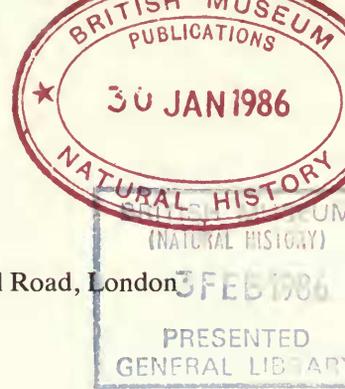


# A classification of the genus *Dryopteris* (Pteridophyta: Dryopteridaceae)

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## Synopsis

The history of the higher and infrageneric classification of *Dryopteris* is briefly discussed and followed by a new classification of the genus into four subgenera, two of which involve new states: *Erythrovariae* (H. Itô) Fraser-Jenkins and *Nephrocystis* (H. Itô) Fraser-Jenkins. Within the subgenera 16 sections are recognised, the following 11 being new: *Hirtipedes* Fraser-Jenkins, *Pandae* Fraser-Jenkins, *Remotae* Fraser-Jenkins, *Pallidae* Fraser-Jenkins, *Splendentes* Fraser-Jenkins, *Cinnamomeae* Fraser-Jenkins, *Marginatae* Fraser-Jenkins, *Aemulae* Fraser-Jenkins, *Politae* Fraser-Jenkins, *Variae* Fraser-Jenkins, and *Purpurascentes* Fraser-Jenkins. The world's species of *Dryopteris* (c. 225) are placed in the various sections and in connection with these a full list of synonyms is included. A list of 89 hybrids is also given. Two new combinations, *D. crassirhizoma* Nakai subsp. *whangshangensis* (Ching) Fraser-Jenkins and *D. goldiana*

(Hook.) A. Gray subsp. *monticola* (Makino) Fraser-Jenkins, are made and *D. reichsteinii* Fraser-Jenkins is a new name for *D. paleacea* var. *madagascariensis* C. Chr. The species *D. parrisiae* Fraser-Jenkins, *D. ruwenzoriensis* C. Chr., *D. subpyncopteroides* Ching ex Fraser-Jenkins, and *D. tingiensis* Ching & S. K. Wu ex Fraser-Jenkins are described.

### Higher classification and relationships of *Dryopteris*

Phyletic and cytogenetic details of *Dryopteris* and its relatives have been discussed in detail by Lovis (1977), who concludes that the genus is probably of dennstaedtioid origin, though the cytological evidence from the base number of 41 is not sufficient to resolve this question. Little fossil evidence for the origin of the dryopteroid ferns exists except for a tertiary fossil, *D. meeteetseana* R. W. Brown (see Lovis, 1977: 251). *Dryopteris* itself may well be of tertiary origin and appears to be relatively ancient, as may be deduced from the existence of a number of widely distinct subgenera within it.

The higher classification of the groups containing *Dryopteris* was set out by Pichi Sermolli (1973, 1977), and a brief survey is included here. In common with a great many other genera, members of the modern genus *Dryopteris* were at one time placed in the family Polypodiaceae which was a vast compendium of many different groups. By the beginning of the present century, the family group had been narrowed down to the Aspidiaceae Mett. ex Frank in the wide sense, which contained both the thelypteroid and aspidioid ferns, many of these being lumped together with *Dryopteris* species into the genera *Nephrodium* or *Lastrea*, or into *Dryopteris* itself. Christensen (1913a, 1920), in his monograph of tropical American *Dryopteris* (see also Christensen, 1938), was the first person to separate the thelypteroid and dryopteroid ferns, followed by Ching (1936, 1940, 1963), who proposed the family Thelypteridaceae, later validated by Pichi Sermolli (1970a). This was the situation at the time of publication of Copeland's *Genera Filicum* (1947), but subsequently Holtum (1947, 1949, 1968–1979), Holtum, Sen & Mitra (1970), and Holtum & Grimes (1980) have carried out much further work in separating and revising the Thelypteridaceae.

The Aspidiaceae, however, were still a large group by today's standards, containing many of the present families of the modern sub-order Aspidiineae, though some groups such as the Elaphoglossaceae and Athyriaceae were only more recently understood to be allied, the latter for example having been placed with the Aspleniaceae (see Sledge 1973a, though he did not recognise the athyrioid ferns as a family). Holtum (1947, 1949, 1960) gave details of the dryopteroid ferns, distinguishing them from other groups within the Aspidiaceae as the Dennstaedtiaceae subfamily Dryopteridoideae. Following the work of Ching (1940, 1965a, 1975), Alston (1956), and Pichi Sermolli (1968 & 1970a), the Aspidiaceae have today been further split so that the equivalent of the wider group is probably best treated as a suborder, the Aspidiineae, as mentioned above, consisting of nine families, the Onocleaceae Pichi-Serm. (1970a), Woodsiaceae (Diels) Herter (1949), Athyriaceae Alston (1956), Hypodematiaceae Ching (1975), Peranemataceae (C. Presl) Ching (1940) nom. cons. (and see Nayar & Kaur, 1966), Dryopteridaceae Ching (1965a), Aspidiaceae Mett. ex Frank (1877) nom. cons., Lomariopsidaceae Alston (1956) and Elaphoglossaceae Pichi-Serm. (1968); nomenclatural details of most of these are given by Pichi Sermolli (1970b). It should be pointed out, however, that a number of authorities prefer to treat the nine families as subfamilies of a family Aspidiaceae taken in the wide sense, in order that this should remain the equivalent of such wide families as the Aspleniaceae sens. lat., etc. Pichi Sermolli (1981) also gave details of a proposal, now accepted, to conserve the family name Aspidiaceae, which was illegitimate being based on the illegitimate name *Aspidium* Sw., a synonym of *Tectaria* Cav. The tectarioid ferns have no other family name and the name Aspidiaceae is therefore used for them in this paper (i.e. in the narrow sense).

In addition Pichi Sermolli proposed the conservation, now accepted, of the name Dryopteridaceae against the name Peranemataceae when the two are combined, and of the name Peranemataceae Ching against Peranemataceae Bütschli, giving details of its spelling which he corrects from '*Peranemaceae*', and showing that the name is illegitimate, whether used for the

fern family or the algal one. Previous details concerning the name Peranemaceae are given by Pichi Sermolli (1970*b*, 1977: 451). The name Peranemataceae is accordingly used here.

Within the modern Dryopteridaceae several modern genera had at one time been included under the name *Dryopteris*, but have subsequently been separated. In particular *Stigmatopteris* was separated by Christensen (1909, 1911*b*, 1913*a*, 1938) (see also Tryon & Tryon, 1981), *Lithostegia* and *Stenolepia* by Ching (1933) and van Alderwerelt van Rosenburgh (1909), *Lastreopsis* by Ching (1938) (and see Tindale, 1957, 1965), and the large and important genus *Ctenitis* by Christensen (1911*b*, 1920, 1934) and Tardieu-Blot & Christensen (1938), followed by Ching (1938), including the often confused *Ctenitis apiciflora* (Wallich ex Mett.) Ching group now placed in *Dryopsis* (Holttum, 1984). *Nothoperanema* was separated as a subgenus by Tagawa (1938), and as a genus by Ching (1966), while two genera often considered intermediate between *Dryopteris* and *Polystichum*, but closer to the latter, have been clarified as *Arachniodes* and *Leptorumohra* (see Ching, 1934, 1938, 1962; Itô, 1935*a* and *b*, 1939; Morton, 1960; Tindale 1961*a* and *b*; Widén et al., 1976, 1978, 1981).

An account of 34 dryopteridaceous genera (from *Nothoperanema* to *Rumohra*), with the Peranemataceae and Aspidiaceae sens. str., under the name Aspidiaceae, is given by Pichi Sermolli (1977), though Holttum (1984) presents a different view. Pichi Sermolli included *Rumohra* as an aspidiaceous fern, a viewpoint which the author tentatively accepts, though it has recently been considered a davallioid fern and thus not related to *Arachniodes*, most of the species of which were once placed in *Rumohra*. The name *Arachniodes* is retained here pending further investigation to determine whether or not the type of the earlier described monotypic genus *Rumohra*, *R. aspidioides* Raddi (= *R. adiantiformis* (G. Forster) Ching), belongs to the same genus as *Arachniodes* species; its present separation, mainly on the basis of its markedly creeping, 'davallioid' rhizome, perhaps being artificial and incorrect; a long, creeping rhizome occurs in some *Arachniodes* species too, which deserves anatomical study (by contrast, see Holttum, 1984).

*Dryopteris* itself in the modern sense has close relationships with several genera and is sometimes not clearly separable from them by definition alone. This is a problem that often affects the delineation of genera or subgenera and too many authors tend to stick rigidly to certain normally characteristic features as the only way to separate species into genera, rather than allowing exceptions in order to follow a more natural arrangement which is usually more workable. These ranks are often more naturally defined by reference to the species groups within them, and the necessity for a description is often allowed to upset generic boundaries unnecessarily. Sledge (1973*a*) has pointed out that the borderline between *Dryopteris* and *Arachniodes* needs further consideration and (1973*b*) has revised several species that had been treated by Ching (1938) according to strict rules based on rigid morphological marker characteristics; much of the difficulty in the past having been caused by members of *Dryopteris* subgenus *Nephrocystis* being placed partly in *Arachniodes*. It is not difficult to make a natural division between the two genera, but nevertheless they are somewhat close, though *Arachniodes* is far more closely related to *Polystichum*, the latter being further removed from *Dryopteris*.

