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NOTES ON THE EXTRA-AUSTRALIAN SPECIES OF DODONAEA (SAPINDACEAE)

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SUMMARY

Outside Australia, five species of *Dodonaea* are accepted, viz. *D. viscosa*, a pantropical coastal species, *D. angustifolia*, an inland species occurring throughout the Tropics and Subtropics, *D. elaeagnoides*, restricted to Florida and part of the Antilles, *D. polyandra*, restricted to a small part of Papua New Guinea and of Queensland, and *D. madagascariensis*, endemic to Madagascar but with clear connections to Australia. Out of these five species three, viz. *D. angustifolia*, *D. elaeagnoides*, and *D. viscosa* were for a long time combined under the last mentioned name. In Chapter II arguments are given for the division of that complex into three species and it is tried to give a historical explanation for the final state of confusion. In Chapter III notes are given on the five accepted species. All further species names used by or after Radlkofer outside Australia are rejected; a discussion of these names is given in Chapter IV.

I. INTRODUCTION

The last complete revision of the genus *Dodonaea* is that given by Radlkofer in his monograph of the Sapindaceae (Engl. Pflanzenr. 98, 1933: 1350–1404). The number of species, accepted in that revision, amounts to 54, and a further one, *D. microcarya* Small, that was unknown to Radlkofer. All but four of these 55 species were restricted to Australia, the exceptions being *D. madagascariensis*, endemic to Madagascar, *D. microcarya*, described from Florida, *D. stenoptera*, a Hawaiian species, and *D. viscosa*, occurring worldwide in the Tropics and Subtropics. With Radlkofer the latter was subdivided into three varieties and these again into a number of forms and subforms.

The main authors after Radlkofer are E.E. Sherff on *D. viscosa*, enriching this complex with several more varieties and forms, and on the Hawaiian species, and H. Lippold on the American species. The Australian species will be treated in a forthcoming publication by Ms. J.G. West, Canberra.

Originally, my only intention was to revise *Dodonaea* for the Flora Malesiana area. Soon, however, it became clear that at least for the *D. viscosa* alliance it would be necessary to broaden the scope of my work considerably, finally following this alliance all around the world. This necessity made it attractive and worthwhile to pay at least some attention to all the few species occurring outside Australia as a counterpart to Ms. West's revision of the Australian species.

II. THE DODONAEA VISCOSA COMPLEX

A. Radlkofer and after

By far the most complex species in Radlkofer's revision of *Dodonaea* is *D. viscosa*, extremely variable and occurring nearly worldwide in the Tropics and Subtropics. On differences in leaf shape and in shape and size of the fruits only, Radlkofer (1933) gave the following subdivision into infraspecific taxa (typical forms and subforms, often not mentioned by Radlkofer, are added in brackets when necessary):

Dodonaea viscosa
- var. *vulgaris* (= var. *viscosa*)
  - f. *repanda* (= f. *viscosa*)
  - f. *schiedeana*
    - (subf. *schiedeana*)
    - subf. *waitziana*
  - f. *burmanniana*
    - (subf. *burmanniana*)
    - subf. *excisa*
    - subf. *laurina*
- var. *angustifolia*
  - (f. *angustifolia*)
  - f. *thunbergiana*
  - f. *microcarpa*
- var. *spatulata*
  - (f. *spatulata*)
    - (subf. *spatulata*)
    - subf. *eriocarpa*
  - f. *elaeagnoides*

Most of these infraspecific taxa are no local endemics but are widely distributed. On the other hand, some to several of these varieties and forms may occur in the same area, though often in a different habitat. This already makes the impression that many of these taxa are defined phenetically, and on rather unimportant characters, rather than genetically.

After Radlkofer, especially Sherff (Field Mus. Nat. Hist. Bot. Ser. 23, 1947: 269–317) enriched and further complicated this system by adding several more varieties and forms, partly again widespread ones. Furthermore, some names placed by Radlkofer in the synonymy of *D. viscosa* were revived by later authors. This happened also to two of Radlkofer's infraspecific taxa, viz. f. *elaeagnoides* and subf. *eriocarpa*. Finally, a few new species were described around *D. viscosa*. One of these newly accepted species, *D. eriocarpa* (a subforma with Radlkofer!), became as complicated as *D. viscosa* itself as, mainly on Hawaii, it was subdivided into some 25–30 varieties and forms (for an enumeration see H. St. John, List Flow. Pl. Hawaiian I., 1973: 223). The weakness of the distinction even between the *D. viscosa* complex and the *D. eriocarpa* complex is clearly demonstrated in a note by Sherff (Amer. J. Bot. 38, 1951: 59, sub *D. eriocarpa* f. *oxyphylla*): a coherent group of Hawaiian forms is placed as a whole under *D. eriocarpa* notwithstanding the fact that as to the characters some of these forms rather belong under *D. viscosa* as defined by him. 'This course, while admittedly arbitrary, has seemed the only practical one to employ.' he argumented.

The only regional revision of some importance since Radlkofer is that by H. Lippold (Wiss. Beitr. Friedr. Schiller Univ. Jena, Beitr. Phytotax. 6, 1978: 79–126) on the American species. He divided the *D. viscosa* complex into five species, viz. *D. arizonica, D. bialata, D. elaeagnoides, D. linearifolia*, and *D. viscosa*.

B. My own approach

In comparison with the complicated taxonomy sketched above, the revision of *Dodonaea* for the Flora Malesiana area seemed to be an easy matter. According to the literature I could expect a widespread and variable *D. viscosa*, which was known to consist in that area of two slightly different forms, one coastal, the other one montane; *D. polyandra*, an apparently rare species from New Guinea, described after Radlkofer's revision came out; furthermore, Sherff (Amer. J. Bot. 32, 1945: 212) described under the mainly Hawaiian *D. eriocarpa* two varieties, viz. var. *minor* and var. *waitziana*, as occurring on Java.

A sorting of the Malesian material, followed by a careful mutual comparison, learned that three entities could be recognized. One of these was *D. polyandra*, restricted to a small part of the Western Dist., Papua New Guinea. Secondly, there was a widespread coastal form with obovate leaves and bisexual flowers, representing *D. viscosa* f. *revanda* of Radlkofer's system. The third one was a montane form, mainly in E. Malesia, which is dioecious or sometimes andromonoecious and bears lanceolate leaves; this represents mainly Radlkofer's *D. viscosa* f. *burmanniana*, sometimes his f. *schiedeana* or f. *angustifolia*, this mainly depending on the relative width of the leaves. This third group could further be divided into two forms, a hairy one on Java, to which Sherff's varieties of *D. eriocarpa* belong, and a glabrous or nearly glabrous one in New Guinea.

The morphological as well as the ecological differences between the second and the third entity mentioned above did arise doubt regarding the correctness of the systems of Radlkofer and of Sherff. The montane form, which apart from the variation in hairiness appears to be a well-circumscribed taxon, in Radlkofer's system should be divided over all three varieties, with Sherff even over two species. On the other hand, however, two clearly different entities, the coastal form and part of the montane form, were both included in the var. *vulgaris* of *D. viscosa*. The main cause for this unsatisfactory system is that it was based mainly on variations in leaf shape, with Sherff moreover on pubescence; no mention was made of the differences in the flower. Therefore, I decided to study the *D. viscosa* complex all through its area of distribution in order to get a better insight in the variability of these two forms and in the constancy of the differences found in Malesia.

The coastal form appeared to be nearly pantropical and is surprisingly uniform. Only in the Caribbean a few specimens had no, or not exclusively, bisexual flowers; they were monoecious, or andromonoecious, or the flowers were all or partly functionally female. With very few exceptions (the Seychelles, Sto. Domingo) it occurred always at low altitudes along or just behind the sea coast.

The inland form appeared to occur all around the world between 35° NL (California, Arizona) and 40° SL (the South I. of New Zealand). It showed a wide but continuous variation in leaf shape and size, with on the one hand the relatively broad-leaved populations from Tahiti and E. Malesia, on the other hand linear-leaved populations growing under rather arid conditions in areas lying as far apart as southern Australia, South Africa, and the southwestern U.S.A. The flowers showed a rather continuous clinal variation from the nearly completely dioecious populations from the Pacific

(except the Galapagos I.), Australia, Malesia and southern Asia via the for a small part andromonoecious or monoecious to exceptionally bisexual condition in South Africa to the predominantly andromonoecious, sometimes dioecious, not rarely bisexual condition in America. As to habitat, this form appeared to be nearly exclusively montane or submontane in the Tropics, reaching the lowland at about 20° NL and SL.

