

# A MONOGRAPHIC REVISION OF THE GENUS *PODOCARPUS* (PODOCARPACEAE): I. HISTORICAL REVIEW

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The taxonomic history of the genus *Podocarpus* (Podocarpaceae) is reviewed as the first part of a revision of the genus. The major taxonomic and other works relating to the genus published during nine time periods (before 1800, 1800–1850, 1851–1875, 1876–1900, 1901–1926, 1927–1947, 1948–1967, 1968–1987 and 1988–present) are briefly but critically discussed. Three landmark works are those by Pilger (1903), Buchholz and Gray (between 1948 and 1962) and de Laubenfels (1985). The paper ends with an outline plan of the revision of the genus to which the paper forms an introduction.

*Keywords.* Classification, history, Podocarpaceae, *Podocarpus*, sections, taxonomy.

## INTRODUCTION

The genus *Podocarpus* L'Hér. ex Pers., nom. cons., is the largest genus of the family Podocarpaceae, itself the second largest conifer family after Pinaceae. It is also the most widely distributed genus of the family, with species found native in every continent except Europe. The largest concentrations of species are found in tropical and subtropical Asia and in South and Central America. Australasia also has numerous species, with Africa having the fewest. Many of its species are important timber trees, and many are threatened with extinction for this or a variety of other reasons such as habitat loss, particularly deforestation, or climate change.

Despite this, our understanding of the genus has long been hampered for want of a satisfactory definitive revision. No comprehensive revision of the genus, with full descriptions of all species, has appeared since the series of papers by Buchholz and Gray that appeared in the *Journal of the Arnold Arboretum* between 1948 and 1962, the contents of which are briefly reviewed later in this paper. The most recent work to deal with the whole genus (other than in books dealing with conifers as a whole) was by de Laubenfels (1985). This work was largely a conspectus of subgenera and sections and did not give full accounts of individual species other than those described as new. Many species of *Podocarpus* remain poorly known or understood and many pose identification problems in the field. Particularly among the Asian species, there are numerous instances of curious, very wide geographical disjunctions that are very

difficult to explain and may be due to species concepts that are too broad, as in the case of *Podocarpus spathoides* de Laub. (Mill & Whiting, 2012).

The time is ripe, therefore, for another full revision of the genus *Podocarpus* to be undertaken. The present paper presents an overview of the taxonomic history of the genus and of research that has been undertaken on it. It is subdivided into nine time periods of 20–25 years each, from the 18th century to the present day. The paper concludes with a very general plan of the revision. It is intended that all subsequent papers in the series will appear in *Edinburgh Journal of Botany*.

## HISTORICAL REVIEW

### *General remarks*

In Appendix III, part E1 of the *International Code of Botanical Nomenclature* (McNeill *et al.*, 2006: 250), *Podocarpus* L'Hér. ex Pers. (Persoon, 1807) is listed as conserved nomenclaturally over the earlier name *Podocarpus* Labill. (Labillardière, 1806). Labillardière's name was based on *Podocarpus aspleniifolius* Labill. which is now regarded as a species of *Phyllocladus* Rich. ex Mirb., *Phyllocladus aspleniifolius* (Labill.) Hook.f. (J. Hooker, 1845; Farjon, 2001). Persoon's genus *Podocarpus* is conserved with *P. elongatus* L'Hér. ex Pers. as the type. *Podocarpus* L'Hér. ex Pers. is itself conserved over the earlier name *Nageia* Gaertn. (Gaertner, 1788) when the two genera are united, but in recent years, beginning with de Laubenfels (1969, as *Decussocarpus*; 1987, as *Nageia*), the consensus, backed up by molecular data as well as morphology, is to treat them as separate genera.

Authors of the 19th and most of the 20th centuries circumscribed *Podocarpus* much more widely than currently. Sections and other infrageneric ranks or groups that were recognised within *Podocarpus*, and within *Dacrydium* Sol. ex Forst., are now regarded as distinct genera. The generic segregation that led from the five or six genera recognised within Podocarpaceae (or its equivalent – often part of Taxaceae) to the 19 accepted today (e.g. Farjon, 2001) led to many changes in the circumscription of *Podocarpus* (de Laubenfels, 1969 – *Dacrycarpus* de Laub., *Decussocarpus* de Laub. [now in part *Retrophyllum* C.N.Page]; de Laubenfels, 1972c – *Parasitaxus* de Laub.; de Laubenfels, 1978b – *Prumnopitys* Phil. reinstated; Page, 1989 – *Afrocarpus* (J.Buchholz & N.E.Gray) Gaussen ex C.N.Page, *Retrophyllum* C.N.Page, *Sundacarpus* (J.Buchholz & N.E.Gray) C.N.Page).

The genus name *Podocarpus* was by very many early authors (and a few more recent ones such as Gaussen) treated as feminine. However, Art. 62.2 Ex. 3 of the *International Code of Nomenclature for Algae, Fungi, and Plants* (McNeill *et al.*, 2012) requires it to be treated as masculine and in this paper I do so throughout regardless of the gender employed in the work being discussed. Where appropriate, the current name (but pending the revisions to come) of a taxon, where different, is inserted in square brackets following the name used in the work being discussed. The name of the section that contains the type of the genus is correctly *Podocarpus* sect. *Podocarpus*

but virtually all the earlier literature uses *Podocarpus* sect. *Eupodocarpus* and that name has therefore been retained in the ensuing discussions of those works.

### *Eighteenth century*

Species of *Podocarpus* began to be described in the 18th century, although not in that genus, which was not described until 1807. The earliest to have been described botanically was the Japanese species *Podocarpus macrophyllus* (Thunb.) Sweet, first described in the pre-Linnaean era as what were regarded as two distinct entities, *Maki spuria* and *Maki foetens*, by Kaempfer (1712), and in the genus *Taxus* L. as *T. macrophylla* Thunb. by Thunberg (1784). (Long before 1712, Christopher Columbus had observed *Podocarpus* in the Caribbean, as I shall point out in more detail in the second paper of this series.) Rumphius (1743) described *Lignum emanum* from the Moluccas (Indonesia); this is now called *Podocarpus rumphii* Blume. In 1789, the African species now known as *Podocarpus elongatus* (Sol.) L'Hér. ex Pers. (and the type of the genus *Podocarpus*) was independently described by Solander as *Taxus elongatus* Sol. in Aiton (Aug/Oct 1789) and by Lamarck (1789) as *Taxus capensis* Lam. Lamarck's work did not appear until 19 October 1789 and thus it is almost certain that Solander's name was published first and takes nomenclatural precedence. *Podocarpus elongatus* is a conserved name with a conserved type, its lectotype being *Masson* s.n. (BM) from South Africa (Leistner, 1966). An old belief that its type, and therefore that of the whole genus, is a cultivated specimen of the Asian species *Podocarpus chinensis* Wall. ex J.Forbes is wrong, as was pointed out by Gray (1953b). At the very end of the 18th century, Thunberg (1800) described *Taxus latifolia* Thunb. from the Cape of Good Hope – this is now known as *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb.

### *Early nineteenth century (1800–1850)*

*Taxonomic works.* – After what is now the type species of *Podocarpus*, *P. elongatus* L'Hér. ex Pers., was described (Persoon, 1807), there followed *P. taxifolius* Kunth in Humboldt *et al.* (1817), now *Prumnopitys montana* (Humb. & Bonpl. ex Willd.) de Laub. (de Laubenfels, 1978b), and *Podocarpus macrophyllus* (Sweet, 1818). In 1824, David Don described five new species of *Podocarpus* as part of his contribution to Lambert's *Genus Pinus* (Don in Lambert, 1824) and Mirbel (1825) published five more species named by Robert Brown, only two of which [*P. latifolius* and *P. spinulosus* (Sm.) R.Br. ex Mirb.] remain in *Podocarpus* today. These were followed by new species from Richard (1826) and Blume (1827).

The next *Podocarpus* species to be described was the New Zealand totara, *Podocarpus totara* G.Benn. ex D.Don, formally described in the second edition of Lambert's *Genus Pinus*, editio minor (Lambert, 1832) but first mentioned by George Bennett (1832: 508) in one of a series of articles describing the uses and wood qualities of various plants from New Zealand, some of which (like the totara) had not yet been

botanically described at that time. Two other members of this very closely related species group were also described during this period: *Podocarpus nivalis* Hook. (W. Hooker, 1843h) and *P. lawrencei* Hook.f. (J. Hooker, 1845).

The first synthesis of the genus was by J. J. Bennett in Bennett & Brown (1838). This gave a history of the genus up to that time and divided it into four sections. The first of these was unnamed and largely, but not entirely, corresponded to *Podocarpus* as circumscribed today, with 16 species listed under four geographical groups. The second section, *Podocarpus* sect. *Taxoideae* Benn., contained the single species *Podocarpus spicatus* R.Br. [*Prumnopitys taxifolia* (Sol. ex D.Don) de Laub.]. The third section, *Podocarpus* sect. *Dacrydioideae* Benn., corresponds to what is now the genus *Dacrycarpus*. The fourth section, *Podocarpus* sect. *Dammaroideae* Benn., contained the single species *Podocarpus latifolius* Wall. non (Thunb.) R.Br. ex Mirb. nec Blume, the correct name for which is now *Nageia wallichiana*. This sectional name was revived in the genus *Nageia* as *N.* sect. *Dammaroideae* (Benn.) R.R.Mill (Mill, 2001).

W. J. Hooker (1842a,b, 1843a–i, 1844) published descriptions of several new species of Podocarpaceae in his *Icones Plantarum* and in the *London Journal of Botany*; of these, only W. J. Hooker (1842a,b, 1843h, 1844) described species of *Podocarpus* as now circumscribed. These were followed by more species from J. D. Hooker (1845) and Siebold & Zuccarini (1846) as the genus began to grow ever larger.

The year 1847 is notable for the appearance of two important early works pertaining to Podocarpaceae: Blume's treatment in the third volume of *Rumphia* (Blume, 1847) and Endlicher's *Synopsis coniferarum* (Endlicher, 1847). Blume followed J. J. Bennett in recognising his sections *Taxoideae*, *Dacrydioideae* and *Dammaroideae* and proposed a fifth, *Nageiae*, that comprised *Podocarpus nageia* R.Br. [*Nageia nag*]. He provided extended descriptions and colour plates of several species and short descriptions of about a dozen more, some of which were newly described.

More important was Endlicher's *Synopsis coniferarum*. In this work, Endlicher proposed Ordo Podocarpeae, equivalent to the family Podocarpaceae as recognised today. This contained three genera, *Podocarpus*, *Dacrydium* and *Microcachrys* Hook.f. which was classed as a 'genus dubium'. Endlicher enumerated 40 species of *Podocarpus*, dividing them between four groups: I. *Nageia* Endl., II. *Eupodocarpus* Endl., III. *Stachycarpus* Endl. and IV. *Dacrycarpus* Endl. Equivalent groups with identical typesetting and layout in his treatments of *Pinus* L. and *Gnetum* L. in the same work were formally awarded the rank of section but these groups in *Podocarpus* were not. Nor were they awarded any formal rank in the subsequent fourth supplement to his *Genera plantarum* (Endlicher, 1848) in which, in any case, he used Sectio for the primary divisions within his highest rank (Regio; and therefore his 'Sectio' is there equivalent to either Subkingdom or Division in today's taxonomic hierarchy) and so these much lower categories cannot, in his *Genera plantarum*, also be sections. In both the main work (Endlicher, 1837) and relevant supplement (Endlicher, 1848), Endlicher classified the conifers as Classis XXII *Coniferae* within Sectio V. Acramphibrya, Cohors I. Gymnospermae. Brizicky (1969) has argued that the

infrageneric names in Endlicher's *Genera plantarum* were rankless. Carrière (1855), however, did regard Endlicher's apparently unranked groups *Nageia*, *Eupodocarpus*, *Stachycarpus* and *Dacrycarpus* as being sections (see his synonymies: Carrière, 1855: 437, 443, 472 and 477 respectively), although he himself treated them as 'tribus' (see below). The earliest work that both accepted the names and definitely assigned sectional rank to the latter three groups appears to be that of Gordon (1858) who, however, regarded *Nageia* as a separate genus. Endlicher's group I. *Nageia* (five species) was equivalent to the genus *Nageia* Gaertn., group III. *Stachycarpus* contained one species now classified in *Afrocarpus* and four species now placed in *Prumnopitys*, while group IV. *Dacrycarpus* comprised two species of *Dacrycarpus* and one now regarded as a member of the genus *Halocarpus* Quinn. Group II. *Eupodocarpus* comprised 28 species, numbered 6–32 with no. 12 being used twice. Of these 28, ten were described as new. However, half of them have since been placed into synonymy of other species. A list very similar to that of Endlicher (1847), but giving only very brief details, was published by Lindley & Gordon (1850); it included 41 species within *Podocarpus* as circumscribed by them.