*Arachniodes* and most of the polystichoid genera share an important feature not found in *Dryopteris*: the apices of the segments and of their basal acroscopic side-lobes, when present, end in an acute point bearing a single stiff, 'cartilaginous' tooth. Although some slight exceptions occur in *Polystichum*, this appears to be a fundamental morphological distinction between the two groups, probably even more so than the presence of a peltate indusium in *Polystichum*, while there is a more or less reniform one in *Dryopteris* and *Arachniodes*. Indeed in *Arachniodes* both indusial conditions occur. *Arachniodes* and most of the species of *Polystichum* also have a markedly more stiffly coriaceous lamina and teeth in contrast to *Dryopteris*, though not surprisingly some exceptions occur and *Arachniodes* species frequently have a creeping rhizome, rare in *Dryopteris*. Members of the genus *Arachniodes* and of the genus *Dryopteris* are readily separable from each other with little difficulty, which emphasises the natural and useful division of the two genera, and the view (e.g. Tryon & Tryon, 1982*b*) that *Arachniodes* should be sunk into *Dryopteris* is certainly unjustified unless *Dryopteris*, *Arachniodes*, *Polystichum*, etc. are all combined, which would be even more impracticable. Tryon &

Tryon (1982*a* and *b*) did not correctly distinguish between polystichoid and dryopteroid ferns when placing the clearly polystichoid genus (as pointed out by Ching, 1965*b*) *Phanerophlebiopsis* Ching into their subgenus *Dryopteris* in error. Indeed, their work contains no mention of the important groups of species within the genera concerned and it should be noted that the vast majority of species of *Arachniodes* are Asiatic and cover a range of form far wider than that found in the American species more familiar to them. They also state that *Dryopteris* and *Arachniodes* combined contain only about 150 species.

*Dryopteris* subgenus *Nephrocystis* (including the genus *Acrorumohra*) is recognised here as representing a discrete transition group towards *Leptorumohra* and *Nothoperanema*, while the subgenus *Erythrovariae*, which may be a more primitive group than subgenus *Dryopteris*, shows some similarities in frond morphology to *Ctenitis*. Subgenus *Erythrovariae* also has some members (section *Variae*) which appear superficially to be distantly related to *Arachniodes*. Some useful information on the genus *Arachniodes*, on its chemistry, and the presence or absence of glands in some of the species nearer the borderline between it and *Dryopteris*, is to be found in Widén, Sarvela & Iwatsuki (1976), Widén, Huure, Sarvela & Iwatsuki (1978), and Widén, Mitsuta & Iwatsuki (1981), though the taxonomic position of the subgenus *Nephrocystis* is not fully brought out. Clearly the relationships between all these groups are complex and reticulate.

### Classification within *Dryopteris*

*Dryopteris* is a large and widespread genus which, not surprisingly, displays a considerable range of form, and contains several rather distinct groups, here treated as four subgenera. Within three of the subgenera there are several sections, particularly in the subgenus *Dryopteris*. The sections are less clear-cut groups of species than the subgenera and often have obvious multidirectional relationships, though still being generally recognisable as groups. A complication that often occurs is the existence of an allopolyploid species derived from two different sections, which has to be assigned to one section or the other, usually somewhat artificially by following the definition of the section, but this does not make the sections any less valid. One of the sections, the *Remotae*, is an artificial one necessary because the ancestral diploid species of the allopolyploid species concerned belong to sections so remote from each other that the resultant species cannot be placed in one or the other section as they have a quite distinct type of 'mixed' morphology unlike either parent. The sections represent natural groups of related species and are more readily defined by means of the groups of species within them than by overall descriptions of the section, which become artificial and often slightly misleading. General descriptions are given but these are necessarily somewhat vague as each contains a wide range of form. It is emphasised that the author attaches by far the more importance to the groupings of species than the sectional descriptions.

Two previous major classifications of *Dryopteris* have been published, Itô (1935*a*, 1936*a*, *b*, *c*, 1939) and Ching (1938), neither of whom were familiar with species on a world-wide scale and whose classifications were based mainly on the species from their own species-rich study areas. Itô dealt with the dryopteroid ferns of Japan and Taiwan and (1936*a*) was the first person to separate *Erythrovariae* as a section. He also (1935*a*) separated *Nephrocystis* as a section of *Dryopteris*, though he immediately afterwards (1935*b*) recognised some species which belong to *Nephrocystis* as the section *Acrorumohra* of the genus *Rumohra* (*Arachniodes*) and later (1939) raised that section to a genus, *Acrorumohra* (H. Itô) H. Itô, which is not recognised here. He also (1939) published a superfluous name, section *Polysticho-drys*, for the *Erythrovariae*. His other sections were less meaningful and were somewhat artificially separated, though some of his subsections correspond at least partially to sections in the present treatment once discordant elements have been removed. Ching's work dealt with the Himalayan species with emphasis on some of the species from south-west China and the east Himalaya in the Indian subcontinent and with reference to additional species in the west Himalaya, south India, and Sri Lanka. It was the first treatment to deal adequately with the subgenus *Pycnopteris* and he also recognised, independently of Itô, the distinction between what he called the sections *Fibrillosae* and

*Bulligerae*, now the equivalent, with some modifications, of the subgenera *Dryopteris* (with its section *Fibrillosae*) and *Erythrovariae* respectively. His treatment, however, did not deal adequately with the subgenus *Nephrocystis*, some members of which he (1964), like Itô, placed in the genus *Acrorumohra*. Ching's 'groups' below his sections, though generally the equivalent of some of the present sections, often contained several discordant elements and were not clear-cut.

The present scheme attempts to place most of the world's *Dryopteris* species and distinguishes more clearly between the major groups as subgenera and the more minor ones as sections; it has involved a reappraisal of the genus world-wide and it is hoped that it is a more natural classification than has previously been produced. Species have been placed in the groups with more emphasis on natural relationships than on rigid adherence to key characteristics, which had previously caused some discordant anomalies. However, it is pertinent to point out here that the author is not as familiar with species from the neotropics, Hawaii, and the Australasian islands as with those from elsewhere. In particular, it has been necessary to obtain help with the species from the neotropical region, which has been most willingly supplied by A. R. Smith of the University of California, Berkeley, though his opinion has not been followed in its entirety. H. Hirabayashi has kindly commented on the Japanese species of subgenus *Erythrovariae*, though I have modified his comments to incorporate work on China. A synopsis of the classification is given below, the details appearing in sequence in the systematic descriptions that follow.

#### *Dryopteris* Adans.

Subgenus 1. *Pycnopteris* (T. Moore) Ching

Subgenus 2. *Dryopteris*

Section 1. *Hirtipedes* Fraser-Jenkins

Section 2. *Fibrillosae* Ching

Section 3. *Pandae* Fraser-Jenkins

Section 4. *Dryopteris*

Section 5. *Remotae* Fraser-Jenkins

Section 6. *Pallidae* Fraser-Jenkins

Section 7. *Splendentes* Fraser-Jenkins

Section 8. *Cinnamomeae* Fraser-Jenkins

Section 9. *Marginatae* Fraser-Jenkins

Section 10. *Aemulae* Fraser-Jenkins

Section 11. *Lophodium* (Newman) C. Chr. ex H. Itô

Subgenus 3. *Erythrovariae* (H. Itô) Fraser-Jenkins

Section 1. *Erythrovariae*

Section 2. *Politae* Fraser-Jenkins

Section 3. *Variae* Fraser-Jenkins

Subgenus 4. *Nephrocystis* (H. Itô) Fraser-Jenkins

Section 1. *Purpurascens* Fraser-Jenkins

Section 2. *Nephrocystis*

## Taxonomy

*Dryopteris* Adans., *Fam. pl.* 2: 20, 551 (1763), nom. cons.

*Psidopodium* Necker, *Elem. bot.* 3: 315 (1790) (fide Christensen, 1906: 590).

*Nephrodium* Rich. in Marthe, *Cat. pl. jard. méd. Paris*: 120 (1801), nom. nud. (Art. 32.1).

*Nephrodium* Rich. in Marthe ex Michaux, *Fl. bor.-amer.* 2: 266 (1803). Lectotype (Pichi Sermolli 1977b):

*Nephrodium marginale* (L.) Michaux (= *Dryopteris marginalis* (L.) A. Gray).

*Arthrobotrys* Wallich, *Num. List*: no. 395, 1034 (1828), nom. nud. (Art. 32.1), represented by *Arthrobotrys macrocarpa* Wallich, nom. nud. (Art. 32.1) (= *Dryopteris cochleata* (Buch.-Ham. ex D. Don) C. Chr.).

*Lophodium* Newman in *Phytologist* 4: 371, app. 16 (1851). Lectotype: *Lophodium multiflorum* (Roth) Newman (= *Dryopteris dilatata* (Hoffm.) A. Gray).

*Dichasium* (A. Braun) Fée, *Mém. foug.* 5: 302 (1852). Lectotype: *Aspidium patentissimum* (Wallich ex Kunze) Franchet (= *Dryopteris wallichiana* (Sprengel) N. Hylander).

*Pycnopteris* T. Moore in *Gdnrs' Chron.* 1855: 468 (1855). Type: *Pycnopteris sieboldii* (Van Houtte ex Mett.) T. Moore (= *Dryopteris sieboldii* (Van Houtte ex Mett.) Kuntze).

*Diclisodon* T. Moore, *Index fil.*: 95 (1857). Type: *Diclisodon deparioides* T. Moore (= *Dryopteris deparioides* (T. Moore) Kuntze).

*Acrorumohra* (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 101 (1939 ['1938']).

Misapplied names: *Polypodium* L., *Polystichum* Roth, *Aspidium* Sw., *Lastrea* Bory, *Rumohra* Raddi, *Phegopteris* Fée, *Polystichopsis* (J. Smith) Holttum, *Arachniodes* Blume, *Byrsopteris* C. Morton.

Type: *Polypodium filix-mas* L. (= *Dryopteris filix-mas* (L.) Schott).