Summarizing, the study of the *D. viscosa* complex all around the world learned that the two forms distinguishable in Malesia are well separated nearly throughout their area. The differences in the flowers won't do completely in America, though even here they hold good for a majority of the material. Moreover, there are several additional characters which enable the easy identification of nearly every specimen (see Chapter III). The clear differentiation between the two forms may be partly due to the differences in distribution and habitat: they simply never meet each other and I have not seen any specimen that could be a hybrid between the two.

My final conclusion is that the coastal and the inland form should be ranked as different, though distinctly allied species. The correct name for the coastal form is *D. viscosa* Jacq., that for the inland form is *D. angustifolia* L. f.

C. Before Radlkofer

As argumented above, the study of *D. viscosa* in the sense of Radlkofer led to the conclusion that this complex included two species (actually three, as apart from *D. viscosa* and *D. angustifolia* the Caribbean *D. elaeagnoides* appeared also to be well separable, but this species was already accepted by H. Lippold, 1978). A first logical question is how it was possible that hardly anybody kept these species separate. A second question, distinctly connected with the first one, is whether and how far the difference between bisexual flowers and polygamy has played a part in the systematics of *Dodonaea*, and especially so in this complex. As *D. viscosa* s.l. was accepted as the type species of its genus, the third question is whether the division of that species will have any influence on the typification. These questions could be answered only by a fairly extensive historical study of literature. The main points resulting from this study will be mentioned and discussed in this subchapter.

a. The name Dodonaea. – The troubles around *Dodonaea* started already in the first half of the 18th century when two completely different plants both were named so. The first to use the name *Dodonaea* was Plumier (Nov. Plant. Amer. Gen., 1703: 20, pl. 12). Linné (Gen. Pl., 1737: index) placed this name in the synonymy of *Ilex*. He did this in a very inconspicuous way which easily could escape attention: in the index he gave first *Dodonaea* in Roman script (accepted names) with a reference to that genus in his own sense, followed by *Dodonaea* in italics (rejected names) with a reference to 91, being the number of the genus *Ilex*. The only later author where I found the name *Dodonaea* used in the sense of Plumier was Adanson (Fam. Pl. 2, 1763: 342), then illegitimate as a later homonym of *Dodonaea* Miller (1754).

In 1737, while rejecting the name *Dodonaea* in the sense of Plumier, Linné (Gen. Pl.: 341) proposed that same name for quite another plant. He gave a fairly extensive diagnosis of the flower, apparently based upon dried material, and as to older litera-

ture he referred to *Carpinus* Burmann (Thes. Zeylan., 1737: 55, pl. 23) and to *Staphylodendron* Plumier (Nov. Plant. Amer. Gen., 1703: 18). In 1738 (Hort. Cliff.: 144) he gave a short description of the vegetative parts. Ludwig (Def. Gen. Pl. ed. 2, 1747: 237) gave a short diagnosis of the flower, probably based upon Linné's diagnosis of 1737. In 1748, Linné (Fl. Zeyl.: 58) gave a new, apparently original description based on fruiting material, and he added some new references. In 1753 (Linné, Sp. Pl.: 118) the name *Dodonaea* in the sense of Linné is regarded as a synonym of *Ptelea viscosa* L. The diagnosis of the genus *Ptelea* now given by Linné (Gen. Pl. ed. 5, 1754: 54) differs in a few additions only from the one given in 1737 (Gen. Pl.: 29) and is absolutely different from his original diagnosis of *Dodonaea* (1737). In 1754, Linné did not give any reference, and the name *Dodonaea* in his own sense is not mentioned at all. In the same year, however, *Dodonaea* was validly published by Miller (Gard. Dict. ed. 4, 1754) with a reference to Linné's Hort. Cliff. and with an original description including flower and fruit. Jacquin (Enum. Syst. Pl., 1760: 19) was the first to publish a species name under *Dodonaea*, i.c. *D. viscosa*, with nothing more than a reference to *Aceri vel palituro affinis* Sloane (Jamaica 2, 1725: 27, pl. 162). In the same year Ludwig (Def. Gen. Pl. ed. 3, 1760: 212) hesitatingly followed Linné in combining *Dodonaea* and *Ptelea*, under the name of the former, however. His diagnosis is mainly based upon *Ptelea*, but with some additions derived from *Dodonaea*, and differs completely from the diagnosis he gave in 1747. With Linné, the name *Dodonaea* reappeared in 1762 (Sp. Pl. ed. 2: 173), still as a synonym of *Ptelea viscosa*. Like in the first edition (1753) the diagnosis is extremely short ('*Ptelea foliis simplicibus*'); he refers to the publications of several botanists, comments on the differences in the descriptions of the flowers by several authors, and finishes with a surprising remark: '*Mihi non floruit*'. No word on his own rather extensive flower diagnosis from 1737! In 1763, Fabricius (Enum. ed. 2: 430, sub *Dodonaea*) and Jacquin (Select. Stirp. Amer. Hist.: 109, sub *D. viscosa*) published extensive original descriptions. In 1764 (Gen. Pl. ed. 6: 60) Linné for the first time commented on the slightly aberrant position of *Ptelea viscosa* in that genus ('*P. viscosa solis staminibus duplicatis videtor differre*'); no mention is made of *Dodonaea* in another than Plumier's sense. The last remark holds also for Linné, Syst. ed. 12 (1767) 125. Finally, in 1771 (Mant. Pl.) Linné changed his mind completely: he accepted *Dodonaea* in his original sense of 1737 as a genus (p. 149) with a description mainly based upon Jacquin (1763). The only species mentioned is *Dodonaea viscosa* (p. 228), which appeared to be out of place under *Ptelea* ('*Removende itaque a Pteleae genere plurium consensum*'). With this publication the confusion around the name *Dodonaea* came to an end, and the genus was generally accepted in the original sense of Linné (1737).

b. The typification of Dodonaea. – The division of *D. viscosa* into three species could have consequences for the typification of the genus. Linné (Gen. Pl., 1737: 341) as well as Miller (Gard. Dict. ed. 4, 1754) described the pistil as being 3-merous. This is possible in *D. viscosa* in the sense accepted here, but far more common in *D. angustifolia*. The first species named under *Dodonaea*, i.c. *D. viscosa* Jacq. (Enum. Syst. Pl., 1760: 19), is based exclusively on a reference to Sloane (Jamaica 2, 1725:

27). Apparently, Sloane included in his text *D. viscosa* as well as *D. angustifolia*, mainly the former (description of the leaf; locality 'Old harbour'), in some points the latter (the description of the fruit as being 2- to 4-merous can hardly be anything but a mixture of the characters of the two species; the locality 'Red Hills' may refer to an inland population). The plate (nr. 162) clearly depicts *D. viscosa* in the sense of the present author. That Sloane did not differentiate between the two species is shown by his herbarium. According to Fawcett and Rendle (Fl. Jamaica 5, 1926: 58–59) the Sloane herbarium includes two collections both named *D. viscosa* and both with the localities 'Old Harbour; Red Hills'. The one, nr. v.97, they cited under typical *D. viscosa*, the other one, nr. v.99, under the var. *angustifolia*. As specimen number v.97 is best in accordance with the main part of the description and with the plate this is proposed as the lecto-type.

c. The flower conditions. – The main cause of the systematic confusion finally resulting in the *Dodonaea viscosa* complex was to all probability the insufficient understanding of the flower conditions, whether the flowers were bisexual or polygamous. As long as this was not well known, let alone the systematic value of it understood, especially differences in shape and size of the leaves were overrated. Finally, when the variation in the flower conditions became known, and notwithstanding the fact that the systematic importance of this character was more or less understood by some botanists, it hardly influenced the system already built up mainly on leaf characters. The for this case more important publications will be mentioned and discussed in chronological order.