The year after the appearance of his *Synopsis*, Endlicher (1848) published the fourth supplement to his *Genera plantarum*. This contained a revised treatment of the conifers in which that of *Podocarpus* was similar to the *Synopsis*, but with the four rankless groups lettered a, b, c and d in boldface rather than given the roman numerals I, II, III and IV. As Brizicky (1969) has pointed out, it appears to be impossible to ascertain what rank(s) should be given to Endlicher's infrageneric groups, of which there appear to be at least four different levels of rank in his 1848 work, denoted by roman numerals (as in *Pinus*, which had been given sectional rank in the 1847 *Synopsis*), boldface letters (as found in *Juniperus* L., *Araucaria* Juss. and *Podocarpus*), boldface roman numerals (as in *Ephedra* L.) and Greek letters (again in *Ephedra*).

Also in 1847 there appeared an apparently much less well known work by Horaninow (1847). Gymnosperms were regarded by Horaninow as the class *Strobilanthae*; within this, Horaninow recognised four 'orders': *Pinopalmae*, corresponding to cycads; *Acerosae* (pines and cypresses, *Araucaria* being included with the pines); *Drupiferae* (yews and podocarps); and *Articulatae* (Gnetaceae plus the angiosperm family Casuarinaceae which during this period was often thought to be a gymnosperm). Order *Drupiferae* comprised the two families Taxaceae and Podocarpaceae and Horaninow was apparently the first person to use the name Podocarpaceae for that family (op. cit.: 27). His concept of Podocarpaceae encompassed only the genus *Podocarpus*; *Dacrydium* and *Phyllocladus* were included in Taxaceae, probably because he stated (op. cit.: 29) that Podocarpaceae differed from Taxaceae by having anatropous ovules. The modern concept of the family includes genera with both anatropous ovules such as *Podocarpus* and orthotropous ones such as *Dacrydium* and *Phyllocladus*. Horaninow (1847) appears not to have accounted for *Microcachrys* at all. He believed that *Podocarpus* contained about 24 species.

*Morphological studies.* – Robert Brown appears to have been the first person (Brown, 1814) to have discovered what he regarded as the ‘true nature’ of the structure of the ‘cone’ of *Podocarpus*. He wrote, ‘certain plants of the order [Coniferae] are even furnished with a double cupula. This is most remarkable in *Podocarpus*, in which the drupa is formed of this external cupula, whose aperture exists not at the apex, but very near its base or point of insertion. The inner cupula in this genus is in every stage entirely enclosed in the outer and is in like manner inverted’. This appears to have been the earliest observation of the structure that specialists on the family now refer to as the epimatium (de Laubenfels, 1992b; Tomlinson, 1992; Tomlinson *et al.*, 1997). Later workers such as Endlicher (1837; see next section) proposed alternative interpretations and the ‘true nature’ of the *Podocarpus* cone was to be a matter of controversy for years to come.

This period also saw some of the earliest work dealing with the structure of the reproductive organs of *Podocarpus* and other members of the family. There was particular controversy concerning the morphology of the ovule, whether it represented an inverted orthotropous structure as put forward by Robert Brown (Brown, 1814; Bennett & Brown, 1838) or an erect anatropous one as originally described by Endlicher in his *Genera plantarum* (Endlicher, 1837: 262) although he later reversed this view and favoured that of Brown (Endlicher, 1847, 1848).

#### *Mid nineteenth century (1851–1875)*

*Taxonomic and horticultural works prior to De Candolle’s Prodrômus.* – The third quarter of the 19th century was notable for the publication of several encyclopaedic horticultural works on conifers: Carrière’s *Traité général des Conifères* in two editions (Carrière, 1855, 1867); Gordon’s *Pinetum* (Gordon, 1858, with *Supplement* in 1862, 2nd edition in 1875 with a reissue in 1879); Courtin’s *Die Familie der Coniferen* (Courtin, 1858); Henkel & Hochstetter’s *Synopsis der Nadelhölzer* (1865); *Pinaceae* by ‘Senilis’, the pseudonym of J. Nelson (Nelson, 1866); Hoopes’s *Book of Evergreens* (1868) and Charles de Kirwan’s *Les conifères indigènes et exotiques*, published in two parts in 1867 and 1868, the Podocarpaceae being treated in the second part (Kirwan, 1868). One of the greatest plant taxonomic works of all time, De Candolle’s *Prodrômus*, was by now well under way and Parlatores’ treatment of Taxaceae for that work, including his account of *Podocarpus*, appeared in its 16th volume (Parlatore, 1868a,b). This period also saw the initial discoveries of the wealth of plant life inhabiting the New Caledonia and Fiji archipelagos (Brongniart & Gris, 1866a,b; Seemann, 1868) as well as accounts of the conifers of New Zealand (J. Hooker, 1853), Tasmania (J. Hooker, 1857) and the West Indies, particularly Cuba (Grisebach, 1862a,b, 1866), as well as miscellaneous other descriptions of new species (Lindley, 1851; Miquel, 1851).

In the fifth volume of Dietrich’s *Synopsis plantarum* (Dietrich, 1852), *Podocarpus* was divided into four unnamed groups lettered a, b, c and d. The composition of

these corresponded very closely to the four groups I. *Nageia*, II. *Eupodocarpus*, III. *Stachycarpus* and IV. *Dacrycarpus* of Endlicher (1847). Group b included only 26 species compared with Endlicher's 28, the omissions being two Australian species. The reason why these were left out is unknown; neither was synonymised with another species.

The treatment of *Podocarpus* in the first edition of Carrière's *Traité général des Conifères* (Carrière, 1855) was fairly similar to that of Endlicher (1847). Forty-eight species were enumerated and described, divided between four 'tribus' (tribes), *Nageia*, *Eupodocarpus*, *Stachycarpus* and *Dacrycarpus*. The use of 'tribe' as a rank between genus and species is contrary to the rules of the *International Code of Botanical Nomenclature* now in force (McNeill *et al.*, 2006); consequently all these new combinations at the rank of 'tribe', based on Endlicher's sections of the same names, were not validly published. 'Tribe' *Eupodocarpus* comprised 36 species of which two were described as new.

Courtin's *Die Familie der Coniferen* (published Jun–Jul 1858) and the *Pinetum* of Gordon (Jun–Dec 1858) are important since they are the first works definitely to award sectional rank to the rankless groups that Endlicher erected within *Podocarpus*, namely *Nageia*, *Eupodocarpus*, *Stachycarpus* and *Dacrycarpus*. Courtin's work treated all four at sectional rank, in the sequence listed above, whereas Gordon awarded full generic rank to *Nageia* and gave sectional rank to the other three, which he treated in the same sequence as Courtin. Unfortunately the exact publication date of either work is not known and they came out at approximately the same time. Courtin (1858) treated 50 species, of which 36 were in section *Eupodocarpus*. Gordon (1858) recognised 42 species in the genus, 35 of them in section *Eupodocarpus*. Courtin's and Gordon's works were very similar, although there are differences in the treatment of a few species. A much enlarged second edition of the *Pinetum* appeared in 1875 with a reissue in 1879. This is discussed below.

The *Synopsis der Nadelhölzer* by Henkel & Hochstetter (1865) adopted a four-section classification of *Podocarpus*. This was identical to the system of Endlicher (1847) except that Endlicher's four rankless groups were all definitely awarded the rank of section including *Podocarpus* sect. *Nageia* for the first time. They recognised 36 species within *Podocarpus* sect. *Eupodocarpus*, none of them new, and 13 among the other three sections. A contemporary work, *The Book of Evergreens* (Hoopes, 1868), listed 43 species of *Podocarpus* but gave detailed accounts of only three.

Very different in nature was the treatment of the conifers and 'taxads' by J. Nelson under the pseudonym 'Senilis' (Nelson, 1866). Nelson had no time for those whom he called 'species-mongers' and who in his estimation had grossly inflated the true number of species amongst the conifers. *Podocarpus* was by him divided into two sections that he named *Calophyllus* and *Stachycarpus*. *Podocarpus* sect. *Calophyllus* Nelson was equivalent to *P.* sect. *Nageia* of earlier authors and comprised just two species. *Podocarpus* sect. *Stachycarpus* encompassed the other three sections of Gordon, Henkel & Hochstetter and others or, in his own words, 'what botanists have been pleased to define as twelve genera'. Within that group he recognised only 13 species,

compared with the 40 or so of earlier but contemporary authors. Of those 13, only five are wholly referable to *Podocarpus* as now circumscribed with a further three comprising elements belonging to both *Podocarpus* and other genera.

One reason for this drastic reduction in species was the fact that Nelson deplored the efforts of those whom he referred to as ‘hair-brained speculators and pedantic systematists, and the small fry who followed their suit,—the species-mongers,’ [to whom] ‘are we indebted for heterogeneous and gratuitous assumptions, and unsustainable and contradictory assertions, which have so obscured the classification and nomenclature of the firs and pines, that at the present time their classification is chaos and their nomenclature cant’ (Nelson, 1866: 20). Unfortunately, Nelson’s extreme lumping simply resulted in more chaos. The most extreme example in *Podocarpus* is the Australian endemic *P. elatus* R.Br. ex Endl., of which he wrote, ‘The same tree, more or less altered by soil, climate and altitude, has been found in Abyssinia, Cape of Good Hope, Brazil, Nepal and New Guinea; and it has been again and again re-introduced and re-christened; for it is to be found with such names as *elongata*, *Lambertiana*, *laeta*, *nobilis*, *spicata*, *spinulosa*, *thetviaefolia*, and *Thunbergii*; their only differences being in the size, form or colour of their leaves’. Nelson’s circumscription of *Podocarpus elatus* was actually a mixture of at least nine good species of *Podocarpus* (including *P. elongatus*, the type of the genus!) and one species of *Prumnopitys*.

J. D. Hooker’s two accounts of the Coniferales of New Zealand and Tasmania were published in 1853 and 1857 respectively. In New Zealand he treated five species of *Podocarpus*, three of which have since been transferred to other genera. In Tasmania only *Podocarpus alpinus* R.Br. ex Hook. was treated; this (J. Hooker, 1857: 356) was the first valid publication of Brown’s epithet which had appeared in several other earlier publications but without meeting all the requirements for validation.

The second edition of Carrière’s *Traité général des Conifères* appeared in 1867. Apart from being a considerably enlarged and revised edition it contained a change in the treatment of the genus *Podocarpus*. *Nageia* which, in the first edition (Carrière, 1855), as well as in the works by Endlicher (1847) before it and Henkel & Hochstetter (1865) after it, had been the first of four rankless groups (Endlicher) or sections of *Podocarpus*, was raised to the level of genus, as had been done by Gordon (1858). As in this author’s work, *Podocarpus* therefore was restricted to the remaining three sections with *Podocarpus* sect. *Eupodocarpus* containing 35 species.