Rhizome normally terrestrial, more or less thick, creeping below but usually with an upright or ascendent apex, closely surrounded by spirally arranged old leaf-bases, rarely becoming elongated so that the leaf-bases are widely separated, often branching, bearing narrow scales at the apex. Fronds usually somewhat large, once to four times pinnate (rarely five times pinnate), may bear glands or hair-like scales (fibrils) but not hairs; stipe and often rachis, costae, etc. bearing scales and often densely scaly; stipe with a ring of several (more than two) separate vascular strands inside it and bearing a deep groove along its upper surface which is continuous with that on the rachis, rachis groove continuous with those on the pinna-costae; lamina herbaceous or somewhat coriaceous, may bear glands or hair-like scales (fibrils) but not hairs, arrangement of (lower) pinnulets usually but not always catadromous; costae and costules canaliculated above and arising from the rachis at a more or less acute angle, the channels being continuous between them; veins in the segments free, simple or pinnate, terminating in small but slightly enlarged vein-endings lying just inside the segment margin; segment base symmetrical or asymmetrical, but though occasionally slightly bluntly auriculate on the acroscopic side, does not bear a marked deltate and pointed auricle ending in a single long-acute or aristate tooth; segment margins frequently toothed, particularly at their apices, but the apex, though often acute, does not end in a single long-acute or aristate tooth at the tip; the teeth range from obtuse crenations to aristate or hair-pointed ones. Sori borne on either side of the pinna-, pinnule-, or ultimate segment-midribs, separate, circular, borne dorsally or rarely apically on the veins, normally indusiate; indusium attached centrally to the receptacle in the middle of the sorus, more or less large, thick or thin, persistent, or shrivelling and deciduous, rounded or cordate, with a deep, narrow sinus at one side reaching in to the point of attachment, thus becoming near to reniform in shape, margins entire or fimbriate, flat or curved down around the sorus. Spores bilateral, perisporate. Base chromosome number 41. Species often polyploid and frequently apomictic, though in the subgenus *Dryopteris* apomixis is mainly but not entirely associated with the presence of genomes from the sections *Hirtipedes* and *Fibrillosae*, or else is frequent in the subgenus *Erythrovariae*. Some further details of *Dryopteris* frond morphology are given by Serizawa (1974, 1976), including details of glands, etc.

*Dryopteris* is a large genus of about 225 species, though others presumably exist in complexes such as the *D. sparsa* and *D. inaequalis* groups which have yet to be elucidated, and probably also in the section *Cinnamomeae* in the neotropics (Smith, 1981 pers. comm.), and doubtless in other groups elsewhere. They largely occupy the forest or sometimes rocky and alpine zones of northern temperate or sub-temperate latitudes, or otherwise subtropical and tropical montane regions. Some species also occur in southern temperate regions, having either spread from the north, or with their nearest relatives in the north. Copeland (1947) has suggested a southern origin for all the modern fern genera, but though this could conceivably be possible for *Dryopteris*, there is no clear evidence. Its centre of distribution and diversity is in south-west China and the east Himalaya, with another centre about Japan (including south-east and south China) and centres of secondary importance in Taiwan, the west Himalaya, south-east Asia and the Australasian/Pacific islands, south India and Sri Lanka, East Africa and Madagascar, Europe (including Macaronesia, west Asia and west and central Siberia), eastern North America and finally Central America and western South America. Species of *Dryopteris* are present in all the continents except Antarctica, though they become scarce in Australasia and

Oceania (17 species) and only one species occurs naturally in mainland Australia, being a south-east Asian element (two extra species are introduced in New Zealand).

The approximate numbers of species from different areas are given below, though it should be noted that only in North America, Europe (in the wide sense), Japan, and the Indian subcontinent has the genus been carefully elucidated according to modern systematic principles. However, the author has been able to make a preliminary study of species from China in Chinese and European herbaria. It should be noted that the figures for endemic species are not so meaningful from the areas in Asia mentioned below as they would be if the natural floristic areas were to be considered, for example, south and south-west China combined with the Indo-Himalaya forms one floristic area, and Japan with east China forms another. If the numbers from the natural floristic areas are considered, the numbers of endemic species increase markedly. North America (U.S.A. and Canada): 16 species (6 endemic). Central and South America (including Easter Island): 15 species (1 introduced, 10 endemic). South Atlantic islands: 4 species (3 endemic). Europe (sens. lat., including north-west Africa, Cape Verde Islands, Macaronesia, western Asia (to Iran), Soviet central Asia and Siberia, east to Irkutsk): 26 species (18 endemic). Africa (including Madagascar, Mascarenes, Seychelles, and south Indian Ocean islands but excluding north-west Africa): 22 species (21 endemic). South Arabia: 1 species (0 endemic). Indian subcontinent: 57 species (13 endemic). China (excluding Taiwan), Tibet, and Mongolia: 103 species (18 endemic). Taiwan: 40 species (3 endemic). Korea: 27 species (3 endemic). Japan: 59 species (12 endemic). Far east Siberia: 8 species (0 endemic). South-east Asia (including the Philippines but excluding Burma): 31 species (1 endemic). Burma: unknown. Australasian and Pacific isles (excluding Hawaii, South America, and Easter Island): 20 species (9 endemic). Australian mainland and New Zealand: 3 species (2 introduced, 0 endemic). Hawaii: 10 species (9 endemic).

**Subgenus 1. Pycnopteris** (T. Moore) Ching in *Bull. Fan meml Inst. Biol. (Bot.)* 8: 365–396 (1938).

*Pycnopteris* T. Moore in *Gdnrs' Chron.* 1855: 468 (1855).

*Dryopteris* group *Pycnopteris* (T. Moore) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).

*Dryopteris* section *Eudryopteris* subsection *Pycnopteris* (T. Moore) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 25 (1939 [‘1938’]).

Type: *Pycnopteris sieboldii* T. Moore (= *Dryopteris sieboldii* (Van Houtte ex Mett.) Kuntze).

Morphology as in subgenus *Dryopteris* except for the fronds being imparipinnate (i.e. with the frond apex ending in a segment similar to one of the lateral pinnae), and only once pinnate, not becoming nearly bipinnatifid, though the pinnae may be shallowly and irregularly lobed. All the species have fronds of a hard-coriaceous texture, harder than those of the other subgenera. One species is exindusiate.

Contains c. four species, confined to eastern Asia: *D. sieboldii* (Van Houtte ex Mett.) Kuntze, *D. pseudosieboldii* Hayata, *D. bodinieri* (Christ) C. Chr., and *D. podophylla* (Hook.) Kuntze\*.

## Subgenus 2. *Dryopteris*

*Lastrea* subgenus *Arthrobotrys* Wallich ex C. Presl, *Tent. pterid.*: 77 (1836).

*Dryopteris* subgenus *Eudryopteris* C. Chr., *Index filic.*: 250 (1905), nom. inval. (Art. 21.3).

*Dryopteris* subgenus *Eudryopteris* C. Chr., *Biol. Arbejd. tileg. Eug. Warming*: 76 (1911), nom. inval. (Art. 21.3).

Type: *Polypodium filix-mas* L. (= *Dryopteris filix-mas* (L.) Schott).

Fronds varying from once to nearly four times pinnate, not imparipinnate, but pinnae gradually reduced to a pinnatifid apex. Stipe and rachis well supplied with scales which are often present

\* The species listed are arranged in a taxonomic order, normally from the least to the most dissect, but taking account of closely related groups. A question-mark (?) denotes a species of doubtful status, requiring further investigation or confirmation.

on the pinna-costae too, at least some scales near the stipe base somewhat wide; scales on the underside of the pinna-costae (as elsewhere) not bullate; lamina coriaceous or lax, but not hard-coriaceous; pinna segments usually more or less symmetrical about their axes and not sloping or auriculate at their acroscopic bases except in a few cases (mostly in the sections *Splendentes* and *Cinnamomeae* with a few examples in the *Pallidae* and *Marginatae*).

Throughout the range of the genus and the only subgenus present in Europe and most of North and South America and Africa.

### Section 1. *Hirtipedes* Fraser-Jenkins, sect. nov.

*Dryopteris* section *Eudryopteris* subsection *Cycadinae* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 19 (1939 [1938]).

Frondes unipinnatae, sed pinnis usque ad medium saepe lobatis.

Type: *Dryopteris hirtipes* (Blume) Kuntze.

Morphology as in section *Dryopteris* except for the fronds being only once pinnate and the pinnae only shallowly lobed or lobed up to half their depth on each side; rarely the lowest basicopic pinna-lobe of the lowest pinnae may become fully separated. Stipe scales narrower than in section *Dryopteris* and, like those of section *Fibrillosae*, usually mostly linear-lanceolate. Several of the species are apomictic. This section is probably distantly related to subgenus *Pycnopteris* and is similar in having shallowly lobed pinnae, though the lobes are somewhat more regular in section *Hirtipedes*; it also shows clear similarities to section *Fibrillosae* and some similarities to the simply pinnate members of subgenus *Erythrovariae*. Two species are exindusiate.

Contains c. 17 species confined to south and eastern Asia and the Australasian and Pacific isles: *D. liankwangensis* Ching, *D. scottii* (Beddome) Ching, *D. hirtipes* (Blume) Kuntze and subspp., ? *D. fatuhivensis* E. Brown, *D. commixta* Tag., *D. darjeelingensis* Fraser-Jenkins in press, *D. cycadina* (Franchet & P. A. L. Savat.) C. Chr., *D. hangchowensis* Ching, *D. stenolepis* (Baker) C. Chr., *D. handeliana* C. Chr., *D. namegatae* Kurata, *D. dickinsii* (Franchet & P. A. L. Savat.) C. Chr., *D. pycnopteroides* (Christ) C. Chr., *D. subpycnopteroides* Ching ex Fraser-Jenkins, *D. microlepis* (Baker) Ching, *D. lunanensis* (Christ) C. Chr., and *D. conjugata* Ching.

### Section 2. *Fibrillosae* Ching in *Bull. Fan meml Inst. Biol.* (Bot.) 8: 366 (1938).

*Aspidium* subgenus *Dichasium* A. Braun in *Flora, Jena* 24: 710 (1841).