Apart from a short note by Sloane (Jamaica 2, 1725: 27, sub *Aceri vel palituro affinis*), Linné (Gen. Pl., 1737: 341) was apparently the first to give a rather extensive description of the flower. As described, the flower makes the impression of being bisexual and accordingly representing *D. viscosa*. Comparable flower descriptions, whether repeating the older ones or original, were published by Linné (Gen. Pl. ed. 2, 1742: 159, sub *Dodonaea*), Ludwig (Def. Gen. Pl. ed. 2, 1747: 237, sub *Dodonaea*), Miller (Gard. Dict. ed. 4, 1754: sub *Dodonaea*), P. Browne (Civ. Nat. Hist. Jamaica, 1756: 191, sub *Triopteris*, and 207, sub *Dodonaea*), Fabricius (Enum. ed. 2, 1763: 430, sub *Dodonaea*), Jacquin (Select. Stirp. Amer. Hist., 1763: 109, sub *Dodonaea viscosa*), Linné (Mant. Pl., 1771: 149, sub *Dodonaea*), and Reichard (Gen. Pl., 1778: 194, sub *Dodonaea*). In 1782 Linné f. (Suppl.: 218) described a second species, *D. angustifolia*. In the name as well as in the diagnosis the difference in leaf shape between the two species is stressed. On the other hand, however, this was the first time that mention was made of polygamy ('*Fructificatio polygama.*'), but this could not play a part as the situation in *D. viscosa* was unknown. The next step was taken by G. Forster (Fl. Ins. Austr., 1786: 27). He mentioned *D. viscosa*, described the leaves only, but added: '*In Soecietatis insulis dioica. In Nova Zeelandia hermaphrodita.*'. This may have added only to the confusion: the failing character of *D. viscosa* was now given, but it was based upon *D. angustifolia* (the form from the Society I. has relatively broad leaves and could with the knowledge of that time only be identified as *D. viscosa*; in New Zealand only *D. angustifolia* occurs and it seems very improbable

that Forster would have had hermaphrodite flowers from that area). Swartz (Obs. Bot., 1791: 150) gave a good original description of *D. angustifolia* from Jamaica. He was the first to give separate descriptions of male and either bisexual or female flowers, moreover indicating that they were from different shrubs. *D. viscosa* was treated very briefly and without flower characters. Moench (Methodus, 1794: 358) on the one hand gave original descriptions of male and female flowers growing on the same tree ('*in eadem stirpe*'). On the other hand, however, he added to the confusion as he gave one species only, *D. lucida*, an illegitimate synonym of *D. viscosa*. Cavanilles (Icon. 4, 1797: pl. 327) depicted male and female flowers but did not mention them in his original description. His description and plate clearly refer to *D. angustifolia*, but though he commented on the differences in leaf shape between his plant and the one depicted by Sloane he considered this as a mere variation, and named his plant *D. viscosa*. Accordingly, the flower condition of *D. viscosa*, with Linné f. still unknown, was incorrectly filled in by Forster, Moench, and Cavanilles. Smith (in Rees Cycl., 1809) listed seven species, described some as being dioecious, but added to the confusion by suggesting the same for *D. viscosa*. Roxburgh (Hort. Beng., 1814: 28; Fl. Ind. ed. 2, 2, 1832: 256) described a dioecious *D. dioeca* in contrast to the polygamous *D. angustifolia*. DeCandolle (Mém. Soc. Phys. Genève 1, 1822: 445) apparently misunderstood Roxburgh's species and described a *D. dioica* ascribed to Roxburgh but actually representing *D. triquetra* Wendl. Furthermore, what different authors from different parts of the world had described as *D. angustifolia* was divided by DeCandolle into some species; only true *D. angustifolia*, unknown to him, was regarded as doubtful. In his influential Prodromus (1, 1824: 616) DeCandolle enumerated 17 species; he described the genus as dioecious or polygamous, and accordingly defined his species primarily on leaf characters, secondarily on the fruits. Sprengel, in the 9th edition of Linné's Genera Plantarum (1830: 318) simply included in the genus diagnosis '*Flores polygami*'. In this way the flower conditions became a genus character, unfit for the distinction of species; for that purpose, the wide variation of the leaves and the fruits offered ample opportunity. Finally, it was Blume (Rumphia 3, 1847: 188) who for the first time correctly described the different conditions of the flowers possible ('*floribus .... hermaphroditis v. abortu unisexualibus, monoicis v. dioicis*') and included this character in the description of his species. But Radlkofer still in 1895 (E. & P., Nat. Pflanzenfam. 3, 5: 356) regarded the flower characters as useless for the distinction of the species: '*Bl. diöcisch (daneben anomaler Weise mitunter scheinbar hermaphrodite)*' (Flowers dioecious, moreover sometimes abnormally seemingly hermaphrodite). But this was the last important misunderstanding of the flower conditions in *Dodonaea*: in 1900 (Mart. Fl. Bras. 13, 3: 639) he recognized a polygamous condition next to a hermaphrodite one, though he did not make use of it for the division of the growing *D. viscosa* complex.

d. The growth of the Dodonaea viscosa complex. – The first botanists publishing on *Dodonaea* had only material from America, mainly the Antilles, and Asia, mainly Ceylon, at their disposal. This means that it represented either *D. angustifolia*, or *D. viscosa*. Moreover, before 1782, when Linné f. described *D. angustifolia, Dodonaea*

was considered to consist of one species only. Surprisingly, it appeared that the descriptions given by most of the older authors clearly refer to *D. angustifolia*, some to a mixture of the two species, hardly any to *D. viscosa*! Examples of names clearly representing *D. angustifolia* are: Breyne's *Acer minus Zeylanicus* (Prodr. 2, 1689: 8) from Ceylon; Plukenet's *Arbuscula viscosa Elaeagnifoliis* (Phytogr., 1692: pl. 141 fig. 1) from America; Plumier's *Staphylodendron foliis lauri angustis* (Cat., 1703: 18) also from America; Hermann's *Waerellaghas* (Mus. Zeylan., 1717: 32) from Ceylon; Burmann's *Carpinus forte viscosa* (Thes. Zeylan., 1736: 55, pl. 23) from Ceylon; probably Linné's *Dodonaea* (Gen. Pl., 1737: 341; Hort. Cliff., 1738: 144; Fl. Zeyl., 1748: 58), the second one from America, the third one from Ceylon; P. Browne's *Triopteris* (Civ. Nat. Hist. Jamaica, 1756: 191, pl. 18 fig. 1) from Jamaica; probably Plumier's *Ptelea foliis simplicibus* (Plant. Amer., 1760: 245, pl. 247 fig. 2) from America; Jacquin's *Dodonaea viscosa* (Select. Stirp. Amer. Hist., 1763: 109) from America; and Linné's *Dodonaea viscosa* (Mant. Pl., 1771: 149, 228) from America. The two species are apparently mixed up in Sloane's *Aceri vel palituro affinis* (Jamaica 2, 1725: 27, fig. 3) from Jamaica and probably Rumphius's *Caryophyllaster litoreus* (Herb. Amb. 4, 1743: 110, pl. 50) from the Moluccas.

Starting with Linné f. (Suppl. Pl., 1782: 218) several authors distinguished between a broad-leaved *D. viscosa* and a narrow-leaved *D. angustifolia*. Examples are Lamarck (Encycl. 2, 1786: 292), Swartz (Obs. Bot., 1791: 150), Murray & Persoon (Syst. Veg. ed. 15, 1797: 386), Willdenow (Sp. Pl. ed. 4, 2, 1, 1799: 343), and Smith (Rees Cycl., 1809). This unreliable character led other authors to a wrong naming, e.g. G. Forster (Fl. Ins. Austr., 1786: 27), Cavanilles (Icon. 4, 1797: 327), and Knuth (in H., B. & K., Nov. Gen. Sp. 5, 1821: 133 of the qu. ed.); in these three cases the name *D. viscosa* was used for what clearly represented *D. angustifolia*.

The splitting of *D. angustifolia* started with DeCandolle: in 1822 (Mém. Soc. Phys. Genève 1: 445; Prodr. 1, 1824: 616) he divided the material identified as such by several authors into 5 species, mainly on leaf characters (the true *D. angustifolia* was added as a sixth one, but was unknown to him). This system was followed by Sprengel (Syst. Veg. ed. 16, 2, 1825: 242) and G. Don (Gen. Hist. 1, 1831: 673); moreover, it led some other botanists to the description of some local *D. angustifolia* forms as species.