In the same year, Sénéclauze (1867) published his monograph of conifers. *Podocarpus* was divided firstly into three ‘tribus’ corresponding largely to *Podocarpus* sensu stricto, *Prumnopitys* and *Dacrycarpus* – an identical division to that of Carrière (1867). The first ‘tribu’, *Podocarpus* sensu stricto, was then divided into geographical groups, with seven [South] American species, four Australian, seven Asian and two from ‘Cap’ [South Africa]. For each species and variety, Sénéclauze gave a short description and these may prove of help when unravelling the true identity of some of the more obscure taxa such as *Podocarpus curvifolius* Carrière that are currently unplaced in lists such as Farjon (2001).

*Parlatore's account of Podocarpaceae for De Candolle's Prodrromus.* – The treatment of *Podocarpus* for De Candolle's *Prodrromus* by Parlatore (1868b) is an important landmark in the systematics of the genus. Parlatore followed the four-section Henkel & Hochstetter (1865) classification of the genus that had its roots in Endlicher's *Synopsis coniferarum*. He enumerated 65 species in the genus, eight (three of them considered doubtful) in *Podocarpus* sect. *Nageia*, 45 (ten doubtful) in *P.* sect. *Eupodocarpus*, six in *P.* sect. *Stachycarpus* and six in *P.* sect. *Dacrycarpus*. Of the six he included in *Podocarpus* sect. *Stachycarpus*, two – 56. *P. nivalis* and 59. *P. alpinus* with its variety  $\beta$  *lawrencii* – are now classified within true *Podocarpus* and it is strange that he placed these in *P.* sect. *Stachycarpus* but included their near relative *P. totara* within *P.* sect. *Eupodocarpus*. His treatment is notable for containing the protologues of eleven new species assigned by him to *Podocarpus*; of these, however, only four remain in the genus as presently delimited. Unlike some of those who had gone before him, notably Carrière as noted by Williams (2004), Parlatore's treatment was backed up by the extensive collections he had seen in the herbaria of Florence, Geneva, London and elsewhere and which form the basis of his type material.

*Post-Prodrromus taxonomic and horticultural works.* – Charles de Kirwan's popular work (Kirwan, 1868) treated 30 species under *Podocarpus* in narrative style, area by area, beginning with those of eastern Asia and progressing via New Guinea, modern Indonesia, Australia and Africa, and finally to the South American and Caribbean species then known. A systematic list was also given at the end of the work. Compared with the contemporary works of Carrière (1867) and Sénéclauze (1867), Kirwan's is much less useful today although for some species such as *Podocarpus chilinus* [*P. salignus* D. Don] it does give dates of introduction that are of historical interest.

The second edition of Gordon's *Pinetum* appeared in 1875 with a reissue in 1879 ('1880' on the title page). This treated 59 species in *Podocarpus*, 46 of them in section *Eupodocarpus*, eleven in *P.* sect. *Stachycarpus* and two 'uncertain and little known kinds', the first of them in fact a *Dacrydium* and the other a *Dacrycarpus*. Unlike Parlatore (1868b), Gordon (1875) continued to retain *Nageia* as a separate genus. He apparently followed Parlatore (1868b) in including *Podocarpus nivalis*, *P. alpinus* and *P. lawrencei* in the circumscription of *Podocarpus* sect. *Stachycarpus* but gave full species rank to all three whereas Parlatore had regarded *P. lawrencei* as a variety of *P. alpinus*.

The early 1860s saw the first descriptions of species of Podocarpaceae from New Caledonia, which is famous today as a centre of gymnosperm diversity with 44 species, all of them save one cycad species being endemic to the island archipelago. Vieillard (1862) described the first species of *Podocarpus* from the island, *Podocarpus novae-caledoniae* Vieill., for which a fuller description was given a few years later by Brongniart & Gris (1866a,b). Petrus de Boer (1866) published a treatment of the conifers of the Indonesian archipelago; this included detailed descriptions of eleven species of *Podocarpus* sensu lato of which seven belong to the genus as currently delimited; most were accompanied by line drawings. Meanwhile, Grisebach (1862a,b, 1866)

published three important works on the flora of the West Indies including treatments of a number of *Podocarpus* species.

*Morphological and other studies.* – This period saw some of the earliest papers dealing with the biology of *Podocarpus* and the family Podocarpaceae in general. One of these was J. D. Hooker's short paper (J. Hooker, 1854) in which he reported the discovery of what he called 'spherical exostoses' on the roots of, first of all, *Podocarpus dacrydioides* A.Rich. [*Dacrycarpus dacrydioides* (A.Rich.) de Laub.] and then of many other conifers, including *Podocarpus* (sensu lato?) itself. These are now known to be the nodules in which live the vesicular arbuscular mycorrhiza that are of widespread occurrence in the conifers other than Pinaceae. Thomas (1863) studied the leaf anatomy of conifers and seems to have been the first person to observe transfusion tissue in the leaves of *Podocarpus* (cf. comment by Bertrand, 1874); transfusion tissue as such was only described some years after Thomas's paper, in *Sciadopitys verticillata* Siebold & Zucc. by von Mohl (1871a,b). Karsten (1849) may also have observed transfusion tissue in *Podocarpus* prior to Thomas, as noted by Bernard (1904), but a thorough search of Karsten's text has failed to reveal the existence of the passage implied by Bernard. Favre (1865) published a note on the female cone of *Podocarpus chinensis*, concluding that the ovule was an erect, anatropous structure covered by a raphe that terminates in a chalazal extension, and enclosed by two integuments that are fused for almost their whole length. Geyley (1867) performed one of the earliest studies on the phyllotaxis and stem architecture of conifers as a whole, publishing details for a number of *Podocarpus* species. Braun (1869) published a paper in which he described a monstrosity, or teratological form, of *Podocarpus chinensis* that displayed the transition from true leaves to ovuliferous scales. Bertrand (1874) published the first really detailed study on the anatomy of leaves and stems of Podocarpaceae, as part of a wider study of all the gymnosperms. Unusually (possibly indeed uniquely), Bertrand reduced the genus *Dacrydium* to a section of *Podocarpus*.

#### *Late nineteenth century (1876–1900)*

*Taxonomic works.* – The last quarter of the 19th century saw relatively little advancement in our knowledge of *Podocarpus*. Further new species were described by Hance (1883), Kirk (1884, 1889), Colenso (1884), Hemsley (1885, 1896), Baker (1885), Masters (1892), Rendle (1894), Bailey (1899) and Franchet (1899), many of which have since been transferred to other genera. The chief work to appear during this otherwise rather fallow period was the *Revisio generum plantarum* by Otto Kuntze, published in 1891. Kuntze reverted to using *Podocarpus* to apply to the genus *Phyllocladus*, as by Labillardière (1806), and used *Nageia* in place of *Podocarpus* L'Hér. ex Pers. As a result, he (Kuntze, 1891: 800) made 65 transfers from *Podocarpus* to *Nageia*, as well as coining four new names to avoid homonymy and adopting ten previous transfers from *Podocarpus* to *Nageia* that had been made by Ferdinand von Mueller, Gordon and Kurz. Because of his nomenclatural viewpoint, Kuntze also

made two reverse transfers from *Phyllocladus* to *Podocarpus*. Baillon (1892) followed this nomenclature.

*Morphological studies.* – In the 1890s there also appeared Masters' comprehensive survey of the morphology and anatomy of the Coniferae (Masters, 1890) as well as the equally extensive treatise on the comparative anatomy of conifer cones by Radais (1894), together with a paper by van Tieghem (1891) erecting the new genus *Stachycarpus* Tiegh. for what had previously been called *Podocarpus* sect. *Stachycarpus*. The latter paper included leaf anatomical details of some 26 species of *Podocarpus* sensu lato, grouped systematically in accordance with their anatomical features. Small-leaved species such as *Podocarpus totara* and *P. nubigenus* Lindl. that lacked abundant transfusion tissue were separated from larger-leaved ones like *P. neriiifolius* D. Don that possessed abundant transfusion tissue.

#### *Early twentieth century (1901–1926)*

*Pilger's taxonomic works.* – The first quarter of the 20th century was marked by two more landmarks in the study of *Podocarpus*, Pilger's accounts of the Taxaceae published in Engler's *Das Pflanzenreich* (Pilger, 1903) and of Podocarpaceae in Engler's *Die natürlichen Pflanzenfamilien* (Pilger, 1926). In between these two major works, as well as afterwards, Pilger also published various other, mainly short papers on Podocarpaceae which, prior to 1916, he included in Taxaceae (Pilger, 1904, 1905, 1913, 1914, 1915, 1916a,b,c, 1923, 1934, 1937).

In his *Pflanzenreich* monograph, Pilger (1903) divided Taxaceae into three subfamilies, Taxaceae subfams. Podocarpoideae Pilg., Phyllocladoideae Pilg. and Taxoideae Pilg. Taxaceae subfam. Podocarpoideae was subdivided into the two tribes Pherosphaereae Pilg. (*Pherosphaera* W. Archer bis) and Podocarpeae (*Microcachrys*, *Saxegothaea* Lindl., *Dacrydium*, *Podocarpus*). Within *Podocarpus*, Pilger slightly modified the hitherto prevailing four-section classification, stemming from the work of Endlicher (1847), by removing *Podocarpus ustus* (Vieill.) Brongn. & Gris from *P.* sect. *Dacrycarpus* to a new, fifth section, *Podocarpus* sect. *Microcarpus* Pilg. He transferred several species from *Podocarpus* sect. *Eupodocarpus* to *P.* sect. *Stachycarpus*, which thereby was composed of ten species, corresponding to the genera *Prumnopitys*, *Sundacarpus* and *Afrocarpus* of today's classifications (e.g. Farjon, 2001, 2010). Conversely he transferred *Podocarpus nivalis* and *P. acutifolius* Kirk from *P.* sect. *Stachycarpus* to *P.* sect. *Eupodocarpus*. *Podocarpus* sect. *Eupodocarpus* thereby comprised 41 species of which two were new.

The most significant of Pilger's papers published between his treatments for *Das Pflanzenreich* and *Die natürlichen Pflanzenfamilien* was Pilger (1916a), in which he proposed a new classification of the Taxaceae (sensu lato). He divided this family into three smaller ones, namely Podocarpaceae, Taxaceae sensu stricto (containing only *Taxus* L. and *Torreya* Arn.) and Cephalotaxaceae. Podocarpaceae itself was subdivided into four subfamilies with *Podocarpus* in subfamily Podocarpoideae (Pilg.) Pilg.

In his treatment of Podocarpaceae for *Die natürlichen Pflanzenfamilien* (Pilger, 1926), Pilger made a further modification to his classification of *Podocarpus*. Two subgenera were recognised: I. *Stachycarpus* (Endl.) Pilg. represented an elevation in rank of *Podocarpus* sect. *Stachycarpus* (Endl.) Gordon while the remaining four sections, *Podocarpus* sects. *Dacrycarpus*, *Microcarpus*, *Nageia* and *Eupodocarpus*, were placed in subgenus 2. *Protopodocarpus* Engl. The latter was first described by Engler in Engler & Prantl (1897: 21) and, since it contained the type of the genus, should correctly be referred to as *Podocarpus* subgen. *Podocarpus*. Within the latter subgenus some 45 species were listed. These were distributed more or less equally between two informal groups, A and B, depending on whether the female cones possessed two small bracts below the receptacle (group B) or not (group A). These groups broadly correspond to the two subgenera first delimited much later by de Laubenfels (1985), *Podocarpus* subgen. *Foliolatus* de Laub. (bracts present) and *Podocarpus* subgen. *Podocarpus* (bracts absent) with one very important difference: the four Afro-Madagascan species including *Podocarpus elongatus* (Sol.) L'Hér. ex Pers., the type of the genus, were all placed in group B (bracts present: i.e. corresponding to *Podocarpus* subgen. *Foliolatus*), rather than in group A (bracts absent: corresponding to *Podocarpus* subgen. *Podocarpus*). As the placement of these Afro-Madagascan species potentially affects the infrageneric nomenclature of the entire genus, the morphological basis of this classification by Pilger (1926) needs very careful checking.