*Dichasium* (A. Braun) Fée, *Mém. foug.* 5: 302 (1852).

*Dryopteris* section *Eudryopteris* subsection *Dichasium* (A. Braun) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 6 (1939 [1938]).

Type: *Dryopteris fibrillosa* (C. B. Clarke) Hand.-Mazz., non (Baker) C. Chr. (= *D. pulcherrima* Ching).

Morphology exactly as in section *Hirtipedes* except for the pinnae being very nearly twice pinnate as the pinna-lobes are cut down nearly to the pinna-costa, leaving them connected only by a very narrow wing of tissue. Some of those at the bases of the lowest few pairs of pinnae may become fully separated into pinnules. Similar to section *Dryopteris* in the fronds being more or less linear-lanceolate, though slightly narrower at the base, but the pinna-lobes are normally markedly regular, parallel-sided, and untoothed at the sides and are either unlobed or more or less shallowly lobed, the side-lobes being rectangular; the lobe-apices have a far more marked tendency to be truncate or rounded-truncate and bear shorter teeth. Differs from section *Dryopteris* in having the lamina more or less coriaceous, somewhat dark-green (often yellowish or pinkish when young) and glossy above, and the stipe and rachis more densely clothed with narrowly lanceolate scales; dense hair-like scales (fibrillae) are also present on the rachis and are often present on the lamina. The indusia are thicker and turned down or inflected at the edges, at least in the early stages, and are more persistent. Most of the species are apomictic.

Members of this section were previously often referred to the *D. filix-mas* group as a result of

early European botanists not distinguishing *D. affinis* (in the present section) from *D. filix-mas*, but it is a markedly distinct section, probably related to the section *Hirtipedes*.

Contains *c.* 21 species, throughout most of the range of the genus except for North America, rare in Africa and only one introduced species in Australasia (New Zealand). Many of the species are apparently derived from *D. wallichiana* or its relatives by hybridisation with a sexual diploid species to form a new species (see also section *Remotae*). Being apomictic, several of the species are markedly variable and may have been divided into unwarranted species by various authors, but it is also possible that further new species may yet be recognised that are at present included in other species. To the section belong *D. parrisiae* Fraser-Jenkins, *D. pulcherrima* Ching., *D. polylepis* (Franchet & P. A. L. Savat.) C. Chr., *D. crassirhizoma* Nakai and subsp. **whangshangensis** (Ching) Fraser-Jenkins **comb. nov.** (basionym: *Dryopteris whangshangensis* Ching in *Bull. Fan meml Inst. Biol. (Bot.)* 8: 421 (1938)), *D. neorosthornii* Ching, *D. redactopinnata* Panigr. & S. K. Basu, *D. rosthornii* (Diels) C. Chr., *D. yigongensis* Ching, *D. acuto-dentata* Ching, *D. incisolobata* Ching & S. K. Wu, *D. wallichiana* (Sprenkel) N. Hylander, ***D. reichsteinii*** Fraser-Jenkins **nom. et stat. nov.** (*D. paleacea* var. *madagascariensis* C. Chr. in *Dansk bot. Ark.* 7: 53 [1932]; type: Madagascar, Mt Tsaratanana, 2400 m, April 1924, *Perrier* 16454 [P!]), *D. chrysocarpa* (Fée) Rothm., *D. affinis* (Lowe) Fraser-Jenkins and subsp., *D. madrasensis* Fraser-Jenkins in press, *D. fusco-atra* (Hillebrand) W. Robinson, *D. lepidopoda* Hayata, *D. sledgei* Fraser-Jenkins in press, *D. pseudo-filix-mas* (Fée) Rothm., *D. khullarii* Fraser-Jenkins in press, and *D. hawaiiensis* (Hillebrand) W. Robinson.

### Section 3. *Pandae* Fraser-Jenkins, **sect. nov.**

*Lastrea* subgenus *Arthrobotrys* Wallich ex C. Presl, *Tent. pterid.*: 77 (1836).

Frondes unipinnatae vel bipinnatae; pinnae herbaceae, haud nitidae, marginibus loborum non parallelis.

Stipes non dense paleaceus.

Type: *Dryopteris panda* (C. B. Clarke) Christ.

Similar to section *Dryopteris* in having more or less linear-lanceolate or lanceolate fronds which are once pinnate, but become twice pinnate as the pinna-lobes may be cut down very nearly to the pinna-costae; some of those at the bases of the pinnae may become fully separated into pinnules, but the connecting wing of tissue between pinnules, when present, is usually slightly wider. As in section *Dryopteris* the lobes or pinnules are only slightly, not markedly, parallel-sided and are either unlobed or more or less shallowly lobed, with side-lobes (when present) not markedly rectangular, in contrast to section *Fibrillosae*. Lamina either thin as in section *Dryopteris*, or somewhat thickly herbaceous and almost very slightly succulent and easily snapped, not coriaceous in texture; pale-green and not glossy above, in contrast to section *Fibrillosae*. Stipe and rachis usually less densely clothed in scales than in sections *Fibrillosae* and *Dryopteris* and lamina more or less devoid of scales or with only a very few. Sori in most species markedly larger than in other sections, with a thick or thin, usually tall indusium which is usually (but not always) curved down at the sides and in some species is inflexed and may not lift even on sporangial maturity. Spores often larger than in other sections (at the diploid level) and often uniquely reddish or chestnut brown under the light microscope.

Contains *c.* 17 species, throughout the range of the genus in the northern hemisphere: *D. ludoviciana* (Kunze) Small, *D. tokyoensis* (Matsum. & Makino) C. Chr., *D. habaensis* Ching, *D. panda* (C. B. Clarke) Christ, *D. bonatiana* (Brause) Fraser-Jenkins in press, *D. costalisora* Tag., *D. woodsii* Hayata, *D. austro-indica* Fraser-Jenkins in press, *D. chrysocoma* (Christ) C. Chr., ? *D. para-chrysocoma* Ching & Z. R. Wang in press, *D. fangii* Ching, Fraser-Jenkins & Z. R. Wang in press, *D. zinongii* Z. R. Wang & Fraser-Jenkins in press, *D. himachalensis* Fraser-Jenkins in press, *D. nobilis* Ching, *D. cristata* (L.) A. Gray, *D. clintoniana* (D. Eaton) Dowell, and *D. celsa* (W. Palmer) Small.

### Section 4. *Dryopteris*

*Aspidium* group *Filix-mas* Christ, *Farnkr. Erde*: 256 (1897), nom. nud. (Art. 32.1).

*Aspidium* group *Fragrantia* Christ, *Farnkr. Erde*: 260 (1897), nom. nud. (Art. 32.1).

*Dryopteris* group *Filix mas* C. Chr., *Index filic.*: XXI (1905), nom. nud. (Art. 32.1).

*Dryopteris* section *Eudryopteris* (C. Chr.) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 5 (1939[‘1938’]), nom. inval. (Art. 21.3).

*Dryopteris* section *Eudryopteris* subsection *Monticolarum* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 23 (1939 [‘1938’]).

*Dryopteris* section *Lophodium* subsection *Fragrantes* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 71 (1939 [‘1938’]).

Type: *Dryopteris filix-mas* (L.) Schott.

Fronds linear-lanceolate to lanceolate, twice pinnate, the pinnules widely attached to the costae except at the bases of the lower pinnae. Pinnules slightly but not markedly parallel-sided, usually somewhat tapering to their apices from about two-thirds of their length, toothed at the sides and markedly so at their apices, with long acute teeth, usually shallowly lobed with pointed side-lobes. Lamina matt and herbaceous, neither coriaceous nor glossy, stipe and rachis sparsely or somewhat densely clothed with scales, scales mostly lanceolate or ovate-lanceolate, though narrow ones also occur, including hair-like ones (fibrils) on the lamina in some species. Sori indusiate, with a thin or somewhat thick indusium which is flat or curved down at the edges, lifting and shrivelling on ripening. Several species are somewhat densely glandular on the costae.

Contains *c.* 15 species, throughout the range of the genus but absent from south-east Asia and Australasia (apart from *D. filix-mas* introduced in New Zealand) and most of Africa and South America: *D. sichotensis* V. Komarov\*, *D. oreades* Fomin, *D. fragrans* (L.) Schott, *D. barbiger*a (T. Moore ex Hook.) Kuntze and subsp., *D. tingiensis* Ching & S. K. Wu ex Fraser-Jenkins, *D. alpestris* Tag., *D. serrato-dentata* (Beddome) Hayata, *D. villarii* (Bellardi) Woyнар ex Schinz & Thell., *D. mindshelkensis* Pavlov†, *D. tyrrhena* Fraser-Jenkins & Reichst., *D. ardechensis* Fraser-Jenkins, *D. filix-mas* (L.) Schott, *D. caucasica* (A. Braun) Fraser-Jenkins & Corley, *D. montigena* Ching, and *D. goldiana* (Hook.) A. Gray and subsp. **monticola** (Makino) Fraser-Jenkins **comb. nov.** (basonym: *Nephrodium monticola* Makino in *Bot. Mag., Tokyo* 13: 80 (1899)).

### Section 5. *Remotae* Fraser-Jenkins, **sect. nov.**

Frondes bipinnatae, anguste lanceolatae; stipes rhachisque aliquantum dense paleacei. Pinnulae in parte inferiora frondis profunde lobatae sed in parte superiora fere non lobatae; lobi rectangulari.

Type: *Dryopteris remota* (A. Braun ex Doell) Druce.

Similar to section *Dryopteris* except that the fronds are lanceolate to very narrowly triangular-lanceolate (i.e. wider at the base), and the pinnules are more narrowly attached to the costa at the bases of the pinnae and are markedly more deeply lobed in the lower part of the frond. The pinnule-lobes are rectangular and the indusia somewhat thick as in section *Fibrillosae*.