The other way, *Dodonaea viscosa* as one big variable species, subdivided into a growing number of varieties and forms, was taken for the first time by Knuth (in H., B. & K., Nov. Gen. Sp. 5, 1821: 133 qu. ed.). He divided what he called *D. viscosa* into three unnamed varieties (actually, all three represent *D. angustifolia*). The basis of Radlkofer's final system was laid by Bentham (Fl. Austral. 1, 1863: 475), however. He enlarged *D. viscosa* as well by the addition of several named species, Australian, but also extra-Australian, as on the strength of much newly collected material. Finally, the complex was divided into three named varieties, based upon leaf and fruit characters (the same characters are nearly exclusively used for the identification of his species, notwithstanding the fact that in the introduction to the genus he remarked: 'The form of the wings of the capsule, which has been much relied on, is as variable as that of the leaves' (p. 472)). As for the reduction of several names to *D.*

viscosa he was followed by Hiern (in J.D. Hook., Fl. Br. India 1, 1875: 697), but the latter gave no subdivision of the complex. Bentham's system was further elaborated by Radlkofer, at first in 1900 (in Mart., Fl. Bras. 13, 3: 639), finally in 1933 (in Engl., Pflanzenr. 98: 1363) in the form given in Subchapter II A of the present paper. Afterwards, that system was on the one hand made still more complicated by the addition of several new varieties and forms, whereas on the other hand parts of it were split off and regarded as distinct, though closely allied species.

The present author's decision to recognize three species in the *D. viscosa* complex, viz. *D. angustifolia, D. elaeagnoides* and *D. viscosa*, actually does not change much. The *D. viscosa* complex is now replaced by a *D. angustifolia* complex and, thanks to the addition of *D. eriocarpa* with all its varieties and forms, the latter is distinctly more unmanageable than the former ever was!

Throughout this chapter attention has been paid to the role of morphological characters in the *D. viscosa* complex. It is worth mentioning, however, that at least one author, i.c. Junghuhn (Java ed. 2, 1, 1853: 296), was aware of the ecological differences between *D. viscosa* and *D. angustifolia* in the Tropics. In Java, he distinguished between a coastal *D. littoralis* (never described) and a montane *D. ferrea* (not described), later renamed *D. montana* and validated by an indirect reference. The differences between these two taxa, both morphological and ecological, remained well known on Java, but they were always considered to represent mere forms of one widespread and variable *D. viscosa* (see e.g. Backer & Bakh. f., Fl. Java 2, 1965: 141, where a beach form and a mountain form are mentioned but not named).

III. THE ACCEPTED SPECIES

KEY TO THE SPECIES

1a. Leaves pinnate. *Madagascar* . . . . . **3. D. madagascariensis**
b. Leaves simple 2
2a. Sepals mostly 5; stamens 12–15; ♀ flowers without staminodes. *New Guinea, Queensland* . . . . . **4. D. polyandra**
b. Sepals mostly 4; stamens 5–9; ♀ flowers with or without staminodes 3
3a. Leaves when dried rather slack, papyraceous to thin-pergamentaceous. Flowers bisexual. Scar of sepals under the fruit mostly strongly lobed around the conspicuous stamen scars; the fruits mostly 2-merous, strawcoloured or brownish. *Tropics, coastal* . . . . . **5. D. viscosa**
b. Leaves when dried rather stiff, pergamentaceous to chartaceous. Flowers mostly at least partly unisexual, often dioecious. Scar of sepals under the fruit usually annular, sometimes slightly lobed, scars of staminodes inconspicuous; fruits often partly 3-merous, sometimes 4-merous, especially the wings tinged reddish when mature 4

4a. Staminodes present in ♀ flowers. Fruit wings not adnate to the style, accordingly incision on top of the fruit between the wings reaching the body of the fruit; fruits conspicuously though often not densely glandular, sometimes sparsely hairy. *Tropics and Subtropics, inland* . . . . . **1. D. angustifolia**

b. Staminodes absent in ♀ flowers. Fruit wings adnate to the style and accordingly the incision on top of the fruit not reaching the body; fruits mostly not conspicuously glandular, glabrous. *Florida, West Indies* . . . . . **2. D. elaeagnoides**

1. Dodonaea angustifolia L. f., Suppl. Pl. (1782) 218. – *D. viscosa* Jacq. var. *angustifolia* Benth., Fl. Austral. 1 (1863) 476. – *D. viscosa* Jacq. f. *angustifolia* Sherff, Amer. J. Bot. 32 (1945) 214. – Type: *herb. Linné 495: 4 and 5* (LINN, microfiche seen).

Most of the rejected names discussed in the next chapter are considered to be synonymous with *D. angustifolia.*

The demarcation between *D. angustifolia* and *D. viscosa* is weakest in America. Therefore, and in order to facilitate a mutual comparison, the following diagnosis is exclusively based upon American material. This diagnosis is followed by notes on the variability in other parts of its area.

Treelet or shrub, 2–6 m high. Young parts, leaf bases, and inflorescences sometimes slightly hairy. *Branchlets* may be more glandular when young and the bark may be more blackish than in *D. viscosa. Leaves* elliptic, 4–9(–12.5) × 1–2.5 cm, 3–6.5 (–12) times as long as wide, widest somewhat above to in the middle, pergamentaceous to stiff pergamentaceous, alive slightly coriaceous, glands conspicuous on both sides, leaves often varnished; apex acute to rounded, the latter mostly narrowly so, mucronate if broadly rounded, sometimes tapering acuminate. *Inflorescences* densely to hardly glandular, all branches covered with a shining varnish. *Flowers:* out of 25 flowering specimens 6 were apparently dioecious (difficult to say for certain, especially if the herbarium specimens are poor), 11 were andromonoecious (part of the flowers considered to be bisexual were probably functionally female as the anthers, though as big as in ♂ flowers, apparently are indehiscent; in that case the plants are actually monoecious), and 8 appeared to be fully bisexual. *Sepals* 4, exceptionally in some flowers 5; scar under the fruit annular to lobed, sepals often fairly long persistent. *Anthers* in some bisexual specimens 1.5 mm long, mostly 2–3 mm in ♂ as well as in bisexual flowers. *Pistil* normally 2-merous, often some to many on a specimen 3-merous, sometimes some to several 4-merous; style mostly for one fourth to more than halfway cleft at the apex, rarely not or hardly so. *Fruits:* the body 7–14 mm high, wings halfway 3.5–6 mm wide; rather stiff, mostly reddish (especially the wings) or exceptionally pale brown, the body conspicuously glandular, glabrous.

Habitat: open vegetation to low shrubby forest on dry soils (sand, limestone), often on rocks, steep slopes, etc., also along rivulets, in secondary vegetation etc. Up to 10° NL and 25° SL always above 1000 m, reaching the lowland at about 20° NL and 25° SL.

Variation. In the western part of the area (America, Africa) variation in flower conditions seems to be clinal, in the eastern part the flower conditions are nearly

constant. The variation in the leaves and in the fruits does not show such a geographical pattern; partly at least it may depend on differences in habitat. This may also hold true for the fact that comparable forms may occur in distant parts of the area. Locally, the range of variation may be rather wide, especially in the Hawaiian I., also in Australia. In these areas it seems warranted to recognize some to several infraspecific taxa, even though most of these will be of value only for that area. In the present paper I have refrained from recognizing any infraspecific taxon, however.

When turning from America in an eastern direction, the flower conditions appear to show a continuous change, widening the gap between the present species and *D. viscosa*. Nearest to the American population comes the Southafrican *D. thunbergiana*. Out of 14 flowering specimens 11 appeared to be dioecious (7 ♀♀, 4 ♂♂), one had ♂ and bisexual flowers, one ♂ and probably ♀, possibly also some bisexual flowers, whereas only one was fully bisexual. In ♂ flowers the pistillode varied from rather well developed to strongly reduced; in ♀ flowers the same holds true for the staminodes, but even if these are well developed the anthers seem normally non-dehiscent. The further material from Tropical Africa and Madagascar, the materials from Asia, Australia, and the Pacific are nearly exclusively polygamous, mostly dioecious, sometimes monoecious or andromonoecious. In the Pacific there is one notable exception: the form called *D. viscosa* var. *spatulata* from the Galapagos I. agrees excellently with the American *D. angustifolia*, is polygamous (bisexual and either ♂ or ♀ flowers on the same specimen), and the staminodes are rather well developed. The other form described from the Galapagos I., *D. viscosa* var. *galapagensis*, is known to me only from one sterile specimen, *H.H. van der Werff 1914* (U). This has rather broad obovate leaves, rounded and apiculate at apex, and resembles strongly *Degener 28355 & 28356* from Hawaii. This may possibly indicate that the Galapagos I. received *Dodonaea* from two sides.