*Other taxonomic and floristic works.* – During this period there were also significant contributions to the taxonomy of the genus by other authors. Foxworthy (1907, 1911) published papers on the genus in the Philippines while Koorders & Valeton (1904, 1915) gave synopses of the species of Java. Laurent (1915) published an important paper on the *Podocarpus* species of Madagascar, and Stapf provided an account of the Bornean species (Stapf, 1914) as well as the first of his two treatments of African species (Stapf, 1917). Of the six species that Stapf (1917) enumerated and comprehensively treated within *Podocarpus* in his account of the tropical African species, only *P. milanjanus* Rendle belongs to *Podocarpus* as circumscribed today; the others all belong to *Afrocarpus*. Compton (1922) provided a critical commentary on the gymnosperms of New Caledonia but there were no taxonomic novelties in *Podocarpus*. Meanwhile, Ignatz Urban, a contemporary of Pilger who also worked at Berlin, published three short notes on the Caribbean species of *Podocarpus* (Urban, 1920, 1922, 1924).

*Morphological and anatomical studies.* – Bernard (1904, 1907) published two papers on centripetal xylem in conifers. The first dealt with this tissue in the leaves while the second discussed it with respect to the reproductive organs. In the first paper he distinguished five types of leaf anatomy based on presence/absence of *hydrostérome* (transfusion tissue), two of which were peculiar to what are now segregated as *Nageia* and *Dacrycarpus*. The other three types were found within *Podocarpus* sensu stricto: (i) no transfusion tissue, no transversely elongated parenchyma cells, little centripetal xylem [*Podocarpus nubigenus*, as well as *Prumnopitys ferruginea* (D. Don ex A. Cunn.)

de Laub.]; (ii) no transfusion tissue, but very well developed centripetal xylem (*Podocarpus elongatus*); and (iii) centripetal xylem and transfusion tissue both well developed (several Asian and Australian *Podocarpus* species as well as what is now *Afrocarpus falcatus* (Thunb.) C.N.Page). The fact that *Podocarpus nubigenus* was found to differ in these characters from *P. totara* and *P. alpinus* is particularly interesting since all three are currently classified in the same section of the genus.

Some early papers on organogenesis of various species of *Podocarpus* were published at the start of the 20th century. Coker (1902) studied the gametophytes and embryo of what he called *Podocarpus coriaceus* Rich. although its true taxonomic identity is questionable since the sources of the material were Jamaica and in cultivation in South Carolina; Buchholz (1941) commented that at least the South Carolina material was probably *Podocarpus macrophyllus* and the Jamaican material was more likely to have been the same species since it too was cultivated. If that is true, Coker did not study *Podocarpus coriaceus* (which is endemic to the Lesser Antilles, although the name has also been misapplied to other species from the Caribbean and South America) at all and we cannot know for certain to which taxon or taxa his results really pertain. Jeffrey & Chrysler (1907) examined *Podocarpus polystachyus* R.Br. ex Endl. as well as species now transferred to *Dacrycarpus* and *Prumnopitys*, while Burlingame (1908) studied *Podocarpus nivalis* and *P. hallii* Kirk [*P. cunninghamii* Colenso] as well as a third species that he surmised might be *Podocarpus elongatus* but which is best regarded as unidentified since that name was then frequently misapplied to *Afrocarpus falcatus*. Burlingame (1908) also provided a summary of the earlier work and stated that his own results were in the main confirmatory.

Hill & de Fraine (1908) studied the seedlings of *Podocarpus chinensis* and noted that each cotyledon had two vascular bundles which together form one pole of the diarch root, as in Gnetales. Interest in teratological forms and the like continued, with a paper on vivipary in *Podocarpus* by Lloyd (1902).

Several papers on aspects of the morphology of *Podocarpus* were published in quick succession in the following decade, by Stiles (1912), Gibbs (1912) and Sinnott (1913). Stiles' paper was a general account of the morphology of the Podocarpaceae based on examination of living and herbarium material; ten species of *Podocarpus* (plus one unidentified) were studied. It was a culmination of a series of earlier papers on the family, of which that by Brooks & Stiles (1910) on *Podocarpus spinulosus* also falls within the scope of this review. That by Gibbs (1912) was a very careful histological study of various stages of development of the female strobilus; eight species of *Podocarpus* were sampled as well as some now removed to *Nageia*, *Dacrycarpus* and *Prumnopitys*. She came to the conclusion that *Podocarpus*, particularly the section *Eupodocarpus*, exhibited the most extreme reduction of the female cone within the family. The study by Sinnott (1913) likewise focused on the morphology and anatomy of the female cones; all the material used came from Australia and New Zealand and included five species of *Podocarpus* in the modern sense. The restriction to Australasian source material means that the full range of variation possibly present in cone structure was not explored but his paper is important in being the first detailed anatomical

examination of the female cones of *Podocarpus*. About this time the first two of John Buchholz's many papers appeared: a study on polycotyledony in conifers (Buchholz, 1919: mainly Pinaceae, with Podocarpaceae only discussed briefly) and a general study of embryo development in conifers (Buchholz, 1920) that discussed all major lineages including the podocarps.

Florin (1920) published one of the earliest studies on the cuticle morphology of gymnosperm leaves. Two species of *Podocarpus*, *P. elongatus* and *P. coriaceus*, as well as one each of *Prumnopitys* and *Dacrycarpus*, were described in detail.

#### *Early mid twentieth century (1927–1947)*

*Taxonomic works.* – The period that elapsed between Pilger's *Pflanzenfamilien* treatment of Podocarpaceae in 1926 and the start of the revision of the genus *Podocarpus* by Buchholz and Gray from 1948 onwards (see next section) yielded relatively few works dealing with *Podocarpus*. Sixteen taxonomic novelties were published in the genus during this period (White, 1933; Lundell, 1937; Pilger, 1937; Carabia, 1941; Chang, 1941; Wasscher, 1941) but five have since been transferred to other genera (mostly *Dacrycarpus*). Stapf (1933) published his treatment of *Podocarpus* for *Flora Capensis*. This contained comprehensive accounts of three species of *Podocarpus* from southern Africa together with treatments of three other species now regarded as members of *Afrocarpus* (Farjon, 2001, 2010).

By far the most significant work on the taxonomy of *Podocarpus* to appear during this period was the incredibly detailed revision of *Podocarpus* in the 'Netherlands Indies' published by Wasscher (1941). The area covered corresponds approximately to modern Indonesia. Because of the Second World War it was not possible for Wasscher to study material in several important herbaria and consequently he was only able to examine limited materials from some adjacent areas such as eastern New Guinea, the Malay peninsula and the northern part of Borneo (then under British control), while examination of materials in Philippines herbaria was impossible. Nevertheless, in what is a considerable understatement, he commented that in his opinion 'I believe this treatment of the genus *Podocarpus* is rather complete for the Netherlands Indies proper'. Indeed, for detail and depth of discussion his work remains unsurpassed today among studies on *Podocarpus* even though many more species have since been described from the region. As was then customary, *Podocarpus* was divided into several sections that correspond to independent genera in current classifications of the family. His classification of the genus was a modification of Pilger's 1926 one and recognised the two subgenera *Stachycarpus* and *Protopodocarpus* although he commented (Wasscher, 1941: 361), 'I doubt whether the subdivision into sub-genera is right. Perhaps we had better not distinguish any sub-genera, but only six equivalent groups which might be either sub-genera or sections'. *Podocarpus* subgen. *Stachycarpus* was represented in the area only by *P. amarus* Blume [*Sundacarpus amarus* (Blume) C.N.Page] while *P.* subgen. *Protopodocarpus* contained the other

24 species, divided among four sections. Three of these (*Podocarpus* sects. *Dacrycarpus*, *Nageia* and *Eupodocarpus*) had been recognised in Pilger's 1926 classification but the remaining one, *Podocarpus* sect. *Polypodiopsis* C.E.Bertr., had not. This section corresponds to the genus *Retrophyllum* C.N.Page. *Podocarpus* sect. *Dacrycarpus* [= *Dacrycarpus*] included eight species (three new), *P.* sect. *Nageia* had two and *P.* sect. *Polypodiopsis* one species. The remaining 13 species were placed in *Podocarpus* sect. *Eupodocarpus*. One of them, *Podocarpus salomoniensis* Wasscher from the Solomon Islands, was described as new, as were seven varieties, one in *P. polystachyus* and the other six within *P. neriifolius*. Some of the latter are now regarded as distinct species.

Another worker whose output was adversely affected by the Second World War was J. P. Carabia, who published an account of the gymnosperms of Cuba (Carabia, 1941). These were principally species of *Podocarpus* in which he recognised five species from Cuba, two of them new. Carabia examined material in United States and Cuban herbaria but was unable to examine types or other specimens in European herbaria such as Berlin. Two years after he published his work, the Berlin herbarium (B) was bombed by Allied forces and much of it was destroyed and, although many of the numbers are duplicated in other herbaria, many collections cited by Pilger (1903) will no doubt have been lost. Some types of Podocarpaceae at B have, however, survived and have been recently digitised and made available online.

*Morphological and other studies.* – The Edinburgh morphologist Orr (1937, 1944) published two significant papers on the anatomy of conifer leaves. The earlier paper was a general study that concentrated on assessing the taxonomic value of various characters. The later paper (Orr, 1944) was a comprehensive anatomical study of the leaves of the genus *Podocarpus*. Like all contemporary workers Orr treated *Podocarpus* in a broad sense including many species since transferred to *Afrocarpus*, *Nageia*, *Prumnopitys*, *Retrophyllum* and *Sundacarpus*. Among the species of *Podocarpus* sensu stricto, Orr noted for the first time that *Podocarpus totara*, *P. nivalis*, *P. acutifolius*, *P. hallii*, *P. gnidioides* and *P. nubigenus* all possessed the common 'negative character' of absence of accessory transfusion tissue in the leaves, a feature that set this group (now *Podocarpus* sect. *Australis* de Laub.) apart from the rest of the genus. He also noted that all the African species he studied possessed five resin canals, again a character that was not found elsewhere in the genus. He found that amongst the large group of Asiatic species (of which he examined material of 22), the occurrence of sclereids had some geographical correlation, sclereids being absent from all examined Philippine and Malay species but present in those from New Guinea and New Caledonia. In some species the hypoderm was continuous, in others discontinuous. Among Australasian species, *Podocarpus drouynianus* F.Muell. and *P. spinulosus* had a unique combination of leaf anatomical characters including a single resin canal and hypoderm interrupted between midrib and margin but continuous over the midrib itself. Thirteen species from Central and South America were examined; these all also had a single resin canal and, except for *Podocarpus parlatorei* Pilg. and *P. salignus*, a continuous hypoderm.

Buchholz continued his researches on the embryogeny of the Podocarpaceae, with papers on *Podocarpus* subgen. *Stachycarpus* (Buchholz, 1936) and a general embryological study of the family (Buchholz, 1941). In the earlier paper, one species still in *Podocarpus* was incidentally discussed. His later paper (Buchholz, 1941) was concerned principally with *Podocarpus*, *Nageia* and *Dacrycarpus* although other genera of the family were also discussed. An important finding was that all the Central and South American *Podocarpus* species studied had very similar embryogeny but that this differed strongly from Australasian members of the genus such as *P. totara* and *P. nivalis*.