This section contains presumed allopolyploid species whose presumed origin is by hybridisation between species from such widely different sections (e.g. *Fibrillosae* and *Lophodium* or *Marginatae*) that their morphology does not fit in any section and they have had to be referred to an artificial section of their own.

Contains *c.* three species, in Europe and the Sino-Himalayan region: *D. remota* (A. Braun ex Doell) Druce, non Hayata, *D. blanfordii* (C. Hope) C. Chr. and subsp., and *D. corleyi* Fraser-Jenkins.

### Section 6. *Pallidae* Fraser-Jenkins, **sect. nov.**

Frondes anguste triangulari-lanceolatae, bipinnatae. Pinnulae in dimidio inferiore pinnae stipitatae, in parte superiore adnatae.

Type: *Dryopteris pallida* (Bory) C. Chr. ex Maire & Petitm.

\* Formerly considered by Fraser-Jenkins & Corley (1973) to be synonymous with *Dryopteris oreades* (under the names *D. coreano-montana* Nakai and *D. abbreviata* (DC.) Newman), but now reinstated as a distinct species related to *D. oreades*.

† Formerly reduced by Fraser-Jenkins (*Candollea* 32: 305–319 (1977)) to a subspecies of *D. villarii*, but now reinstated as a species close to the latter.

Similar to section *Dryopteris* except that the fronds are markedly wider at their bases, being  $\pm$  narrowly triangular-lanceolate, and the pinnules are stalked, or with narrow bases up to about half way up the pinna and are more or less parallel-sided with rounded or more pointed apices, usually bearing somewhat wider-based acute teeth, lobed or unlobed at the sides. Lamina often slightly more crispaceous. The stipe is much longer and well-clothed with more ovate-lanceolate and more glossy scales, scaly only at the base, scales usually becoming more scattered than in section *Dryopteris* or absent further up, and with very much fewer or no fibrillae. Indusia small but slightly thicker than in section *Dryopteris*, usually curved down at the edges, but not tightly enclosing the sorus. As in section *Dryopteris* several species are somewhat densely glandular on the costae. Several of the species are apomictic.

Contains c. 17 species, throughout the range of the genus except South America, Africa (but present in western North Africa), south-east Asia, Australasia, north Europe and north Asia: *D. marginalis* (L.) A. Gray, *D. sericea* C. Chr., *D. peninsulae* Kitagawa, *D. lacera* (Thunb.) Kuntze, *D. uniformis* (Makino) Makino, *D. sublacera* Christ, *D. basisora* Christ, *D. odontoloma* (Beddome) C. Chr., *D. juxtaposita* Christ, *D. nigropaleacea* (Fraser-Jenkins) Fraser-Jenkins, *D. pallida* (Bory) C. Chr. ex Maire & Petitm. and subsp., *D. submontana* (Fraser-Jenkins & Jermy) Fraser-Jenkins, *D. arguta* (Kaulf.) Watt, *D. aitoniana* Pichi-Serm., *D. stewartii* Fraser-Jenkins, *D. lachoogensis* (Beddome) Nayar & Kaur, and *D. fructuosa* (Christ) C. Chr.

### Section 7. *Splendentes* Fraser-Jenkins, sect. nov.

Frondes bipinnatae vel in una specie fere tripinnatae, lanceolatae vel elongate triangulari-lanceolatae.

Pinnulae praeter in partem superiorem pinnae ad costam anguste affixae, basi valde asymmetricae, latere acroscopico quam latere basiscopico longiori, sed basi acroscopica non auriculata.

Type: *Dryopteris splendens* (Hook.) Kuntze.

Similar to section *Pallidae* except that the fronds are generally longer, elongated triangular-lanceolate, but still with a wide base, and in one species nearly tripinnate. The pinnules are distinct in being markedly asymmetrical at their bases with the lobes on the acroscopical side longer and larger than the more obliquely sloping and narrow ones on the basiscopical side, but not auriculate at the acroscopical base (as in *Polystichum*). The stipe is usually thicker and often dark-coloured. In its remarkable asymmetric pinnules this section shows a similarity to subgenus *Nephrocystis*, but in other features it is clearly more like subgenus *Dryopteris* and in particular section *Pallidae*.

Contains c. six species, confined to the east Himalaya, China including Taiwan, and New Guinea: *D. bamleriana* Rosenstock, *D. splendens* (Hook.) Kuntze, *D. kwanzanensis* Tag., *D. reflexosquamata* Hayata, *D. rubripes* Ching & Chu in prep., and *D. sikkimensis* (Beddome) Kuntze.

### Section 8. *Cinnamomeae* Fraser-Jenkins, sect. nov.

Frondes unipinnatae (sed fere bipinnatae) vel bipinnatae vel fere tripinnatae. Pinnulae valde devexae, non lobatae vel profunde lobatae vel pinnatisectae; lobi pinnularum basi inaequilateri, latere acroscopico quam basiscopico plerumque leviter longiori.

Type: *Dryopteris cinnamomea* (Cav.) C. Chr.

Fronds varying from once pinnate (but nearly bipinnate) to bipinnate or nearly tripinnate and from lanceolate to narrowly triangular-lanceolate. Differs from the other sections in the lamina usually being more thinly herbaceous and brittle, and in the pinnules markedly obliquely sloping and often somewhat narrowed to their bases. Pinnule-lobes, when present, somewhat similar, but not as extreme as in section *Splendentes*, in being narrow and usually slightly longer at the base of the acroscopical side of the pinnule than at the base of the basiscopical side. Indusia thin, but tall and curved down at the edges as in many species of section *Pandae*. Several species are markedly glandular. This section contains a group of species of rather wide morphological diversity in the degree of pinnation and dissection, but they appear to form a distinct natural

group connected by their sloping pinnules, usually with narrower bases, and are perhaps not particularly closely related to the other sections.

Contains *c.* 12 species, mainly in South and Central America with two species reaching southern California and another reaching Easter Island; three species are also present in Africa. To the section belong *D. saffordii* C. Chr., *D. cinnamomea* (Cav.) C. Chr., *D. patula* (Sw.) L. Underw., *D. glandulifera* (Liebm.) C. Chr., *D. huberi* (Christ) C. Chr., *D. schnellii* Tard., *D. munchii* A. Reid Smith, *D. mexicana* (C. Presl) C. Chr., *D. maxonii* L. Underw. & C. Chr., *D. ahamantica* (Kunze) Kuntze, *D. esterhuyseniae* Schelpe & N. C. Anthony, and *D. karwinskyana* (Mett.) Kuntze. Information about the species has been taken partly from Christensen (1911a & 1913a), A. R. Smith (1981 pers. comm.), and from preliminary study by the present author.

### Section 9. *Marginatae* Fraser-Jenkins, sect. nov.

Frondes magnae, bipinnatae vel plerumque tripinnatae interdum quadripinnatae, plerumque late triangulariter lanceolatae; dentes segmentorum acumen capillaceum aristatum haud ferentes.

Type: *Dryopteris marginata* (Wallich ex C. B. Clarke) Christ.

Differs from section *Dryopteris* in its usually large fronds which range from bipinnate to, more normally, tripinnate or sometimes four times pinnate, with the pinnules and often pinnulets mostly stalked or narrowly attached except in the upper parts of the pinnae. The fronds differ markedly in their usually widely triangular-lanceolate shape, and unlike most species of other sections often arise from a prostrate or creeping rhizome; the ultimate segments are somewhat distant and, unlike section *Lophodium*, do not bear aristate hair-points. As in section *Dryopteris* the lamina is mid-green, herbaceous, and matt, but it differs markedly in having a long stipe, often as long as the lamina (as in section *Pallidae*), clothed with scattered, thin, usually matt, ovate-lanceolate scales. The indusia (as in section *Dryopteris*) are small, thin, slightly curved down at the edges and lift and shrivel on ripening except in two species which are exindusiate (*D. ruwenzoriensis* and *D. chaerophyllifolia*). The spores are similar to section *Dryopteris* and are not minutely spinulose as in section *Lophodium*, with which this section might sometimes be confused, except that one species has bluntly echinate spores (*D. ruwenzoriensis*). A few of the species are apomictic.

Contains *c.* 26 species, throughout southern and eastern Asia and Africa, with one species reaching Yemen: *D. cochleata* (Buch.-Ham. ex D. Don) C. Chr., *D. pteridiiformis* Christ, *D. angustifrons* (T. Moore ex Hook.) Kuntze, *D. subimpressa* Loyal, *D. schimperiana* (Hochst. ex A. Braun) C. Chr., *D. ruwenzoriensis* C. Chr., *D. approximata* Sledge, *D. pentheri* (Krasser) C. Chr., *D. fadenii* Pichi-Serm., *D. lewalleana* Pichi-Serm., *D. dracomontana* Schelpe & N. C. Anthony, *D. inaequalis* (Schldl.) Kuntze, *D. goeringiana* (Kunze) Koidz., *D. ramosa* (C. Hope) C. Chr., *D. shiromensis* Kurata & Nakaike, *D. bojeri* (Baker) Kuntze, *D. oligodonta* (Desv.) Pichi-Serm., *D. caroli-hopei* Fraser-Jenkins in press, *D. marginata* (Wallich ex C. B. Clarke) Christ, *D. subarborea* (Baker) C. Chr., *D. chaerophyllifolia* (Zipp.) C. Chr., *D. aquilinoidea* (Desv.) C. Chr., *D. porosa* Ching, *D. mangindranensis* Tard., *D. manniana* (Hook) C. Chr., and ? *D. manniana* auct. [S. and E. Africa].

### Section 10. *Aemulae* Fraser-Jenkins, sect. nov.

Frondes tripinnatae, deltatae vel deltato-lanceolatae; dentes segmentorum acumen capillaceum aristatum ferentes. Sporae spinulis minutis haud munitae.

Type: *Dryopteris aemula* (Aiton) Kuntze.

Similar to section *Lophodium* but with lanceolate (not ovate-lanceolate), matt, concolorous stipe-base scales, more deltate or widely triangular-lanceolate fronds and the spores not minutely spinulose.