Most specimens are glabrous or only the inflorescences are thinly, shortly, and patently hairy. The main exception is the form from Java, the Lesser Sunda I., and Celebes, which has especially the leaf axils and the bases of the leaves rather densely, the buds, young twigs, inflorescences, and infructescences densely to sparsely hairy. The hairiness of the pistils, and accordingly of the fruits, is variable but only rarely conspicuous.

The variation of the leaves as a whole is wide and may regard all kinds of characters, like length and width, ratio, texture, nervation, etc. Locally, the variation is often much narrower. Some extreme forms are on the one hand *D. thunbergiana* var. *linearis* in South Africa (leaves 3–6.5 × 0.3–0.75 cm, ratio c. 5.5–21), *D. microcarpa* from Bourbon I., and some forms from Australia, comparable with *D. arizonica* from North America. On the other hand, the population from the Society I. is rather constant and easily recognizable, being characterized by large and relatively broad obovate leaves (c. 7–10 × 2–3 cm, ratio c. 4) with a conspicuous and dense nervation.

In the Hawaiian I. the variation is probably wider than in any other area and regards more characters. The principal characters are leaf shape and size, hairiness, especially of the fruit, the number of locules in pistil and fruit, size and shape of the

fruits, and the width of the fruit wings. Mainly on these characters three species were distinguished, viz. *D. eriocarpa, D. sandwicensis*, and *D. stenoptera. D. eriocarpa* was subdivided into some 35 varieties and forms, the other two encompassed each a few varieties and forms (see St. John, List Flow. Pl. Hawaiian I., 1973: 223–224). As the pattern appeared different from elsewhere it seemed desirable to pay special attention to the Hawaiian population. For this I had at my disposal a varied collection of about 65 specimens, including representatives of all three species and of a good number of the varieties and forms. Irrespective of the identifications given on the sheets the material was sorted into a number of morphologically rather uniform or clearly coherent entities. Most of these entities were not sharply delimited against each other but formed together a gradual series with the largest, most variable, but clearly coherent group in the center. It turned out that even the species locally recognized did not or hardly take up a special position. *D. eriocarpa*, with its many varieties and forms, appeared to encompass nearly the whole wide range of variability. *D. sandwicensis*, of which one paratype (*Rock s.n.* in L 214568) and some identical collections were available, fell under the central group. Another member of this group, nearly identical with the paratype of *D. sandwicensis* and collected at the same locality, is *Heller 2871*, the type of *D. eriocarpa* var. *glabrescens*. Only the third 'species', *D. stenoptera*, takes at least an extreme position because of its peculiar fruits. These are inflated with 3 or 4 rib-like wings no more than 1 mm wide; the body is glabrous but strongly glandular. This extreme form appeared to be gradually connected with the central group, however. Gradually, the fruits become less inflated, the wings broader, finally shouldered so as to form the typical incision at the top, and the body becomes slightly hairy. Even with the restricted material available it seemed hardly possible to define clearcut infraspecific entities or even to recognize the varieties or forms already described. And the Hawaiian material as a whole even does not take a position of its own; some specimens from the central group are hardly or not at all distinguishable from the inland populations of New Guinea.

Distribution. Because of the separation between *D. angustifolia* and *D. viscosa* it seems desirable to give a rather detailed account of the distribution of both species, justifying it by the citation of the most important literature and/or some selected collections. The collections cited are from FI, L, M, RSA, SING, and U. If not stated otherwise the literature citations were under *D. viscosa*. The geographical sequence is that used by the Kew herbarium.

ORIENT. Iraq: Groenhart in L 946.329-153. – Iran: see Sherff, Field Mus. Nat. Hist. Bot. Ser. 23 (1947) 294. – Afghanistan: Griffith herb. 1020/1. – Arabia: Schimper 261, 266.

JAPAN. Ryukyu I.: Fosberg 37873, Walker & Tawada 6549. – Bonin I.: Fujita & Shimizu 65.

CHINA. Yunnan: see Ming in Wu, Fl. Yunnan 1 (1978) 282, pl. 66 fig. 7 & 8. – Fukien: see Sherff, op. cit. 294. – Amoy: Chung 188. – Kwantung: see Sherff, op. cit. 294. – Hainan: Chun & Tso 43932, Lei 396. – Taiwan: Keng 1362, Liao & Kuo 2147, Odashima 17825, 17880; see Li, Woody Fl. Taiwan (1963) 494, fig. 189.

INDIAN SUBCONTINENT. Pakistan: Siddiqi & Nasir 17; see Stewart, Cat. Fl. W. Pakistan (1972) 463. – India: see Brandis, Indian Trees (1906) 186; Talbot, For. Fl. Bombay 1 (1909) 342, fig. 202; Troup, Silvic. Indian Trees (1921) 225. – Punjab: Koelz 4046, Schlagintweit 10846. – Madhya Pradesh: Panigrahi 6616. – Tamil Nadu: 6 colls., incl. Hohenacker 1067, 1068,

Shetty 27984. – Ceylon: 7 colls., incl. Fosberg 50675, 50676; see Trimen, Fl. Ceyl. 1 (1893) 312.

INDO-CHINA. See Lecomte, Fl. Indo-Chine 1 (1912) 1005. – Vietnam: Chevalier 30454, Poilane 976.

MALESIA. Java: 31 colls. from West, Central, and East. – Lesser Sunda I.: 18 colls. from Bali, Timor, the Babar and Tanimbar I. – Philippines: Britton 416, Clemens 17184, PNH 20391, Vanoverbergh 1032, all from Luzon. – Celebes: Bünnemeijer 12093, Meijer 11049, Yoshida 995 & 1376, all from the southwestern peninsula. – New Guinea: 87 colls. from the whole island.

AUSTRALIA. Western Australia: Mills in L 220574. – Northern Territory: Chippendale 4950, Kanis 1746. – Queensland: 20 colls., incl. Blake 2567, Dietrich 190, L.S. Smith 3549. – South Australia: 21 colls., incl. Eichler 12605, Kraehenbuehl 2481, Haegi 1295. – New South Wales: 49 colls., incl. Constable NSW 41747, Hartley, Craven & Adams 13559, Maiden & Boorman NSW 119215. – Victoria: 6 colls., incl. Streimann 2619, 2837, 2839. – Tasmania: Gunn 377; see Curtis & Morris, Stud. Fl. Tasmania, ed. 2, 1 (1975) 122, fig. 35. – Lord Howe I.: van Balgooy 1136, Johnson & Rudd 1215.

NEW ZEALAND. New Zealand: Fosberg 30288, Gomez in herb. Hooker 9035, J.L.N. in L 953.111–945; see Allan, Fl. New Zealand 1 (1961) 429: Davies, New Zeal. Native Pl. Stud. ed. 2 (1961) 29, pl. 2 & 3; Salmon, New Zealand Flowers and Plants in Colour, ed. 2 (1967) 52, fig. 123–125; Rivers, New Zealand J. Bot. 9 (1971) 549–554; reaches as far South as Banks Peninsula, c. 43°30' SL. – Norfolk I.: Hoogland 6652, Robinson NSW 131760.