The final important paper to appear in the 1940s was Wilde's study of conifer cones (Wilde, 1944). This proposed a new, evolutionary and morphological classification of the male and female cones of Podocarpaceae and introduced new terminology to describe their arrangement. This was based on internodal reduction. The apparently primitive state was termed 'primary clusters' which could be reduced to a single cone. Internodal reduction in the secondary vegetative branches could result in the formation of 'secondary clusters' of male cones, while internodal reduction in the primary vegetative branch could further aggregate these into 'tertiary clusters'. Based on her studies of male cone evolution she hypothesised that *Podocarpus drouynianus* and *P. nivalis* were, of the species she studied, the most primitive. She noted strong similarities between Podocarpaceae and Araucariaceae in the nature and arrangement of the fertile branches, a significant finding in the light of today's molecular phylogenetics work which places them as sister families. She also hypothesised that in *Podocarpus* (sensu lato including *Prumnopitys* etc.) there had been progressive sterilisation of the fertile branches, with the most primitive being those of *Prumnopitys taxifolia* and *Prumnopitys andina* (Poepp. ex Endl.) de Laub.

#### *Later mid twentieth century (1948–1967)*

*The taxonomic work of Buchholz and Gray.* – Post-war research on *Podocarpus* and Podocarpaceae in general was dominated by the team of John Theodore Buchholz (1888–1951) and Netta Elizabeth Gray (1913–1970) who between them produced a series of papers between 1948 and 1962 in which the bulk of *Podocarpus* as then delimited was critically revised (Buchholz & Gray, 1948a,b,c; Gray & Buchholz, 1948, 1951a,b; Gray, 1953a,b, 1955, 1956, 1958a, 1960, 1962a). The first three parts of their revision of *Podocarpus* were published in 1948 (Buchholz & Gray, 1948a,b,c). The first instalment (Buchholz & Gray, 1948a) set out their sectional classification, which was based largely upon a consideration of leaf anatomy. They followed the suggestion Wasscher had made earlier (1941: 361, quoted above) and abandoned the two subgenera recognised by Pilger (1926). Instead they delimited eight sections, two of them new (*Podocarpus* sect. *Afrocarpus* J.Buchholz & N.E.Gray, *P.* sect. *Sundacarpus* J.Buchholz & N.E.Gray). These are listed in Table 1 together with the relevant paper number(s) and reference(s) and the current name and rank of the section.

TABLE 1. Sections of *Podocarpus* recognised by Buchholz & Gray (1948a). 'Paper number': I–XIII as given in the individual titles

Section	Paper number(s)	Reference(s)	Current rank and name (Farjon, 2010)
1. <i>Dacrycarpus</i> (Endl.) Gordon	Not revised	—	Genus <i>Dacrycarpus</i>
2. <i>Microcarpus</i> Pilg.	XII	Gray (1960)	Genus <i>Parasitaxus</i>
3. <i>Nageia</i> (Endl.) Henkel & Hochst.	Not revised	—	Genus <i>Nageia</i>
4. <i>Afrocarpus</i> J. Buchholz & N.E. Gray	VII	Gray (1953a)	Genus <i>Afrocarpus</i>
5. <i>Polypodioopsis</i> C.E. Bertr.	III, XIII	Gray & Buchholz (1948), Gray (1962a)	Genus <i>Retrophyltum</i>
6. <i>Sundacarpus</i> J. Buchholz & N.E. Gray	VI	Gray & Buchholz (1951b)	Genus <i>Sundacarpus</i>
7. <i>Stachycarpus</i> (Endl.) Gordon, in part	II, V	Buchholz & Gray (1948b), Gray & Buchholz (1951a)	Genus <i>Prunnopitys</i>
8. <i>Eupodocarpus</i> (Endl.) Gordon	IV, VIII, IX, X, XI	Buchholz & Gray (1948c), Gray (1953b, 1955, 1956, 1958a)	Genus <i>Podocarpus</i>
Sections and key	I	Buchholz & Gray (1948a)	n/a

The remainder of this discussion will concern only the papers relating to *Podocarpus* as currently delimited, i.e. numbers IV, VIII–XI in the series (for references see Tables 1 and 2 and the following paragraph).

In total, Buchholz and Gray treated 75 species of *Podocarpus* as currently delimited, of which 18 were described as new (Table 2). With additional papers (Buchholz, 1949; Gray, 1959) the two authors described 20 new species of *Podocarpus* during the course of their work, and recognised 77. Buchholz and Gray's work was for the most part extremely careful and their revisionary series remains the standard reference for research on *Podocarpus*.

*Other taxonomic and floristic works.* – Buchholz and Gray were not the only workers on *Podocarpus* in the immediate post-war period. Ronald Melville of Kew published both a research paper (Melville, 1955) and a floristic revision (Melville, 1958) on the Podocarpaceae of East Africa. David de Laubenfels described the first of his many new species of *Podocarpus* (de Laubenfels, 1960). His main works have appeared from 1970 onwards and are discussed in the following sections. Finally, Hu (1964) also described a new *Podocarpus* from Zhejiang, SE China in this period.

Floristic accounts of the family, or of *Podocarpus* in particular, appeared for many regions including the Cape peninsula (Adamson, 1950), New South Wales (Anderson, 1956), Venezuela (Buchholz & Gray, 1957; Veillon, 1962), New Caledonia (Sarlin, 1954; Chevalier, 1957), Guadeloupe (Questel, 1951), Guatemala (Gray, 1958b), Tonga (Gray, 1959), New Zealand (Allan, 1961), southern Africa (Breitenbach, 1965; Leistner, 1966), China (Hu, 1964), Taiwan (Li, 1963), tropical Africa (Lewis, 1960) and Mexico (McVaugh, 1966), while Gray (1962b) published an account of the *Podocarpus* species cultivated in the United States.

*Morphological and other studies.* – It was in 1953 that David de Laubenfels, who later became so important as a student of the Podocarpaceae, published his first major paper (de Laubenfels, 1953). This discussed the external morphology of conifer leaves, which he classified into four broad groups labelled Types I–IV. Leaves of *Podocarpus* and similar genera were classified as Type II, defined as being linear or lanceolate, bifacially flattened with a single vascular bundle. This was regarded as being the commonest type amongst living conifers. Shortly afterwards, Griffith (1957) published a detailed account of the leaf anatomy and development of *Podocarpus macrophyllus*, focusing on the development of transfusion tissue.

Several more embryological studies were published during this period, especially by Doyle and co-workers (Doyle, 1945, 1954; Boyle & Doyle, 1953, 1954) but also by Brownlie (1953) who studied the New Zealand species.

Papers by Hair & Beuzenberg (1958) and Hair (1963) represent the earliest significant studies of cytology of Podocarpaceae. The paper published in 1958 in particular remains a standard reference for chromosome numbers although care must now be taken to 'translate' the names given into current nomenclature. Eight species of *Podocarpus* as now circumscribed were studied, the chromosome numbers of which ranged from  $2n = 20$  in *Podocarpus latifolius* to  $2n = 38$  in *P. salignus* which was later

TABLE 2. Papers by Buchholz and/or Gray dealing with species of *Podocarpus* as now delimited. 'Subsection': in the sense of Buchholz & Gray (1948a)

Paper	Subsection	Area treated	Number of species treated	Number of new species	Other novelties	Reference
IV	C and D	Caribbean, Central and South America	29	10	3 new varieties, 3 new combinations	Buchholz & Gray (1948c)
VIII	A and E	Africa	7	0		Gray (1953b)
IX	F	New Caledonia and Fiji	3	2		Gray (1955)
X	D	New Zealand, Tasmania, New Caledonia,	7	0		Gray (1956)
XI	B	temperate S America 'South Pacific'	29	6	3 new varieties, 1 change of rank	Gray (1958a)
Totals			75	18	6 new varieties, 4 new combinations	

recorded as also having  $2n = 40$  (Hair, 1966). Hair (1966) interpreted these as a reduction series, from  $2n = 40$  to  $2n = 20$ . However, molecular phylogenetics research conducted within the last decade suggests that this is a simplistic view since taxa with identical chromosome numbers have originated more than once. The variation has been explained in terms of Robertsonian transformation but as yet it is not possible to determine whether the range in number has arisen through fusion, fission or a combination of both (Jones, 1978, 1998). Indeed the validity of the whole hypothesis that Robertsonian transformation is the explanation for the variation has recently been questioned (Murray & de Lange, 2011).

Knowledge of wood anatomy of *Podocarpus* and other members of the family advanced through the work of Greguss (1951, 1955, 1957), Kaeiser (1954), Patel (1967) and Tegnér (1967). Kaeiser (1954) examined a particularly large number of samples – 186, belonging to nearly 80 species of *Podocarpus* sensu lato, c.50 of them belonging to *Podocarpus* as presently circumscribed – and her work must be regarded as one of the most comprehensive studies in terms of coverage. She adopted the six informal subsections A–F recognised within *Podocarpus* by Buchholz & Gray although she was unable to examine any material of subsection E (*Podocarpus rostratus* L. Laurent from Madagascar). She found that the other five sections were all homogeneous in nearly all characters she scored, except that piceoid pits were lacking in subsection A (all African species) and C (all American species) though present in subsections B (Asia and Pacific), D (equivalent to *Podocarpus* sect. *Australis*) and F (Pacific). Subsection F was also unique in totally lacking ray indentures and radial pits in the tracheids were not frequently twinned as in the other four subsections studied. *Podocarpus* could be distinguished from *Sundacarpus* and all species of *Prumnopitys* except *P. andina* by the presence of abundant xylem parenchyma. Greguss (1955) described the wood of 13 species, all of them also examined by Kaeiser (1954).

Palynological examination of the Podocarpaceae began in detail. Ueno (1960a) studied almost 40 species of *Podocarpus* (and 81 of the family as a whole), measuring various standard parameters. Pollen grains were assigned to ‘types’ according to the relative ratios of breadth, depth and height. Of twelve possible combinations, only seven were found in both the body and the cappa, with four of the seven being common to both. Body type was listed before cappa type in a style resembling a ratio, e.g. ‘3 : 9’ indicated body type 3 and cappa type 9. Combination ‘11 : 9’ was commonest in *Podocarpus* (22 species) followed by ‘3 : 9’ (11 species), ‘2 : 9’ (4), with single species having combinations ‘1 : 9’, ‘9 : 5’, ‘11 : 1’ and ‘11 : 10’. Sometimes different samples of the same species had different combinations of types, e.g. *Podocarpus alpinus* had both ‘11 : 1’ and ‘1 : 9’, and species generally thought to be closely related in other respects also sometimes differed, e.g. *Podocarpus drouynianus* (‘3 : 9’) and *P. spinulosus* (‘11 : 9’). The significance of these ‘types’ and/or the data upon which they were based are therefore perhaps questionable. His second paper (Ueno, 1960b) was a much more general survey of pollen grain biology and germination in gymnosperms. Erdtman (1957, 1965) published descriptions, accompanied by photographs or diagrams, of the pollen of about 30 species still in *Podocarpus*.

Detailed phytochemical studies on the Podocarpaceae as a whole began about this time. The most active teams were based in New Zealand, particularly that headed by Cambie, which published at least 75 papers under the series title 'Chemistry of the Podocarpaceae' in a variety of journals including *Australian Journal of Chemistry* and *Phytochemistry* between 1962 and 1990. Some of the earliest papers concerned the identification of the chemical constituents of some of the New Zealand *Podocarpus* species such as *P. totara* (Cambie & Mander, 1962), *P. hallii* (Cambie *et al.*, 1963), *P. acutifolius* and *P. nivalis* (both Bennett & Cambie, 1967), and so of potential taxonomic interest, but later papers were much more analytical and of little use in plant systematics. Nakanishi *et al.* (1966) isolated the insect moulting hormone ponasterone A from *Podocarpus nakaii* Hayata in Japan while simultaneously Galbraith & Horn (1966) published their initial discovery of 20-hydroxyecdysone (by them called crustecdysone) in *Podocarpus elatus* in Australia. These were the first discoveries of the group of steroidal compounds initially called phytoecdysones and now termed phytoecdysteroids, initially found in Podocarpaceae and subsequently in Taxaceae, ferns and angiosperms (Abubakirov, 1982).