Species of this section are intermediate in morphology between the sections *Pallidae* and *Lophodium*.

Contains *c.* three species in Europe and far eastern Asia: *D. chinensis* (Baker) Koidz., *D. gymnophylla* (Baker) C. Chr., and *D. aemula* (Aiton) Kuntze.

**Section 11. Lophodium** (Newman) C. Chr. ex H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 65 (1939 ['1938']).

*Lophodium* Newman in *Phytologist* 4: 371, appendix XVI (1851).

*Aspidium* group *Spinulosa* Christ, *Farnkr. Erde*: 261 (1897), nom. nud. (Art. 32.1).

*Dryopteris* group *Lophodium* (Newman) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).

Lectotype: *Lophodium multiflorum* (Roth) Newman (= *Dryopteris dilatata* (Hoffm.) A. Gray). Christensen (1905: XXI) selected *D. spinulosa* auct. as the type, which was included within *L. multiflorum* by Newman. The type mentioned by Tryon & Tryon (1982*b*) was *L. foeniseeii* (Lowe) Newman (= *D. aemula* (Aiton) Kuntze), but this was not included by Newman in his first circumscription of his genus (p. 371).

Similar to section *Marginatae* but with the stipe-base scales usually thicker and more glossy and usually bicoloured; the lobes of the ultimate segments are usually narrower and more pointed and they end in long hair-pointed aristate teeth (as in *Polystichum*) which are slightly longer than those in section *Aemulae*. The spores are (apparently) unique in being minutely spinulose on the surface of the perispore.

Contains *c.* 10 species, throughout the north temperate zones of the world and in Macaronesia and Africa (also one species, *D. dilatata*, introduced in the Falkland Islands): *D. carthusiana* (Villars) H. P. Fuchs, *D. antarctica* (Baker) C. Chr., *D. guanchica* Gibby & Jermy, *D. crispifolia* Rasbach, Reichst. & Vida, *D. intermedia* (Muhlenb. ex Willd.) A. Gray and subsp., *D. azorica* (Christ) Alston, *D. campyloptera* (Kunze) Clarkson, *D. dilatata* (Hoffm.) A. Gray, *D. expansa* (C. Presl) Fraser-Jenkins & Jermy, and *D. amurensis* Christ.

**Subgenus 3. Erythrovariae** (H. Itô) Fraser-Jenkins, *stat. nov.*

*Dryopteris* section *Erythro-variae* H. Itô in *Bot. Mag., Tokyo* 50: 32 (1936).

*Dryopteris* section *Polysticho-drys* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 36 (1939 ['1938']).

Type (lectotype, H. Itô (1939)): *Dryopteris erythrosora* (D. Eaton) Kuntze.

Fronds once to nearly four times pinnate and similar to subgenus *Dryopteris* except that the stipe-base usually bears a tuft of distinctive, stiff, narrow scales and the rest of the stipe in most species is more or less devoid of scales, those present usually being very narrow and more or less stiff, but a few species have the stipe clothed with wider scales throughout its length. It differs markedly in having almost all the species with very small bullate, or bullate-based scales, often appearing to be almost saccate, on the underside of the pinna-costae and often on the underside of the tip of the rachis and the pinnule-centres as well. The pinnules may be symmetrical as in subgenus *Dryopteris*, but are more usually asymmetrical about their axes and often sloping and slightly auriculate at their acroscopic bases. The lamina is usually more brittle than in subgenus *Dryopteris*. Most of the species are apomictic.

This subgenus shows some similarities to all the other subgenera and also, though more distantly, to *Nothoperanema*, *Ctenitis*, and *Arachniodes*; in view of this, and its wide range of form, it is possible that it could be the most primitive subgenus in *Dryopteris*. A few species (*D. assamensis*, *D. cyclopeltidiformis*, *D. integriloba* (some south-east Asian specimens), *D. polita*, and *D. yepingensis*) usually or always do not have any bullate scales, which has caused some confusion as they are in all other respects clearly members of subgenus *Erythrovariae* and cannot be placed in subgenus *Dryopteris*. This subgenus is confined to eastern Asia, with one species in New Guinea, the main centre of distribution being in Japan and east China (including Taiwan), extending to west China, Korea, south-east Asia, and north-east India. The species do not grow at high altitudes. The present author has not studied the Japanese and Korean species of the subgenus in as much detail as most of the other species in this account, and in drawing up the lists below has relied considerably on the following authors, none of whom have worked diagnosti-

cally on the subgenus throughout Asia: Itô in Nakai & Honda (1939), Nakai (1952), Hirabayashi (1974, 1982 pers. comm.), and Nakaike (1975). However, a full assessment of Chinese and Japanese species of the subgenus has not yet been carried out, and only the more obvious cases are integrated here, following the author's work in Peking.

### Section 1. *Erythrovariae*

*Dryopteris* section *Bulligerae* Ching in *Bull. Fan meml Inst. Biol. (Bot.)* 8: 366, 371 and 475 (1938).

*Dryopteris* section *Polysticho-drys* subsection *Erythro-variae* (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 37 (1939 ['1938']).

*Dryopteris* section *Polysticho-drys* subsection *Gymnosorae* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 64 (1939 ['1938']).

Type (lectotype, H. Itô (1939)): *Dryopteris erythrosora* (D. Eaton) Kuntze.

Fronds with a herbaceous or somewhat coriaceous lamina, but not markedly stiffly coriaceous. Pinnules without caudate apices and lobes normally rounded and not pointed. Stipe scales wide or narrow; costae and costules with (or occasionally without) bullate scales below.

Contains c. 25 species, throughout the range of the subgenus, as follows: *D. cyclopeltidiformis* C. Chr., *D. decipiens* (Hook.) Kuntze, *D. cordipinna* Ching & Shing, *D. fuscipes* C. Chr., *D. assamensis* (C. Hope) C. Chr. & Ching, *D. purpurella* Tag., *D. integriloba* C. Chr., *D. yepingensis* C. Chr. & Ching ex Ching, *D. championii* (Benth.) C. Chr., *D. kinkiensis* Koidz. ex Tag., *D. kenzoi* Kurata, *D. tsugiwoi* Kurata, *D. koidzumiana* Tag., ? *D. liyangensis* Ching & Lan, *D. erythrosora* (D. Eaton) Kuntze, ? *D. caudipinna* Nakai, *D. kinokuniensis* Kurata, *D. hondoensis* Koidz., *D. cystolepidota* (Miq.) Makino, *D. ryo-itoana* Kurata, *D. tenuicula* C. Matthew & Christ, *D. simasakii* (H. Itô) Kurata, *D. tenuipes* (Rosenstock) Seriz., *D. subtrian-gularis* (C. Hope) C. Chr., and *D. gymnosora* (Makino) C. Chr.

### Section 2. *Politae* Fraser-Jenkins, sect. nov.

Stipes longissimus paleas paucas basi ferens, super glaber. Frondes glabrae; pinnae longe stipitatae; pinnulae valde asymmetricae, infimae basicopicae prolongatae.

Type: *Dryopteris polita* Rosenstock.

Differs from section *Erythrovariae* in being completely glabrous and without any scales except for a tuft of narrow ones at the very base; lowest pinnae with long stalks and pinnules markedly sloping and asymmetrical, the lowest one extended.

In some respects intermediate between the subgenera *Erythrovariae* and *Nephrocystis*; the lack of bullate scales has caused its only species to be referred to *Nephrocystis* (Itô in Nakai & Honda, 1939), sub *D. laurisilvicola* T. Suzuki, but bullate scales are absent in a few other members of subgenus *Erythrovariae*, and the frond morphology is closer to subgenus *Erythrovariae* than to subgenus *Nephrocystis*.

Contains a single, somewhat isolated species distributed in south-east Asia, the Australasian islands, south China including Taiwan, and south Japan: *D. polita* Rosenstock.

### Section 3. *Variae* Fraser-Jenkins, sect. nov.

*Dryopteris* section *Polysticho-drys* subsection *Formosanae* H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 62 (1939 ['1938']).

Stipes paleas angustas ferens, costis costulisque paleas bullatas ferentibus. Lamina rigide coriacea; pinnulae apice caudatae lobis acutis.

Type: *Dryopteris varia* (L.) Kuntze.

Differs from section *Erythrovariae* in the fronds having a stiffly coriaceous lamina and the pinnules with caudate apices and pointed lobes; the lowest pinnule on the lowest pinna considerably longer than the rest, as in section *Politae*, but not as dissect as in that section. Stipe scales all narrow and the costae and costules with slightly bullate-based scales in contrast to the more bullate scales of section *Erythrovariae*.

Contains *c.* 10 species, in north-east India, China including Taiwan, Japan, Korea, and the northern parts of south-east Asia, as follows: *D. saxifraga* H. Itô, *D. bissetiana* (Baker) C. Chr., *D. varia* (L.) Kuntze, *D. pacifica* (Nakai) Tag., *D. sacrosancta* Koidz., *D. hadanoi* Kurata, *D. shibipedis* Kurata, *D. insularis* Kodama, *D. sordidipes* Tag., and *D. formosana* (Christ) C. Chr.

#### Subgenus 4. *Nephrocystis* (H. Itô) Fraser-Jenkins, *stat. nov.*

*Dryopteris* section *Nephrocystis* H. Itô in *Bot. Mag., Tokyo* 49: 437 (July 1935).

*Aspidium* group *Diclisodon* (T. Moore) Christ, *Farnkr. Erde*: 262 (1897) (Art. 35.2).

*Aspidium* group *Sparsa* Christ, *Farnkr. Erde*: 262 (1897), nom. nud. (Art. 32.1).

*Dryopteris* group *Diclisodon* (T. Moore) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).

Type: *Dryopteris hayatae* Tag. (= *D. subexaltata* (Christ) C. Chr.).