PACIFIC. New Hebrides: Chew RSNH 55 A, Morrison in L 117587. – New Caledonia: 16 colls., incl. Balansa 3304, Bernardi 10034, 12577, 12744; mainly and most common in low scrub on serpentine. – Fiji I.: 11 colls., incl. Degener 14299, 15347, A.C. Smith 4253, 6593, from the Yasawa Group, Vanua Levu, Viti Levu, and the Malolo Group; see Parham, Plants Fiji I., rev. ed. (1972) 246. – Samoa: see Christophersen, Bernice P. Bishop Mus. Bull. 128 (1935) 133. – Tonga: Hotta 4750 from Vava'u I.; see Yuncker, Bernice P. Bishop Mus. Bull. 220 (1959) 176, at least partly. – Niue I.: see Sykes, Fl. Niue (1970) 186. – S.E. Polynesia: see Brown, Bernice P. Bishop Mus. Bull. 130 (1935) 163–164. – Tahiti & Society I.: 6 colls., incl. Moore 8, 189, Setchell & Parks 547, from Tahiti and Raiatea. – Rarotonga: Philipson 10238. – Guam: see Stone, Micronesica 6 (1970) 396, fig. 62. – Hawaii: 67 colls., incl. Degener 31549, 31550, 31551, Herbst 824, from Kanai, Oahu, Molokai, Lanai, Maui, Hawaii, etc.; see Rock, Indig. Trees Hawaii (1913) 278, 281, pl. 109 (partly as *D. eriocarpa*); Degener, Fl. Hawaii (1956, 1959) as *D. eriocarpa* and *D. sandwicensis*.

TROPICAL AFRICA. Ghana: see Irvine, Woody Pl. Ghana (1961) pl. 5. – Congo Republic: Lebrun 8141, Malaisse 6088; see Robijns, Fl. Parc Albert I (1948) 523, pl. 51; Hauman, Fl. Congo Belge 9 (1960) 382, pl. 39. – Sudan Republic: see Crowfoot, Flow. Pl. N. and Central Sudan (1928) fig. 104(2); Andrews, Fl. Pl. Anglo-Egypt. Sudan (1952) 339, fig. 126. – Ethiopia: Schimper 314, 705; see Cufodontis, Bull. Jard. Bot. Etat Suppl. (1958) 494. – Uganda: see Eggeling & Dale, Indig. Trees Uganda, ed. 2 (1952) 378, pl. 19. – Kenya: Maas Geesteranus 5033, 5835. – Tanganyika: see Sherff, op. cit. 282. – South Tropical Africa: see Exell, Fl. Zambesiaca 2 (1966) 542, pl. 117. – Mozambique: see Exell & Sousa, Fl. Moçamb. 51 (1973) 44. – Malawi: Stolz 892. – Zambia: see White, For. Fl. N. Rhodesia (1962) 224. – Rhodesia: see Sherff, op. cit. 282. – Angola: see Exell & Mendonça, Consp. Fl. Angol. 2 (1954) 91.

MADAGASCAR and the MASCARENE ISLANDS. Madagascar: d'Alleizette in L 951.64–405, Decary 10242; see Capuron, Mém. Mus. Natl. Hist. Nat. Sér. B, Bot. 19 (1969) 27, pl. 4 fig. 12–19. – Mauritius: Sieber 287. – Reunion: 5 colls. incl. Lam & Meeuse 5284.

SOUTH AFRICA. See Marloth, Fl. S. Afr. 2, 2 (1925) 158, pl. 53: B (as *D. thunbergiana*); Palmer & Pitman, Trees S. Afr., 2nd ed., 2 (1972) 1368–1370. – Cape Prov.: 9 colls. incl. Lotsy & Goddijn 1685, Lütjeharms 7176, van Steenis 23916.

NORTH AMERICA. Florida: see Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 89, as *D. bialata*. – New Mexico: Bourgeau 312. – Arizona: Goodding 15567; see Lippold, op. cit. 84, as *D. arizonica*. – California: M.E. Jones 27087. – Bermuda: see Lippold, op. cit. 90, as *D. bialata*.

CENTRAL AMERICA. Mexico: 17 colls., incl. Palmer 143, 181, 290, Stanford, Lauber & Taylor 2022, 2051, 2453, from Sonora, Chihuahua, Nuovo Leon, Tamanlipas, Hidalgo, Morelos, and Veracruz. – Guatemala: see Sherff, op. cit. 278. – British Honduras: see Sherff, op. cit. 278, 289. – Honduras: see Lippold, op. cit. 90, as *D. bialata*. – Nicaragua: see Lippold, op. cit. 90, as *D. bialata*. – Costa Rica: Durkee 75–63.

WEST INDIES. Bahamas: see Sherff, op. cit. 305. – Cuba: Curtiss 263, Rutten-Pekelharing 179; see Lippold, op. cit. 88, 101, as *D. bialata*, resp. *D. linearifolia*. – Jamaica: Proctor 23306, 27744, 27745. – Haiti: Picarda 1333. – Sto. Domingo: Eggers 1885, Fuertes 189, von Türckheim 2970. – Puerto Rico: see Lippold, op. cit. 90, as *D. bialata*.

SOUTH AMERICA. Brazil: 11 colls., incl. Irwin, Harley & Smith 32455, Rambo 44006, 44066, Reitz & Klein 57, 3971, 15022, from Bahia, Rio de Janeiro, Sao Paulo, Paranà, Sta. Catarina, Rio Grande do Sul; see Lippold, op. cit. 91, as *D. bialata*. – Panama: see Croat, Ann. Missouri Bot. Gard. 63 (1977) 446, fig. 5. – Colombia: Cuatrecasas 20475, Cuatrecasas, Schultes & Smith 12140. – Venezuela: Benitez de Rojas 998, Breteler 4097, de Bruijn 1020. – Ecuador: Fosberg 23195. – Peru: 6 colls., incl. Dombey 887, Fosberg 27696, 27703; see Macbride, Fl. Peru 3 A (1956) 390. – Bolivia: 9 colls., incl. Fiebrig 2501, Krukoff 10707, Steinbach 173. – Galapagos I.: van der Werff 1040, 1539, 1914, 2334; see Wiggins & Porter, Fl. Galapagos I. (1971) 751, at least as to *D. viscosa* var. *galapagensis*. – Argentina: see Sherff, op. cit. 281, 291. – Uruguay: Herter 5040, 5229, 85049, 96921; see Herter, Fl. Illust. Urug. (1942) fig. 2074.

2. Dodonaea elaeagnoides Rudolph ex Ledeb. & Alderstam, Diss. Bot. Pl. Doming. (1805) 18 (not seen); H. Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 95, pl. 1–5, map 2. – *D. viscosa* Jacq. f. *elaeagnoides* Radlk., Engl. Pflanzenr. 98 (1933) 1371. – Type: *Rudolphi in herb. Willdenow 7515* (B, seen on microfiche). – **Fig. 1 b.**

The following diagnosis may facilitate the comparison with *D. viscosa*:

Shrub up to 3 m high. *Branches* soon, sometimes nearly from the beginning, terete, rather gnarly, greyish, often fairly densely or scurfy glandular. *Leaves* obovate, 2.5–8 (–10) × 1–2.25(–4) cm, ratio 1.75–4.5, widest at most 0.25 of the length below the apex; apex rounded or sometimes nearly truncate, sometimes either apiculate or emarginate; chartaceous to stiff pergamentaceous, drying brownish to sometimes greenish, usually not very glandular and accordingly not varnished. *Inflorescences* glabrous but variably glandular. *Flowers* unisexual, mostly dioecious, rarely monoecious. *Sepals* 4. *Stamens* 6 or 7; the anther 1.5–1.8 mm long; in ♀ flowers completely suppressed. *Pistil* 2-merous, sometimes partly 3-merous; style 4.5–5 mm long, knobbed or slightly lobed at apex. *Fruits:* body 4–7 mm high, the wings 2–4 mm wide, at the apex adnate to the style base for 1.5–2.5 mm, thin-pergamentaceous (slightly more stiff than in *D. viscosa*), mostly not conspicuously glandular, glabrous, possibly brownish to reddish.

Habitat: coastal and inland, up to c. 350 m alt.; acc. to Lippold (l.c.) restricted to coral limestone near the coast.

Distribution. (acc. to Lippold, l.c., if not otherwise mentioned).

NORTH AMERICA. Florida and the Florida Keys.

WEST INDIES. The Bahamas, Cuba, Sto. Domingo, Puerto Rico (P. Sintenis 859), the Virgin I., St. Eustatius (Arnoldo 3182, Boldingh several colls. in U, Stoffers 3503, Suringar several colls. in L), La Désirade, Grenada.