This period was also marked by the publication of two key papers by Rudolf Florin, those on female reproductive organs (Florin, 1954) and conifer distribution and biogeography (Florin, 1963). The latter paper included a lengthy discussion (pp. 182–200) on the distribution of Podocarpaceae. In this Florin followed the Buchholz & Gray infrageneric classification of *Podocarpus* which at that time had only just been completed. He noted the primarily Asian distribution of *Podocarpus* subsect. B (equivalent to the bulk of present-day *Podocarpus* subgen. *Foliolatus*), the African distribution of subsections A and E (equivalent to *Podocarpus* subgen. *Podocarpus* sects. *Podocarpus* and *Scytopodium*), the primarily Australasian distribution of subsection D (= *P.* subgen. *Podocarpus* sect. *Australis*) and the exclusively American distribution of subsection C (the rest of *Podocarpus* subgen. *Podocarpus*). He hypothesised that the two big subsections, B and C, might both have had Australasian origins with B migrating into Asia and C into the Americas, and that the ancestor of the single species of subsection D in the Americas (*Podocarpus nubigenus*) may have reached there from Australasia via Antarctica. With modern techniques of phylogenetic and biogeographic analyses it is now possible to test these hypotheses rigorously although to date no such study has been performed for *Podocarpus*. During this period Florin (1958) also published a short paper on the systematics of the Podocarpaceae, covering aspects such as vegetative and reproductive morphology, embryology, cytology and relationships with other conifer families, particularly Taxaceae and Cephalotaxaceae (today recognised as a single family: Christenhusz *et al.*, 2011). This paper contained little about *Podocarpus* in particular.

#### *Twentieth century (1968–1987)*

*Taxonomic works.* – One person has dominated research on Podocarpaceae systematics, and the description of new taxa within *Podocarpus*, from the mid-20th

century until the beginning of the 21st – David de Laubenfels. De Laubenfels took over the mantle from Buchholz and Gray (see preceding section) and in his first major paper (de Laubenfels, 1969) began what was originally conceived as a revision, to be published in two parts, of nine genera of Podocarpaceae, four of them being newly segregated by him from *Podocarpus*. Only the first part of that revision, containing detailed accounts of six genera (*Phyllocladus*, *Dacrydium*, *Falcatifolium* de Laub., *Dacrycarpus*, *Acropyle* and *Decussocarpus*), actually appeared in its intended form, although he did later account for the three remaining genera in briefer treatments (*Parasitaxus* as part of de Laubenfels, 1972b; *Prumnopitys* as de Laubenfels, 1978b; and *Podocarpus* sensu stricto as de Laubenfels, 1985). His 1969 paper is important for its removal from the genus, at last, of *Podocarpus* sects. *Dacrycarpus*, *Nageia*, *Polypodiopsis* and *Afrocarpus* as part of what he called (1969: 276) an attempt ‘to produce a more balanced treatment of the family’. *Podocarpus* sect. *Dacrycarpus* became an independent genus, *Dacrycarpus*, while the other three sections initially became the genus *Decussocarpus* although he was later obliged, by a change in the rules of the *International Code of Botanical Nomenclature*, to revert to the genus *Nageia* (de Laubenfels, 1987). De Laubenfels also transferred *Podocarpus* sect. *Sundacarpus* J.Buchholz & N.E.Gray to *Prumnopitys* as a monospecific section (de Laubenfels, 1978b). Subsequently, Page (1989) treated them all as independent genera [*Nageia*, *Afrocarpus*, *Retrophyllum* and *Sundacarpus* respectively], which remains their current status.

In 1972 de Laubenfels published two important floristic treatments of the gymnosperms of Madagascar (de Laubenfels, 1972b) and New Caledonia (de Laubenfels, 1972c). The former work was preceded by a precursor paper (de Laubenfels, 1972a) in which two new Madagascan species of *Podocarpus* were described. His New Caledonian account treated seven species of which one was new.

De Laubenfels (1978a) next revised the conifers of the Philippines and described three new species of *Podocarpus*. Papers on the *Podocarpus* species of Ambon in the Moluccas (de Laubenfels, 1979) and New Guinea (de Laubenfels, 1980) followed, with one new species being described in each. Next was a floristic revision of the Podocarpaceae of Venezuela (de Laubenfels, 1982) in which three new species were described, then he described one new species from the Caribbean (de Laubenfels, 1984a), and contributed accounts of each genus of Podocarpaceae occurring in the Pacific area, including *Podocarpus* (de Laubenfels, 1984b), to Balgooy’s *Pacific Plant Areas*.

His revision of *Podocarpus* (de Laubenfels, 1985) enumerated 94 species, of which eleven were new and one was an elevation to species rank of a former variety. The most notable feature of this paper, however, was his novel classification of the genus *Podocarpus*. Two subgenera were recognised, each with nine sections. *Podocarpus* subgen. *Podocarpus* contained 41 species while *P.* subgen. *Foliolatus* comprised the remaining 53. The subgenera were defined primarily on presence or absence of ‘foliola’ (small bracts) below the normally fleshy and coloured structure (the so-called ‘receptacle’) that subtends the ovule(s), and the presence or absence of a Florin ring

around each stoma. *Podocarpus* subgen. *Podocarpus* (receptacle without subtending foliola; Florin rings present) contained all the South American and Afro-Madagascan species together with all those on New Zealand, while *P.* subgen. *Foliolatus* de Laub. comprised the Asiatic and Pacific representatives of the genus. Both subgenera are represented in New Caledonia and Australia. Subsequent research, including molecular phylogenetics, has borne out the validity of these subgenera as distinct taxa (see next section). However, the validity of the character of the subtending foliola of the receptacle that was the primary character used to separate the subgenera was soon called into question by Stoffberg (1991b), who noted the occasional presence of one or two spreading foliola in *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb., which de Laubenfels (1985) classified in *Podocarpus* subgen. *Podocarpus* sect. *Podocarpus*. Small bract-like structures at the top of the peduncle, but  $\pm$  adnate to the receptacle rather than free from it and spreading, have also been observed in various South American species of *Podocarpus* subgen. *Podocarpus* by the present author, as will be noted in later papers of this series. Therefore another character, apart from Florin ring presence/absence, may need to be sought to delimit the two subgenera of de Laubenfels (1985) morphologically.

Whether or not all or any of the 18 sections of *Podocarpus* delimited by de Laubenfels should continue to be recognised, and if so how many and in what circumscriptions, is much more debatable. The sections were distinguished principally on vegetative characters, particularly those of the bud scales. Infrageneric taxa, and indeed genera and families, that are based primarily on vegetative features tend to have had a chequered history. *Phyllocladus*, for example, long kept separate from the rest of Podocarpaceae by virtue of its specialised phylloclades (cf. Keng, 1973), has been found using molecular phylogenetic analyses to be nested within the family in a clade that also contains *Lagarostrobos* Quinn, *Halocarpus* Quinn, *Parasitaxus*, *Prumnopitys* and other genera (Conran *et al.*, 2000). Similarly, few of de Laubenfels's sections within either subgenus of *Podocarpus* stand up to phylogenetic scrutiny. The species of *Podocarpus* in the Caribbean and Central America fall into four of the nine sections of *P.* subgen. *Podocarpus* (de Laubenfels, 1985) and, of those sections with more than one species in the area, none was monophyletic (Stark Schilling, 2004). Conversely, several very closely related species from the Greater Antilles, that did form a monophyletic lineage, are currently classified in two different sections (Stark Schilling, 2004). Similar results can be obtained when almost any biogeographic area is considered. Detailed character scoring of a large number of characters – vegetative, reproductive and micromorphological – is currently under way in order to attempt a new infrageneric classification that will place morphology in the context of the available molecular data.

With 94 species recognised, de Laubenfels's 1985 paper represents a major landmark in the history of *Podocarpus* taxonomy. The constituent species of each section were keyed out and listed, with brief synonymy when thought necessary (34 instances out of the 83 previously described species). They were, however, not described in detail unless new to science. Consequently, although it introduced a novel

infrageneric classification and described taxonomic novelties, de Laubenfels's work is really a conspectus or *catalogue raisonnée*, not a revision in the usually accepted sense of the term. Great care must be taken when reading the protologues of de Laubenfels's species in his 1985 paper because although in most cases only the holotype is given, to validate the name, it has been discovered that in at least some instances the protologue was actually founded on the basis of many other specimens, and in at least one instance (*Podocarpus spathoides* de Laub.: Mill & Whiting, 2012) some of these specimens have subsequently been found not to belong to the taxon described.

*The Gausсен school.* – De Laubenfels was not, however, the only person to publish works on Podocarpaceae or the genus *Podocarpus* in the mid-20th century. Henri Gausсен, based at Toulouse, had for a long time been producing an encyclopaedic work entitled *Les Gymnospermes actuelles et fossiles*. This appeared as a large number of fascicles of the in-house publication *Travaux du Laboratoire forestière de Toulouse*. It had a very complex hierarchical construction of Tomes, Sections, Volumes (some divided into Parties), Fascicules and Chapitres, with each chapter of each fascicule being independently paginated. Thus, for an unambiguous citation, the tome, section, volume, part (if relevant), fascicule and chapter must all be given as well as the pagination. Having previously dealt with cycads, *Ginkgo* L., Pinaceae, Cupressaceae and Araucariaceae, in the early 1970s Gausсен reached the Podocarpaceae ('les Podocarpinés'). These were treated as fascicles XII, XIII and XIV of tome 2 vol. 1. Fascicle XII (Gausсен, 1973) was a general introduction, fascicle XIII (Gausсен, 1974) treated all genera except *Podocarpus* and fascicle XIV (Gausсен, 1976) was an account of *Podocarpus*. Gausсен's circumscription of *Podocarpus* was unique. As well as *Podocarpus* sensu stricto, it included *Nageia* and *Retrophyllum* as *Podocarpus* sects. *Nageia* and *Polypodiopsis* respectively but excluded the other sections *Dacrycarpus* and *Stachycarpus* which he treated (under those names) at generic rank, with Buchholz & Gray's *Podocarpus* sect. *Sundacarpus* being treated as a section of *Stachycarpus*. *Podocarpus* sect. *Afrocarpus* was also excluded and raised to genus rank as '*Afrocarpus* Gausсен' but he did not fulfil all the requirements of the *International Code of Botanical Nomenclature* then in force and his generic name, and all combinations within it, were not validly published: validation did not take place until the paper by Page (1989). Just why Gausсен excluded *Afrocarpus* but not *Nageia* or *Retrophyllum* from *Podocarpus* is unclear.

Gausсен's work was very derivative, almost all illustrations being re-used from other publications, and described no new species. In separate papers, however, he did publish two new species from Madagascar. Gausсен's colleague Woltz also named a new species, *Podocarpus gausсенii* Woltz, after him (Woltz, 1969, 1970) but that has been transferred to *Afrocarpus*. Gausсен and Woltz were particularly interested in the podocarps of Madagascar and published significant papers on their leaf anatomy (Woltz, 1973; Gausсен & Woltz, 1975), seedling anatomy and morphology (Woltz, 1970) and wood anatomy (Marguerier & Woltz, 1977). The latter paper was billed as being the 'first part' and covered only three species; a second part, that would have

dealt with the other Madagascan *Podocarpus* species, was promised (Marguerier & Woltz, 1977: 158) but apparently never appeared. Woltz and other colleagues such as Ferré and Rouane also published more general papers on the seedling anatomy of the Podocarpaceae (Ferré *et al.*, 1975, 1977) and on particular genera such as *Saxegothaea* and *Sundacarpus*.