Fronds twice to four times pinnate and similar to subgenus *Dryopteris* except that they are always  $\pm$  wide at the base and the stipe is long and smooth and bears fewer scales which are narrow to ovate and partly deciduous unlike subgenus *Dryopteris*; the upper stipe, rachis, and costae are glabrous or bear a few very small and very narrow scales, but do not bear bullate scales as in subgenus *Erythrovariae*. The arrangement of the pinnules or pinnulets at the base of the lamina is either catadromous as in subgenus *Dryopteris* or anadromous as in *Arachniodes*. Pinnules or pinnulets always asymmetrical and sloping, with their acroscopic sides developed, especially at their base where they often become slightly auriculate with a rounded auricle, but not as developed as in *Arachniodes* and not pointed; in subgenus *Dryopteris* only two sections have asymmetrical sloping pinnules. The lamina is usually markedly smoother and more glabrous than in subgenus *Dryopteris*.

This subgenus has been considerably confused as the arrangement of the segments can be either anadromous or catadromous; when anadromous, the species have often been placed in the genus *Arachniodes* or in the separate genus, *Acrorumohra*, disregarding their close natural relationships to other species placed in *Dryopteris*. Thus Itô (1935*a* and *b*) placed some of the species in *Dryopteris* section *Nephrocystis* and some in *Rumohra* (i.e. *Arachniodes*) section *Acrorumohra*, which he later (1939) raised to a separate genus. Ching (1964) followed Itô and did not observe the close relationship between the catadromous *D. sparsa* and anadromous *D. macrochlamys*, etc. and placed the two into the two separate genera, *Dryopteris* and *Acrorumohra*. However, Sledge (1973*a* and *b*) commented on the inconsistencies and problems arising from such a treatment and, although at first sight there is a marked difference between the very divided-leaved species such as *D. diffracta* and the less divided ones, Sledge (1973*b*) also pointed out that *D. macrochlamys* (sub *D. obtusissima*) contains a range of form that links the two together, as had been noticed by some earlier authors. The difficulties with this group have also blurred the distinction between *Dryopteris* and *Arachniodes* (and related genera) and though the subgenus *Nephrocystis* is perhaps distantly related to *Arachniodes* and in particular, to *Leptorumohra*, the three genera *Dryopteris*, *Arachniodes* and *Leptorumohra* appear to be both natural and readily distinguishable. *Nephrocystis* is confined to Africa, Asia, Australasia, and Oceania apart from one species in Central America; most of the species are south-east Asian and Sri Lankan.

#### Section 1. *Purpurascens* Fraser-Jenkins, *sect. nov.*

Frondes magnae, tripinnatae vel quadripinnatae, segmentis parvis remotis asymmetricis. Stipes paleas angustas ferens.

Type: *Dryopteris purpurascens* (Blume) Christ.

Similar to section *Nephrocystis* except that the fronds are large, very well developed, finely dissect, three to four times pinnate and with small, more or less remote ultimate segments which are usually more or less pointed at their apices and auriculate at their acroscopic bases. The rhizome can be either creeping (often markedly so) or, as in section *Nephrocystis*, ascendent. Unlike section *Nephrocystis* the stipe bears very narrow scales particularly in a tuft near the

base, and the frond usually bears very small, narrow scales in tufts near the junctions of the rachis, costae, and costules underneath. Some members of this section are perhaps somewhat intermediate in morphology between the rest of subgenus *Nephrocystis* and some members of the section *Marginatae* in subgenus *Dryopteris*, while clearly being closely related to the section *Nephrocystis*. This emphasises the connection between the two subgenera and indicates that *Acrorumohra* is a part of *Dryopteris*.

Contains c. 13 species, mainly in south-east Asia and the Australasian and Pacific islands, but extending to Hawaii and Africa and with one species in tropical America. To the section belong *D. futura* A. Reid Smith, *D. kilemensis* (Kuhn) Kuntze, *D. remotipinnulata* Bonap., *D. purpurascens* (Blume) Christ, *D. arborescens* (Baker) Kuntze, *D. wardii* (Baker) Kuntze, *D. permagna* M. Price, *D. dicksonioides* (Mett. ex Kuhn) Copel., *D. powellii* (Baker) C. Chr., *D. pseudoparasitica* Alderw., *D. papuana* C. Chr., *D. parvula* W. Robinson, and *D. pulvinulifera* (Beddome) Kuntze.

## Section 2. *Nephrocystis*

*Rumohra* section *Acrorumohra* H. Itô in *J. Jap. Bot.* 11: 583 (August 1935).

*Acrorumohra* (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* 4: 101 (1939 [1938]).

Type: *Dryopteris hayatae* Tag. (= *D. subexaltata* (Christ) C. Chr.).

Rhizome ascendent; stipe long, bearing ovate-lanceolate scales, rachis and costae more or less glabrous. Fronds medium sized, twice to four times pinnate, becoming a fifth time pinnate in one species, with small, remote segments or large ones, segments normally rounded, asymmetrical.

This section contains less dissected catadromous species showing some similarities to the subgenus *Erythrovariae* as well as to the section *Purpurascens* and perhaps, though distantly, to the genus *Arachniodes*; it also contains more dissected anadromous species previously placed in the genus *Acrorumohra* (including its type, *D. diffracta*) and showing some similarity to *Leptorumohra*. However the Sri Lankan (Ceylonese) species, *D. macrochlamys*, is remarkable for having both less divided and more divided fronds, even on the same rhizome, thus underlining the connection between the two frond-types.

Contains c. 14 species, confined to Asia and the Australasian and Pacific islands and Australia, and well represented in south-east Asia and Sri Lanka: ? *D. aneitensis* (Hook.) C. Chr., *D. hasseltii* (Blume) C. Chr., *D. platypus* (Kunze) Kuntze, *D. sparsa* (Buch.-Ham. ex D. Don) Kuntze, *D. viridescens* (Baker) Kuntze, *D. subexaltata* (Christ) C. Chr., *D. cacaiana* Tag., *D. sabae* (Franchet & P. A. L. Savat.) C. Chr., *D. yoroii* Seriz., *D. deparioides* (T. Moore) Kuntze and subspp., *D. sri-lankensis* Fraser-Jenkins in press, *D. macrochlamys* (Fée) Fraser-Jenkins in press, *D. subreflexipinna* Ogata, and *D. diffracta* (Baker) C. Chr.

## Species not placed in the classification

It has not yet been possible to place 12 species, mostly from Hawaii and the south Atlantic islands, into the classification outlined here, as their morphology is not sufficiently close to other species; they need further study to ascertain their natural relationships. The unplaced species are as follows:

Madagascar: *Dryopteris perrieriana* C. Chr., *D. subcrenulata* (Baker) C. Chr.

Hawaii: *Dryopteris acutidens* C. Chr., non Ching, *D. crinalis* (Hook. & Arn.) C. Chr. (probably a *Ctenitis*), *D. glabra* (Brackenr.) Kuntze, *D. nuda* L. Underw., *D. sandwiciensis* (Hook. & Arn.) C. Chr., *D. unidentata* (Hook. & Arn.) C. Chr.

Central America: *Dryopteris nubigena* Maxon & C. Morton.

South Atlantic islands: *Dryopteris ascensionis* (Hook.) Kuntze, *D. cognata* (C. Presl) Kuntze, *D. napoleonis* (Bory) Kuntze. These three species all appear to be related and form a distinct group with a frond shape similar to many *Ctenitis* species; the group needs further study with a view to recognising it taxonomically, perhaps as a fifth subgenus of *Dryopteris* if they belong to *Dryopteris* at all.

## New species

### 1. *Dryopteris subpyncnopteroides* Ching ex Fraser-Jenkins, sp. nov.

Fig. 1

Species inter *D. conjugatam* et *D. pyncnopteroidem* intermedia. Stipes dense paleaceus, lamina aliquanto tenui laevique, pinnis quam eis *D. conjugatae* minus profunde lobatis. Sori in medio pinnae inserti.

Morphology intermediate between that of *D. conjugata* and *D. pyncnopteroides*. Stipe densely clothed with narrow, mid-brown scales, which are slightly paler than in *D. conjugata* and more dense than in *D. pyncnopteroides*. Lamina slightly larger and wider than in *D. pyncnopteroides*, but similar to it in texture and thus thinner, softer, and smoother than in *D. conjugata*, with the veins slightly darkened and presumably very slightly impressed in the upper surface in the living state as in *D. pyncnopteroides* and *D. dickinsii*. Pinnae less deeply lobed than in *D. conjugata*, with wide square lobes which are slightly deeper than in normal *D. pyncnopteroides*; the lowest pair of pinnae often slightly deflexed and as long as those above, so that the frond has a wide base; pinna-lobes bearing a few long, narrow teeth at the corners. Sori indusiate, medial along the centre of the pinnae reaching close to the costa. Spores of relatively medium size; *c.* 45  $\mu\text{m}$  long. Cytotype unknown.

Holotype: Yunnan, Yangbi, 6 Nov. 1929, R. C. Ching 25498 (PE!). Paratypes: Yunnan, Yangbi, R. C. Ching 22469 (PE!); Yunnan, Yangbi, 2500m, 4 June 1963, Jingsaijiang team 4265 (PE!).

The dense scales and more deeply lobed pinnae separate this species quite distinctly from *D. pyncnopteroides* to which it is closely related. The somewhat small spores suggest that the species may perhaps be a diploid apomict, but it is to be hoped that living material with more spores may become available from China for further study. *D. subpyncnopteroides* is so far known only from Yunnan, SW. China.

### 2. *Dryopteris parrisiae* Fraser-Jenkins, sp. nov.

Fig. 2

Species *D. wallichianae* similis, sed fronde parviora, stipe valde relative longiori, pinnis brevioribus, basibus pinnarum latiore conjunctibus, pinnis apicalibus altiore conjunctibus differt. Cytotypus triploideus.