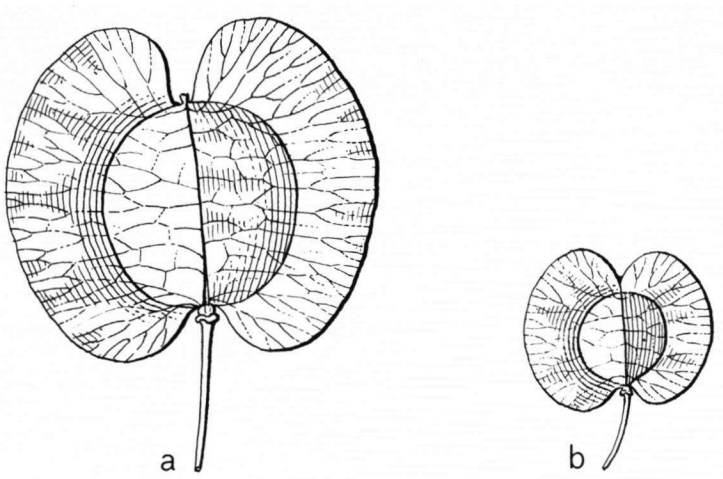

Fig. 1. *Dodonaea* fruits. a. *D. viscosa*: wings free from the style (Sieber Fl. Martinique 101). – b. *D. elaeagnoides*: wings adnate to the style (Suringar s.n. in herb. L 905.136-157). Both x 2. Drawing by Ruth van Crevel.

Note. Especially the unisexual flowers and the clearly different fruits – smaller and with the wings apically adnate to the style base (fig. 1b) – are for me strong arguments to consider this a good species, allied with *viscosa* but sufficiently different.

3. Dodonaea madagascariensis Radlk., Abh. Naturwiss. Vereine Bremen 8 (1884) 470; Engl. Pflanzenr. 98 (1933) 1384; Capuron, Mém. Mus. Natl. Hist. Nat. Sér. B, Bot. 19 (1969) 28, pl. 4 fig. 1–6. – Syntypes: *J.M. Hillebrandt 3604, Hilsenberg s.n.* (BM) (neither seen).

This species, endemic to Madagascar, is the only one outside of Australia that does not belong to the *D. viscosa* group. It resembles mostly *D. polyzyga* F. Muell. from inland NW. Australia.

4. Dodonaea polyandra Merr. & Perry, J. Arn. Arb. 21 (1940) 525. – Type: *L.J. Brass 8379* (iso in L).

This species is distinctly allied to *D. viscosa*; it differs mainly in the number of sepals (5 instead of 4) and of stamens (12–15 instead of 5–9). It is restricted to SE. New Guinea (Western Dist., Bensbach and Morehead Subdists.) and NE. Queensland.

5. Dodonaea viscosa Jacq., Enum. Syst. Pl. (1760) 19. – Lectotype (present author): *Sloane herb. v.97* (BM, seen on microfiche). – **Fig. 1 a.**

In America, the difference between *D. viscosa* and *D. angustifolia* is slighter than anywhere else. Moreover, *D. viscosa* meets here with an other closely allied species, viz. *D. elaeagnoides*. In order to facilitate the comparison between *D. viscosa* and the two other species the following diagnosis is exclusively based upon American material.

Shrub or rarely treelet, 1.5–3 m high. Glabrous. *Branchlets* not essentially different from both other American species, but more uniform, nearly always hardly glandular, often somewhat thicker, nearly always remaining reddish brown, sometimes soon becoming more terete and blackish, fissuring lengthwise reticulately. *Leaves* obovate, 5–12.5 × 1.5–4.5 cm, 2.25–3.75 times as long as wide, widest slightly above or sometimes in the middle, thin-pergamentaceous (papyraceous to pergamentaceous), drying greenish, glands nearly always inconspicuous, leaves not varnished (only so in bud); apex usually rounded and apiculate, sometimes in some leaves either just rounded, or acute. *Inflorescences* hardly glandular, accordingly not varnished or rarely so. *Flowers* bisexual. *Sepals* 4 (not rarely in some flowers 5), caducous, scar under the fruit varying from deeply lobed to nearly annular. *Anthers* 1.1–1.66 mm. *Pistil* mostly 2-merous, but often some to several 3-merous ones on the same specimen; style not to slightly cleft at the apex. *Fruits:* the body 9–13 mm high, wings halfway (3.5–)4–6 mm wide; membranous, straw coloured, the body not conspicuously glandular, glabrous.

Habitat: coastal, mostly on sandy beaches, once at 250 m alt. (Sto. Domingo).

The present species is surprisingly uniform throughout its nearly worldwide area of distribution. Only some specimens different in one character or the other should be mentioned. *F. Bøgesen s.n.* in *U 24337 B* from St. Croix is monoecious with ♂ and ♀ flowers. *M. Fuertes 317* from Santo Domingo is mainly bisexual but has some ♂ flowers, and occurs at 250 m altitude. *Hekking 1091* from Surinam has the flowers partly functionally ♀; the same holds true for *Pons L.B.B. 12702*, also from Surinam. All these are undisputable *D. viscosa*. The only really doubtful specimen is *Curtiss 263* from Isla de Piños, Cuba. Vegetatively it resembles *D. viscosa* but for the clearly glandular leaves; the flowers are partly bisexual, partly functionally female, the pistil is often 3-merous, the style is clearly lobed, the fruits resemble those of *D. angustifolia*. Probably, it is no hybrid as the seeds are well developed.

Distribution. The distribution is given in the same way as under *D. angustifolia* and for the same reason.

INDIAN SUBCONTINENT. Burma: Griffith herb. 1020/2; see Kurz, Forest Fl. Burma 1 (1877) 287. – Andamans: King's coll. in L 908.270-147.

INDO-CHINA. Thailand: Maxwell 75-1004, 76-659, both from Chon Buri Prov., Ira I. – Vietnam: Pierre 4121, from Phu Quoi I.

MALESIA. Sumatra: 5 colls., incl. Ajoeb 25, Diepenhorst HB 2222, Lesger 120, from West Coast, East Coast, Benkulen, and Krakatau. – Malay Peninsula: 31 colls. from Thailand, Perak, Dindings, Kelantan, Pahang, Johore, Langkawi I., P. Penang. – Java: 25 colls., from West Java and neighbouring islands, East Java, and P. Bawean. – Lesser Sunda I.: 9 colls., incl. Iboet 350, Kostermans 22071, Teijsmann 11177, from Sumba, Flores, and Timor. – Borneo: 8 colls. incl. Ashton S 17829, Dewol & Bindin SAN 80333, Hou 551, from Sarawak, Sabah, and Balambangan I. – Philippines: 15 colls., incl. Elmer 10452a, 12179, 16760, Merrill Sp. Blanc. 601, from Palawan, Mindoro, Luzon, Polillo, Sibuyan, and Mindanao. – Celebes: 4 colls., incl. Koorders 18818, Rachmat 343, from North, Central, and Southwest. – Moluccas: 18 colls., incl. Bloembergen 4755, Buwalda 6073, Robinson Pl. Rumph. 1, from Morotai, Halmaheira, Ternate, Obi and Sula I., Buru, Ceram, and Ambon. – New Guinea: 11 colls., incl. BW 2229, 3488, 12079, NGF 31703, from all over the island, New Britain, New Hanover, and Mapia I.

AUSTRALIA. Northern Territory: Latz 3282 from Wessel I. – Queensland: 5 colls., incl. Hubbard 3478, L.S. Smith 11013, 12525.

PACIFIC. Solomon I.: Kajewski 2458 from Guadalcanal. – New Caledonia: 2 colls., incl. Balansa 157. – Samoa: Reinecke 356 from Savaii. – Niue I.: Sykes Niue I. coll. 1965 nr. 293. – Marquesas: Gagné 1290 from Eiao I. – Marianas: McGregor 460 from Guam. – Marshall I.: 4 colls., viz. St.John & Cowan 21799, 22015, Taylor 46-1095, 46-1442, from Wotje, Likiep, and Bikini Atoll.

TROPICAL AFRICA. Senegal: Anonymus in L 908.269-1219, Type of *D. senegalensis*. – Ghana: Deaw Sp. 184. – Togo: Warnecke 306.

MADAGASCAR and the MASCARENE ISLANDS. Comoro I.: Lam & Meeuse 6577. – Seychelles: Jeffrey 778 from Mahe, Procter 3948 from Praslin.

NORTH AMERICA. Florida: see Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 106.