*Floristic works.* – Floristic treatments of *Podocarpus* appeared for many parts of the world during this period. Apart from those for Madagascar, New Caledonia, Malesia, the Philippines, and Venezuela, all by de Laubenfels and discussed above, examples include accounts for Australia (Boland *et al.*, 1984; Bennett, 1987), China (Cheng & Fu, 1978), Tasmania (Curtis & Morris, 1975), Mozambique (Graça Silva, 1983), southern Africa (Palmer & Pitman, 1972; Breitenbach, 1974; Palgrave, 1977, 1983), Fiji (Parham, 1972; Smith, 1979), Thailand (Phengkklai, 1973, 1975), New Zealand (Salmon, 1980), and alpine New Guinea (van Royen, 1979) as well as for the *European Garden Flora* (Nelson, 1986). John Silba's two conifer works also appeared during this period. The first (*International Census of the Coniferae*: J. Silba, 1984) took the form of a checklist and was a precursor to the more detailed second one, the *Encyclopaedia Coniferae* (J. Silba, 1986). Like Gausson's before him, Silba's works of 1984 and 1986 were derived compilations with no new taxa within *Podocarpus* (although he did publish novelties later; see next section).

*Morphological and other studies.* – Morphological and/or anatomical studies were published concerning seedlings (Woltz, 1970, 1986; Ferré *et al.*, 1975; Siqueira & Ferreira, 1987), vegetative shoots and leaves (Schoonraad & van der Schijff, 1974, 1975, South African species of *Podocarpus* and *Afrocarpus*; Woltz, 1973 and Gausson & Woltz, 1975, Madagascan species; Kausik, 1975, *Podocarpus brevifolius* (Stapf) Foxw.; Ferré *et al.*, 1977, New Caledonian species; Ho *et al.*, 1983, SE Asian species mainly from China; Offler, 1984, Asia and New Guinea; Woltz *et al.*, 1987, worldwide), female strobili (Jain, 1978, *Podocarpus neriifolius*; Morvan, 1968, 1971a,b, 1973, 1975, *P. macrophyllus*) and wood (Greguss, 1972; Marguerier & Woltz, 1977; Suzuki, 1979; Diaz-Vaz, 1986, *Podocarpus nubigenus*). The leaf anatomical study by Woltz *et al.* (1987) examined 122 species of Podocarpaceae of which an unspecified number belonged to *Podocarpus* itself. They found that groups could be established based on anatomical characters of the midrib and associated structures such as resin canals. Various evolutionary series within the family were proposed, with some of them ending in so-called 'over-evolved' taxa that showed a reversal to the hypothesised ancestral condition.

Dodd & van Staden (1981) published a study of the germination and viability of the recalcitrant seeds of *Podocarpus henkelii* Stapf ex Dallim. & A.B.Jacks.

Alvin & Boulter (1974) published a paper describing a new controlled method to prepare gymnosperm cuticles for examination under the scanning electron microscope and this paved the way for a new field of study that in Podocarpaceae has proved extremely useful and informative although until very recently *Podocarpus*

itself had scarcely been studied. Morvan (1982, 1987) undertook studies of the epicuticular waxes of the leaves and strobili of *Podocarpus macrophyllus*.

Doyle & Brennan (1971a,b) published important work on cleavage polyembryony in conifers, with the Podocarpaceae being surveyed in the first of the two papers.

Vasil & Aldrich (1973) studied the ultrastructure of the pollen in *Podocarpus macrophyllus*. Ueno (1984, 1985a) continued his studies on gymnosperm pollen and published a more detailed account of Podocarpaceae pollen (Ueno, 1985b).

Phytochemical studies included papers on anthocyanins by Lowry (1968), whose identification of delphinidin-3,5-diglucoside in *Podocarpus polystachyus* was the first record of any anthocyanin in Podocarpaceae. Other papers on anthocyanins in Podocarpaceae soon followed (Crowden & Grubb, 1971; Lowry, 1972; Crowden, 1974). However, there have been very few subsequent studies, despite the obvious presence of anthocyanins in the receptacles and young leaves, and it would be interesting to determine whether the pigment characteristics of species with dark-coloured (violet, purple or blackish) receptacles are different to those with red ones such as *Podocarpus nivalis*. Norditerpene dilactones are widespread in the genus and are cytotoxic; these compounds have been named and isolated from many species from both subgenera of *Podocarpus* such as *P. milanjanus* (Hembree *et al.*, 1979, 1980), *P. nubigenus* (Silva *et al.*, 1973), *P. purdieanus* Hook. (Wenkert & Chang, 1974), *P. sellowii* Klotzsch ex Endl. (Hembree *et al.*, 1979), *P. salignus* (Matlin *et al.*, 1982, 1984a,b) and *P. macrophyllus* (Itô *et al.*, 1968). The biflavones and other flavonoid compounds present in the genus were studied by Kumar Roy *et al.* (1987) and in New Zealand by Markham *et al.* (1984, 1985). Research on phytoecdysteroids at first advanced rapidly, with these compounds being discovered in many members of the Podocarpaceae as well as in Taxaceae, ferns and some angiosperms. Compounds of this group identified in Podocarpaceae during this period included ponasterones B and C from *Podocarpus nakaii* (Nakanishi *et al.*, 1968), makisterones A, B, C and D from *P. macrophyllus* (Imai *et al.*, 1968a,b), and podecdysone B from *P. elatus* (Galbraith *et al.*, 1969).

Lastly, the first morphological cladistics analysis of conifer families was published (Hart, 1987). This found only one unique character that united the family – the binucleate embryonal cell of the proembryo – although the presence of an epimatium was also found in all but two of the 15 genera studied (including *Phyllocladus* but treating *Afrocarpus*, *Nageia* and *Retrophyllum* within *Decussocarpus* and presumably including *Sundacarpus* within *Prumnopitys*, since that was the classification then prevailing). His work revealed nothing of the phylogeny within *Podocarpus* since it was concerned with the levels of family and genus only.

#### *The past 25 years (1988–present)*

*Taxonomic works.* – The first important taxonomic work on *Podocarpus* of the past 25 years was the revision of the family in *Flora Malesiana* by de Laubenfels (1988).

This treated 30 species, none of which was new; however, unlike in his 1985 paper, all were fully described and mapped and some were also illustrated. Three further new Asiatic species (de Laubenfels & Silba, 1988a) and one Brazilian species (de Laubenfels & Silba, 1988b) were described very shortly afterwards.

De Laubenfels published several more short floristic papers in the early 1990s in which a total of five further new species of *Podocarpus* were described (Silba, 1990 [without de Laubenfels's permission: de Laubenfels, pers. comm. 2012]; de Laubenfels, 1991a,b, 1992a, 1994). Since then he has also described one more species (de Laubenfels, 2003) and elevated another to species rank (de Laubenfels, 2005) giving a total of nine New Caledonian species, for all of which he provided a key in the later paper. However, there is currently some debate as to whether either or both of these two last-described species are distinct (Farjon, 2010; Jaffré *et al.*, 2010).

Staszkievicz (1988) published a paper on the *Podocarpus* species of the Antilles in which he used morphometrics as an aid to delimiting the taxa. He proposed a novel treatment of the species occurring on those islands that will be discussed in more detail in the second paper of this series.

Silba (1990) published a supplement to his 1984 and 1986 works discussed in the previous section. Unlike those it contained taxonomic novelties. Between this 1990 work and a later paper (Silba, 2000), Silba described 14 varieties within ten species of *Podocarpus*, all of which were synonymised within their parent species by Farjon (2001) but require proper evaluation of their status. Farjon (1998, 2001) published two editions of a world checklist of conifers, in the later of which 107 species of *Podocarpus* were accepted. Silba (2008a,b, 2009) described or validated two new species (*Podocarpus ballivianensis* Silba and *P. tixieri* Gausson ex Silba) and a new subspecies of *Podocarpus lawrencei*, and the following year (Silba, 2010) he published an updated version of his 1984 checklist of *Podocarpus* in which 108 species were listed; this contained 39 new subspecific combinations, many of these being elevations to subspecies of varieties that he had described in earlier publications. Since then Silba has published a new species from New Caledonia (Silba, 2014).

Treatments of *Podocarpus* appeared in two compendia of the world's conifers, by Eckenwalder (2009) and Farjon (2010). These recognised 82 and 97 species respectively. Both represent reductions from the 107 species that had been accepted by Farjon (2001) and Eckenwalder's treatment with its sometimes incomprehensibly broad species concept recognises three fewer than the 85 that de Laubenfels had enumerated in his 1985 revision of the genus. Farjon (2010) lectotypified the names of several species for the first time and Farjon & Filer (2013) mapped all species of *Podocarpus* accepted by them as part of a larger atlas of the world's conifers.

Between 1996 and 2000, Bobrov and various Russian co-workers published a series of papers, mostly in obscure conference proceedings, on aspects of the systematics of various genera of Podocarpaceae, especially the smaller or more aberrant ones (Bobrov & Melikian, 1998b; Bobrov & Kostrikin, 1999), and particularly emphasising carpological characters. This work culminated in two papers (Bobrov & Melikian, 1998a; Melikian & Bobrov, 2000) outlining a new and radically different classification

of the family. In the earlier paper, *Podocarpus* subgen. *Foliolatus* was raised to generic rank as *Margbensonia* Bobrov & Melikian. Twenty new combinations were made, far fewer than would actually be required were this classification to become generally accepted. That, however, has not been the case, except in the later paper by Melikian & Bobrov (2000). *Margbensonia* was regarded as a synonym of *Podocarpus* by Farjon (2010) and by Christenhusz *et al.* (2011). In the paper by Melikian & Bobrov (2000), Podocarpaceae as circumscribed over the past 40 or so years was drastically carved up into 14 families spread over six orders. In their strict sense, the Podocarpaceae itself comprised only the four genera *Podocarpus*, *Margbensonia*, *Afrocarpus* and *Sundacarpus*. Subsequently Doweld (2001) modified this arrangement somewhat, bringing all genera of 'pre-Bobrov & Melikian' Podocarpaceae together again as the class Podocarpopsida, which was divided into four orders and twelve families, with one order and three families of those erected by Melikian & Bobrov (2000) being reduced to synonymy. Christenhusz *et al.* (2011) on the other hand regarded Podocarpaceae (in its usual circumscription, of 19 genera) and its sister family Araucariaceae as constituting the order Araucariales, which is the view accepted here.

*Podocarpus macrophyllus* in Japan has very recently been revised by Akiyama & Ohba (2012) with notes on typification. Also very recently, the new species *Podocarpus orarius* R.R.Mill & M.Whiting has been described from the Solomon Islands (Mill & Whiting, 2012), segregated from *P. spathoides* after careful work involving morphology and cuticle micromorphology, while A. D. Silba & J. A. de Silva [= John Silba: see table of contents of Silba & de Silva (2014)] have described three new taxa (Silba & de Silva, 2013a,b, 2014) that require critical evaluation before acceptance.

*Floristic works.* – Floristic treatments appeared for Costa Rica (de Laubenfels, 1991a; Merello, 2003), the Guianas (Stevenson & Zanoni, 1991), Ecuador (Stevenson, 1999), Colombia (Torres-Romero, 1988), Bolivia (Martín, 1993), Peru (de Laubenfels, 1991b, 1994; Brako & Zarucchi, 1993; Vicuña-Miñano, 2005), Chile (Marticorena & Rodríguez, 1995), Argentina (Covas, 1995), Australia (Stanley & Ross, 1989, Queensland; Harden, 1990, New South Wales; Hill, 1998, whole continent), New Zealand (Eagle, 2006), China (Fu *et al.*, 1999), Taiwan (Yang & Lu in Li & Keng, 1994), Cambodia, Laos and Vietnam (Hiệp & Vidal, 1996) and Japan (Yamazaki, 1995).

