot.sav.sk/icbn/main.htm
- Nesom GL (1981) Ant dispersal in *Wedelia hispida* HBK (Heliantheae: Compositae). Southwestern Naturalist 26: 5–12. http://www.jstor.org/stable/3671323, doi: 10.2307/3671323
- Noroozi J, Yousef A, Nordenstam B (2010) A new annual species of *Senecio* (Compositae-Senecioneae) from subnival zone of southern Iran with comments on phytogeographical aspects of the area. Compositae Newsletter 48: 43–62.
- Paulson RE, Srivastava LM (1968) The fine structure of the embryo of *Lactuca sativa*. I. Dry embryo. Canadian Journal of Botany 46: 1437–1445. doi: 10.1139/b68-195
- Sernander R (1906) Entwurf einer Monographie der europäischen Myrmekochoren. Kongliga Svenska Vetenskaps Academiens Handlingar 41: 1–410.
- Srivastava LM, Paulson RE (1968) The fine structure of the embryo of *Lactuca sativa*. II. Changes during germination. Canadian Journal of Botany 46: 1447–1453. doi: 10.1139/ b68-196
- Thiers B (2008+) Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden. http://sweetgum.nybg.org/ih/
- Triebel D, Scholz P (2001+) IndExs Index of Exsiccatae. Botanische Staatssammlung München: http://indexs.botanischestaatssammlung.de [accessed 20.2.2012].
- Tuisl G (1968) Der Verwandtschaftskreis der Gattung *Lactuca* L. im iranischen Hochland. Vorarbeiten zur Flora Iranica Nr. 16. Annalen des Naturhistorischen Museums Wien 72: 587–638.
- Tuisl G (1977) *Lactuca.* In: Rechinger KH (Ed), Flora Iranica 122. Graz, Akademische Druckund Verlagsanstalt, 185–196.

Wagenitz G, Gamal-Eldin E (1983) Die Gattung *Sclerostephane* Chiov. (Compositae, Inuleae). Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 104: 91–113.
Wanner G (2004) Mikroskopisch-botanisches Praktikum. – Stuttgart, Georg Thieme.

Wikipedia (2012) Dena. http://en.wikipedia.org/wiki/Dena [accessed 20.2.2012]

Appendix

Specimens of related species investigated

Lactuca rosularis

Iran. Khorasan: prope Robat-e-Safid inter Mashad et Torbat-e-Heydariyeh, [c. 35.72°N, 59.38°E], 1800–2000 m, 29 May 1977, Renz & Runemark in Rechinger 55980 (B). Semnan: Momen-abad [c. 35°32.5'N, 53°17.5'E], 1100–1150 m, 26 Jun 1992, Termeh, Moussavi & Tehrani (IRAN 54459). Tehran: 13 km E Eyvanki, [35°20.9'N, 52°12.3'E], 1100 m, 8 Jul 1974, Renz & Iranshahr, Rechinger 16608 (IRAN 10627). Tehran: 13 km W Garmsar [35°15.3'N, 52°11.8'E], 25 May 1984, Moussavi & Karavar (IRAN 10626). Qom: Qom to Qomrud, [c. 34°42.9'N, 50°57.3'E], 16 Oct 1972, Iranshahr & Moussavi (IRAN 10629). Kerman: Bam, Deh Bakri, 29.054°N, 57.913°E, 6 May 1969, Pazouki & Hashemi (IRAN 10628).

Cicerbita polyclada

Iran. Kogiluyeh & Boyer Ahmad: [in glareosis alpis] Kuh-Daena [c. 30°56'N, 51°28'E], [Jul 1842], [Kotschy 603 ed. R. F.] Hohenacker (B 100312954 isolectotype). Markazi: Kuh-Shasinde [nr. Shahsand, c. 33°56'N, 49°22'E], Conglomeratabhänge, 18 Jul 1902, T. Strauss 14091 (B 100312952, 100312953).