WEST INDIES. Cuba: Curtiss 263; see Lippold, l.c. – Jamaica: see Lippold, l.c. – Santo Domingo: Fuertes 317; see Lippold, l.c. – Puerto Rico: Heller 4507, Sintenis 108, Wagner 442; see Lippold, l.c. – Virgin I.: Eggers 44 from St. Thomas. – Saint Croix: Bøgesen in U 24337 B; see Lippold, l.c. – St. Martin: Boldingh 2504 B, 3031 B, Suringar in L 905.136-159. – Antigua: see Lippold, l.c. – Guadeloupe: Duss 2904, 3627; see Lippold, l.c. – Martinique: Sieber 101; see Lippold, l.c. – Grenada: Beard 210, Broadway 3743. – Trinidad: Broadway 8996. – Tobago: Webster & Miller 9830.

SOUTH AMERICA. Surinam: 10 colls. – Brazil: Martius 397; see Lippold, l.c. from Bahia.

IV. REJECTED SPECIES NAMES

In this chapter all species names, accepted either by Radlkofer (1933) or by some later author but rejected by the present author, are discussed.

1. Dodonaea arborea Herter, Revista Sudamer. Bot. 5 (1937) 55; Fl. Illust. Urug. (1942) fig. 2243. – Type: not mentioned.

Reduced by Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 86, to *D. bialata*, by the present author to **D. angustifolia**.

2. Dodonaea arizonica A. Nelson, Amer. J. Bot. 21 (1934) 576; H. Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 82, pl. 1–5, map 1. – *D. viscosa* Jacq. f. *arizonica* Sherff, Amer. J. Bot. 32 (1945) 214; Field Mus. Natl. Hist. Bot. Ser. 23 (1947) 295. – Type: *A. Nelson 11276* (RM, not seen).

Mentioned by Sherff (1947) as occurring in the U.S.A. (Arizona, Texas) and Mexico (Sonora). Characterized by being a shrub no more than 1.5 m high with at least the young parts fairly densely minutely patent hairy and the leaves very narrow (up to 9 cm × 4–8 mm, c. 10 times as long as wide). The few specimens seen by me appeared to be dioecious. This seems to be an extreme form of **D. angustifolia**, occurring farther North than any other American *Dodonaea* and growing under drier conditions. A nearly identical collection, *Steinbach 173*, is known from Bolivia; other extremely narrow-leaved forms occur in South Africa (*D. thunbergiana* var. *linearis*) and in Central and southern Australia. The occurrence of comparable forms under extreme conditions in different parts of the world strengthens the impression that these are phenotypically rather than genetically defined taxa.

3. Dodonaea bialata H., B. & K., Nov. Gen. Sp. 5 (1821) 104, pl. 442; H. Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 85, pl. 1–5, map 1. – Type: *Humboldt & Bonpland 355 = herb. Willdenow 7316* (B, P; seen on microfiche).

For a description may be referred to Chapter III, the diagnosis of American *D. angustifolia.*

Reduced by Radlkofer (1933) to *D. viscosa* Jacq. f. *burmanniana* Radlk., by the present author to **D. angustifolia.**

4. Dodonaea eriocarpa Smith in Rees, Cyclop. 12 (1809); Sherff, Amer. J. Bot. 32 (1945) 204–213; Occas. Pap. Bernice P. Bishop Mus. 20 (1949) 4–7; Amer. J. Bot. 38 (1951) 57–61; Bot. Leafl. 8 (1953) 15; Degener, Fl. Hawaii (1956); St.John, List Flow. Pl. Hawaiian I. (1975) 223. – *D. viscosa* Jacq. subf. *eriocarpa* Radlk., Engl. Pflanzenr. 98 (1933) 1369. – Type: *Menzies* (not seen).

See Chapter III, the discussion on *D. angustifolia.*

Reduced to **D. angustifolia.**

5. Dodonaea lagunensis M.E. Jones, Contrib. West. Bot. 18 (1933) 57. – Type: *M.E. Jones 27087* (RSA).

Apparently, this name has been overlooked by nearly every author, even by Lippold. I found it only mentioned by Sherff (Field Mus. Nat. Hist. Bot. Ser. 23, 1947: 273), who cited it under *D. viscosa* Jacq. f. *repanda* Radlk. This reduction to true *D. viscosa* seemed geographically as well as ecologically improbable. *D. viscosa* s.s. is a coastal plant and is restricted to the Tropics, but unknown from the American West coast. *D. lagunensis*, on the contrary, is described from the Laguna Mts. in California, i.e. inland and in the Subtropics. These arguments as well as a study of the type collection led me to the conclusion that *D. lagunensis* is a synonym of **D. angustifolia** rather than of *D. viscosa.*

As Jones' original description of *D. lagunensis* includes only very few essential characters it seems worthwhile to give at least a short diagnosis based upon the type:

Twigs, petioles, and leaves thinly shortly hairy, the latter above on the base of the midrib only, beneath mainly on the midrib, very sparsely on the minor veins. *Twigs* at first angular, brown, and slightly glandular, soon becoming terete and black. *Leaves* c. 4–7 × 1.75–2 cm, about 2.25–3.5 times as long as wide, widest slightly above the middle, glands conspicuous especially on the upper side, leaves varnished; apex rounded, apiculate. *Inflorescences* short and few-flowered, hardly glandular. *Flowers* probably unisexual as under the fruit the scars of the stamens are not conspicuous and the scar of the calyx is annular. *Sepals* 4, partly persistent. *Fruits* 2-merous, the body c. 1 cm high, distinctly glandular and very sparsely short-hairy, the wings up to 7.5 mm wide, sometimes reddish.

6. Dodonaea linearifolia Linden ex Turcz., Bull. Soc. Imp. Naturalistes Moscou 31 (1858) 407; H. Lippold, Wiss. Beitr. Friedr. Schiller Univ. Jena Beitr. Phytotax. 6 (1978) 100, pl. 1–5, map 2. – Type: *Linden 2070* (KW; iso in A, G, NY; not seen).

Reduced by Radlkofer (1933: 1366) to *D. viscosa* Jacq. var. *angustifolia* Benth. This seems to be one of the narrow-leaved forms of **D. angustifolia**.

7. Dodonaea microcarya Small, Torreya 25 (1925) 39. – Type: *Small, Cuthbert & Matthaus 9105* (NY; not seen).

Reduced by Lippold (1978: 95) to **D. elaeagnoides** Ledeb. & Alderstam. This opinion is shared by the present author.

8. Dodonaea sandwicensis Sherff, Amer. J. Bot. 32 (1945) 202; Bot. Leafl. 9 (1954) 6; Degener, Fl. Hawaii (1959) with fig.; St.John, List Flow. Pl. Hawaiian I. (1973) 224. – Type: *Jules Remy 567* (P; not seen).

See Chapter III, the discussion on the variability of *D. angustifolia*. Reduced to **D. angustifolia**.

9. Dodonaea stenoptera Hillebr., Fl. Hawaiian Isl. (1888) 88; Radlk., Engl. Pflanzenr. 98 (1933) 1374; Sherff, Amer. J. Bot. 32 (1945) 213; St.John, List Flow. Pl. Hawaiian I. (1973) 224. – Type: *Hillebrand* (B; not seen).

Among *D. angustifolia* in the broad sense accepted by the present author, this is the most deviating form because of its fruits. These are inflated, slightly horny, and with rib-like wings no more than 1–1.5 mm broad. However, there is a gradual transition from the extreme kind of fruit to the 'normal' less-inflated and broad-winged fruits.

To be reduced to **D. angustifolia**.

10. Dodonaea thunbergiana Ecklon & Zeyher, Enum. Pl. Afric. Austral. 1 (1835) 54; Marloth, Fl. S. Afr. 2, 2 (1925) 158, pl. 53; Adamson & Salter, Fl. Cape Pen. (1950) 569. – *D. viscosa* Jacq. f. *thunbergiana* Radlk., Engl. Pflanzenr. 98 (1933) 1372. – Type: *Ecklon & Zeyher 419* (iso in L).

D. thunbergiana var. *linearis* Sonder in Harvey & Sonder, Fl. Cap. 1 (1860) 242. – Type: *Drège* (not seen).

Especially the var. *linearis* has very narrow leaves, comparable with *D. arizonica* and *D. linearifolia* in America and with certain Australian forms. These leaves are 3–6.5 cm × 3–7.5 mm, c. 5.5–21 times as long as wide.

To be reduced to **D. angustifolia**.