Enright & Ogden (1995) published an important book on the ecology of the conifers of the southern hemisphere whose chapters contain much on the ecology of *Podocarpus* species, while Hill & Brodribb (1999) published a now-classic paper documenting the history of the southern hemisphere conifers. Much more recently a volume (Turner & Cernusak, 2011) has appeared containing twelve papers, some of a seminal nature, on the ecology of podocarps in tropical forests. Many of these papers deal with aspects of the ecology of various tropical species of *Podocarpus*. However, much still remains at best poorly known and often unknown, particularly in less well known areas such as New Guinea, the Indonesian archipelago and New Caledonia and in areas such as animal/plant interactions and dispersal biology.

*Morphological and other studies.* – Macêdo & Leite (1999) studied the leaf anatomy of *Podocarpus lambertii* Klotzsch ex Endl. while that of *P. parlatoarei* was documented by del Fueyo (1988). Del Fueyo (1989) also studied the wood anatomy of *Podocarpus parlatoarei*, while the fungi associated with that species have been the subject of a long series of papers by Catania and co-workers (Catania, 2005; Catania & Romero, 2001, 2005, 2006, 2008, 2009, 2010a,b). This is the only species of the genus for which such detailed information on mycological associations is available.

Stoffberg (1991a,b) published a pair of papers in which she developed studies begun in her two earlier papers (published under the name of Schoonraad: Schoonraad & van der Schijff, 1974, 1975) already mentioned. In the first paper (Stoffberg, 1991a) she provided valuable information concerning the initiation of female strobili in *Podocarpus*. In the second paper (Stoffberg, 1991b) she gave details of the initiation of the seed scale complex primordium, the nucellus and integument, and the epimatium. She regarded the integument of gymnosperms as being homologous with the outer integument of a bitegmic angiospermous ovule, on account of the subdermal origin of both. In that paper she also pointed out that free bracts or foliola were sometimes developed in *Podocarpus latifolius* of subgenus *Podocarpus*, thus contradicting de Laubenfels (1985) who regarded possession of that feature as unique to the other subgenus, *Foliolatus*.

The first paper on the cuticle micromorphology of *Podocarpus* as revealed by scanning electron microscopy appeared (Stockey *et al.*, 1998). This followed a series of papers by Stockey and her co-workers that had dealt with several other genera of the family. Lavalley (2000) also studied the cuticles of some South American species but using light microscopy. Until very recently these were the only modern papers dealing with the cuticle of living *Podocarpus* species. However, a paper on the cuticle micromorphology of the Caribbean and Central American species has recently been published (Stark Schilling & Mill, 2011) while Whiting (2009) studied a wide variety of species.

Studies on the ultrastructure and biochemistry of the seeds of *Podocarpus henkelii* were conducted by Dodd *et al.* (1989a,b) as a follow-up to their 1981 paper alluded to in the previous section. The 'Gausson school' continued their studies on the seedling anatomy of Podocarpaceae (Rouane *et al.*, 1988; Woltz, 1988).

The reproductive biology and cytoplasmic inheritance of *Podocarpus totara* was carefully unravelled (Wilson & Owens, 1999, 2003) while more general aspects of Podocarpaceae reproduction were investigated by Tomlinson and co-workers (Tomlinson, 1992, 1994, 2000; Tomlinson & Takaso, 1998; Tomlinson *et al.*, 1991, 1997). Nuclear magnetic resonance imaging techniques were used by Masson *et al.* (2001) to investigate the internal structure of the receptacle and seed of *Podocarpus nivalis* non-invasively as part of a more wide-ranging programme of research investigating the use of NMR as a tool to examine the internal anatomy of various podocarp 'fruits' particularly species of *Afrocarpus* and *Prumnopitys*.

Cytological work included a paper by Hizume *et al.* (1988) that reported the presence of sex chromosomes in *Podocarpus macrophyllus*. Later, Davies *et al.* (1997)

studied the karyology of New Zealand species and Murray *et al.* (2002) used fluorescent *in situ* hybridisation techniques on *Podocarpus totara* and four closely related species, all belonging to *Podocarpus* sect. *Australis*. Zhou & Gu (2001) studied the karyomorphology of *Podocarpus* (including *Dacrycarpus* and *Nageia*) in China and found that the sections *Podocarpus*, *Nageia* and *Dacrycarpus* were each characterised by a different type of resting nucleus, so supporting their recognition as distinct genera. The three *Podocarpus* species investigated all had  $2n = 38$  but differed in the numbers of chromosome types (metacentrics, submetacentrics, subtelocentrics and telocentrics). Del Fueyo (1996, 1999) studied microsporogenesis, microgametogenesis and cone and ovule development in Argentinean species.

Abdillahi *et al.* (2010) published an important summary of the phytochemistry of Podocarpaceae and its relation to ethnobotany and pharmacology. Other phytochemical discoveries included the occurrence of anthocyanins with neohesperidose as the sugar unit, apparently unique to Podocarpaceae (Andersen, 1989). A major review of the podolactone compounds so widespread in the family appeared (Barrero *et al.*, 2003). This summarised the more than 70 such compounds that had been isolated from *Podocarpus* and related genera up until that time and their importance as biologically active compounds. There has also been renewed interest in the structure and functions of phytoecdysteroids and their potential applications as insecticides and in phytomedicine, with several recent important reviews (Dinan, 2001, 2009; Kubo, 2006; Dinan *et al.*, 2009; Lafont & Dinan, 2009; Fahrbach *et al.*, 2012) as well as a dedicated website, Ecdybase ([www.ecdybase.org](http://www.ecdybase.org); Lafont *et al.*, 2002 onwards).

Papers on the phylogenetics of the Podocarpaceae began to appear. The first was that by Kelch (1997) who performed an analysis based purely on morphological data. He quickly followed this up with one combining the morphological data with evidence from 18S rDNA (Kelch, 1998). In the latter study, only two species of *Podocarpus* were studied and these did not form a clade, rendering *Podocarpus* paraphyletic. Later studies by Conran *et al.* (2000) and Sinclair *et al.* (2002), however, sampled more species and in both sets of analyses *Podocarpus* was monophyletic with the two subgenera moderately to strongly supported. Muller *et al.* (2004) focused on the African species of *Podocarpus* and *Afrocarpus* while Su *et al.* (2004) performed a Bayesian analysis with rather low sampling within *Podocarpus*. Since 2011 three important papers on the molecular phylogenetics of Podocarpaceae have appeared (Biffin *et al.*, 2011, 2012; Knopf *et al.*, 2012). Biffin *et al.* (2011) sampled about 90 species of the family including 31 *Podocarpus* using two chloroplast genes (*matK* and *rbcL*) and nuclear ITS2, while the following year (Biffin *et al.*, 2012) they published a phylogenetic tree of Podocarpaceae based on an even larger sample (56 species), this time based on three chloroplast genome subunits, *rbcL*, partial *matK* and *trnL-F*. However, Biffin *et al.* (2012) did not discuss this phylogeny in detail since the paper in which it was published (as an electronic data supplement) was primarily concerned with leaf evolution in the family. In both their papers, and in that by Knopf *et al.* (2012), the two subgenera of *Podocarpus* formed robust clades. The sampling by Knopf *et al.* (2012) was still more comprehensive and covered 183 accessions of

145 taxa, 77 of which were species of *Podocarpus*. Their paper is the most definitive molecular phylogenetic analysis of *Podocarpus* to date.

Using *rbcL*, nr ITS1 (rather than ITS2 as in Biffin *et al.*, 2011) and the *NEEDLY* intron, they obtained a well-resolved topology that was supported by their analyses of morphology and leaf anatomy and was well correlated with geographical distribution. The paper by Knopf *et al.* (2012) was the only paper of these three to discuss the results obtained in a taxonomic context. Once again both subgenera were strongly supported, as were various smaller subclades within each. The composition of the subclades conflicted with the sectional classification of de Laubenfels (1985) in many cases. For example, the New Caledonian species, which de Laubenfels (1985) classified in four different sections of *Podocarpus* subgen. *Foliolatus*, formed a monophyletic group. Other unexpected apparent relationships were found in *Podocarpus* subgen. *Podocarpus*. These will be discussed in more detail in the taxonomic revisions.

Within the past few years, population genetics or phylogeographic techniques have been employed to unravel the phylogenetic history of particular species of *Podocarpus*. Examples include *Podocarpus matudae* Lundell (Ornelas *et al.*, 2010), *P. nubigenus* (Quiroga & Premoli, 2010), *P. parlatorei* (Quiroga & Premoli, 2007, 2013; Quiroga *et al.*, 2012), *P. salignus* (Allnutt *et al.*, 2001) and the *Podocarpus latifolius/milanjanus* species complex of tropical and southern Africa (Muller *et al.*, 2004). No similar studies appear yet to have been undertaken for any of the species of *Podocarpus* subgen. *Foliolatus* although our understanding of some of them (particularly *P. neriifolius* and the *P. macrophyllus/P. chinensis* complex in China and Japan) would benefit from them.

#### PLAN OF THE REVISION

As mentioned in the historical review above, the emerging consensus view from molecular phylogenetic studies is that although the two subgenera of *Podocarpus*, subgenera *Podocarpus* and *Foliolatus*, are strongly supported, the many sections delimited within them by de Laubenfels (1985) do not all withstand phylogenetic scrutiny. Consequently, this revision will adopt the subgenera but, initially, not the sections. Instead, species will be revised within geographic areas, with each part devoted to a single geographic area and the species in each part treated alphabetically. Rather than use political boundaries it has been decided to adopt the World Wildlife Fund's bioregional classification, in which the world is classified into a small number of large areas called bioregions which are then subdivided into 867 smaller subunits called ecoregions, arranged in 14 biomes. Although published accounts of these units in book form do not yet exist for the whole world, they do for South America (Dinerstein *et al.*, 1995), Africa (Burgess *et al.*, 2004) and the Indo-Pacific region (Wikramanayake *et al.*, 2000) and these together account for almost all of the areas of the world inhabited by species of *Podocarpus*.

*Podocarpus* subgen. *Podocarpus* will be revised first, then *Podocarpus* subgen. *Foliolatus*. The first part to appear will deal with the species of *Podocarpus* subgen.

*Podocarpus* of the Caribbean Islands. The next part will treat the species of Central America. Subsequent parts will deal with the remaining South American species, the African and Madagascan species, and the Australasian species of subgenus *Podocarpus*. The species of *Podocarpus* subgen. *Foliolatus* will then be revised. Broadly speaking, the later parts of the revision will deal with the species of New Caledonia, New Guinea, the rest of Malesia, and mainland Asia. Once all species have been revised, it will then be possible to construct a new sectional classification, which will be the subject of the final part. A small number of species occur in more than one bioregion (the most widely distributed species is *Podocarpus neriifolius* which in its current circumscription extends from Nepal to Fiji although that could change after revision). In such cases the species will be treated more than once, with description and specimen citations applicable to the area being covered. However, papers will as far as possible be structured to minimise such overlaps.

Each species account will contain, as well as synonymy, typification of accepted names and all synonyms, etymologies of the accepted name and all synonyms, a full description and citation of all specimens seen, and any taxonomic and/or nomenclatural notes, paragraphs summarising what is known about many aspects of the biology of the species. These include (in order): vernacular names (with countries where used indicated); a paragraph summarising key distinguishing features; and notes on phenology, distribution, bioregion(s) and ecoregion(s) where present, ecology (including habitat, altitude, and associated species), plant–plant interactions, mycological associations, plant–animal interactions, IUCN conservation status (the current assessment, or one proposed in the species account) and any uses.

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