Morphology similar to *D. wallichiana* but fronds smaller when mature (usually up to *c.* 90 cm long). Stipe relatively much longer (between 2/3 the length to the same length as the lamina) and bearing long, narrow, paler-edged scales with dark streaks near to their centres or bases, sometimes becoming mostly dark. Lamina noticeably more stiffly coriaceous than in *D. wallichiana*, and wide at the base with the lowest pair or pairs of pinnae often somewhat deflexed. Pinnae shorter and pinna-lobes markedly widely fused together up to about half the width of the pinna at their bases (except the first pair on each pinna), much more so than in *D. wallichiana*; lower basiscopic pinnules of the lowest pair of pinnae in larger fronds becoming extended and longer than the acroscopic ones, and curving slightly towards the pinna apex. Pinna-lobe apices markedly truncate, bearing a few wide-based, short teeth. Pinnae at the frond apex joined at their bases over a longer distance than in *D. wallichiana*, thus making the frond apex more caudate. Spores partially abortive. Cytotype triploid (apomictic),  $2n = 123$ , determined on B. S. Parris' collections of small plants growing at the base of the type plant and cultivated at Chelsea Physic Garden as nos 3396 and 3397 (Gibby, 1985).

Holotype: Papua New Guinea, Western Highlands Province, Tomba Path, Mt Hagen, above Tomba village and saw-mill, on rotting log in very mossy cut-over mid-montane *Nothofagus* forest with much *Pandanus*, locally common, *c.* 2600 m, 19 Sept. 1980, B. S. Parris & J. P. Croxall 10295 (K!).

Other specimens seen: Papua, E. side of Lake Myola, Kokoda District, no. 1 sub-district, 2000 m, 22 July 1974, J. R. Croft et al., LAE 61928 (L!K!), 61848 (L!), 61615 (L!); Papua, NW. slopes of Mt Giluwe, above Kagoba, 3300 m, 22 Jan. 1979, J. R. Croft 728 & J. I. Marsh (K!); Papua, E. slopes of Mt. Saruwaged, 4 km



**Fig. 1** *Dryopteris subpyncopteroides* Ching ex Fraser-Jenkins. Holotype (25498) (PE).



Fig. 2 *Dryopteris parrisiae* Fraser-Jenkins. Holotype (Parris & Croxall 10295) (K).

SE. of Lake Gwam, Huon Peninsula, 7 July 1981, *J. R. Croft* 1295 (K!); Papua, Isuani Grassland, SE. slope of Mt Victoria, Port Moresby Subdistrict, Central District, 2700 m, 3 July 1974, *J. R. Croft*, LAE 61615 (K!), 17 July 1974, 61848 (K!); Papua, Mt Giluwe, 3110 m, 18 Aug. 1961, *R. Schodde* 1906 (K! L!); New Guinea, Sirunki, Western Highlands, beyond Kaiamanda, 2560 m, young leaves eaten by natives, 4 Sept. 1962, *D. Walker* ANV 651 (K!), 657 (L!); NE. New Guinea, 2440 m, Jan. 1968, *D. Walker* 8836 (K!); Dutch New Guinea, Lake Habbema, 3225 m, *L. J. Brass* 9138 (L! BM!); Papua, Eastern Highlands, Mt Wilhelm, E. slope, 3560 m, 18 June 1959, *L. J. Brass* 30002 (K!L!), 2600 m, 18 July 1959, 30596 (K!L!), 3300 m, 29 June 1959, 30194 (K!L!), 2770 m, 5 July 1959, *L. J. Brass* 30329 (K!); Papua, Milne Bay District, N. slope of Mt Dayman, Maneau Range, 2230–2250 m, 9 June 1953, *L. J. Brass* 22841 (BM!); Papua, Mt Albert Edward, Central Division, 3680 m, May–July 1933, *L. J. Brass* 4409 (BM!); Papua, Ibiwara, *C. Kalkman* 4704 (L!); Papua, South Highlands, Ibiwara, *W. Vink* 17206 (L!), 17220 (L!); Papua, Mt Ambu, *W. Vink* 17399 (L!); Papua, South Highlands, Tari, Mt Né, *W. Vink* 17266 (L!); New Guinea, Kegl Sugl, in forest around camp at ANU store, c. 2550 m, 23 Feb. 1970, *A. C. Jermy* 5249 (BM!), 5271 (BM!), 5272 (BM!); New Guinea, Mt Wilhelm, in *Pandanus-Podocarpus* forest, 2700 m, 24 Feb. 1970, *A. C. Jermy* 5257–5260 (BM!); New Guinea, Mount Abilala, in moss forest, c. 2740 m, 19 Nov. 1969, *A. C. Jermy* 4265 (BM!); New Guinea, S. side of Lake Naho, Finisterre Mountains, 17 Nov. 1969, *A. C. Jermy* 4220 (BM!).

This species almost replaces *D. wallichiana* in New Guinea, though that species also occurs there as a rarity. Intermediate specimens occur in Java, Borneo, and New Guinea, but are connected to normal *D. wallichiana* by a range of intermediates. Such a plant of *D. wallichiana*, somewhat approaching *D. parrisiae*, but as always more deeply lobed in its pinnae, has been investigated by Gibby (1985) (Sabah, Borneo, Pakka Cave, Kinabalu National Park, 6 Dec. 1980, *A. C. Jermy* 15145 (BM!)) and found to be diploid,  $2n = 82$ , as in normal *D. wallichiana*. Such plants do not have the extreme *D. parrisiae* morphology, and are presumed to represent variation within *D. wallichiana* as a further example of imitation among closely related *Dryopteris* species, occurring more or less sympatrically. *D. parrisiae* is named after Dr Barbara S. Parris (formerly Croxall) of the Royal Botanic Gardens, Kew, who collected the type specimen. It is so far known only from New Guinea.

### 3. *Dryopteris tingiensis* Ching & S. K. Wu ex Fraser-Jenkins, sp. nov.

Fig. 3

Species *D. barbigeræ* subsp. *komarovii* similis, sed paleis stipitis valde fuscioris, lobis pinnarum truncatioribus, sporis maioribus partim abortivis differt.

Morphology similar to *D. barbigeræ* subsp. *komarovii*, but stipe scales markedly darker and of a castaneous dark brownish black, sometimes with a yellowish tint around their edges. They differ markedly from those of *D. acuto-dentata* by being larger, more numerous, thicker, and without the slightly crinkled, coal-like appearance of the more deciduous scales of that species, as well as in their less black colour, and are thus more similar to those of *D. barbigeræ* subsp. *komarovii* except in having a markedly darker colour than even the somewhat dark-scaled specimens of the latter that sometimes occur in SE. Tibet and SW. China. Lamina upper surface less glossy and less coriaceous than in *D. acuto-dentata* (which is very slightly coriaceous) and similar to *D. barbigeræ* subsp. *komarovii*. Pinna-lobes somewhat crowded, incised at the margins in a similar manner to the latter, slightly but recognisably more truncate at their apices, but not as much as in *D. acuto-dentata*. Spores partially abortive, good spores up to c. 49  $\mu\text{m}$  long (excluding perispore), and thus larger than in *D. barbigeræ* subsp. *komarovii*. Cytotype unknown, but the spores suggest that the plant could well be a triploid apomict. It is to be hoped that living material may become available from China for further study.

Holotype: Xizang [Sichang, = Tibet], Kong Chu Hsien, 4200 m, 21 Aug. 1976, *Chang Chung* team 9525 (PE!). Paratype: Xizang [Sichang, = Tibet], Ting Tze Hsien, Ka Ta region, Dang Ga village, 3600–4000 m, 19 June 1976, *Chang Chung* team 4053 (PE!) (spores immature).

This species, though having slightly truncate pinnules, recognisably more so than in *D. barbigeræ* subsp. *komarovii*, nevertheless looks far closer to it in lamina morphology than to *D. acuto-dentata*, but it is clearly of a different cytotype, from its spores, than the diploid sexual *D. barbigeræ* subsp. *komarovii*. Ching & Wu named this species, while studying the fern flora of



**Fig. 3** *Dryopteris tingiensis* Ching & S. K. Wu ex Fraser-Jenkins. Holotype (Chang Chung team 9525) (PE).

Tibet, from the single, immature specimen from Ting Tze which has immature spores. Although they have accepted other such specimens for publication as new species, often erroneously, they did not publish *D. tingiensis* along with their other Tibetan species. I agreed with their original recognition of it on seeing the specimen, and became reinforced in my view that it is a new species on studying the specimen that I have designated the type, which was unidentified in a new collection Professor Ching passed to me to examine while I was visiting him in Peking. It is named after Ting Tze county, Tibet, and is so far only known from SE. Tibet.

#### 4. *Dryopteris ruwenzoriensis* C. Chr., sp. nov.

Fig. 4

'*Eudryopteris* rhizomate virisimiliter obliquo; stipite valido, 60 cm vel ultra longo, brunneo-stramineo, paleis paucis (plerisque abrais) luteo-brunneis, lanceolatis, integris, ad 2 cm longis, aliis multo minoribus filiformibus mixtis vestito, superne sulcato. Lamina ovata, magna (metrali?), 60 cm vel ultra lata, papyraceo-herbacea, laete viridi, tripinnata. Pinnis alternis, ad 10 cm inter se remotis, basalibus maximis, ad 35 cm longis, breviter petiolatis, 15 cm latis, latere basiscopico producto inaequilateralibus, acuminatis, sequentibus subaequilateralibus, subdeltoideo-oblongis, subsessilibus, costis sursum alatis; pinnulis II. ord. basiscopicis pinnarum basialium 11–12 cm longis 3 cm latis, pinnis primariis supremis similibus, acropiscis iis pinnarum ceterum similibus, 4–5 cm longis 1.5–2 cm latis, sessilibus, e basi paulo aequali truncata latiore subgradatim in apicem acuminatum attenuatis omnibus alternis, 3–2 cm inter se remotis, ad costulam plus minusve late alatum profunde pinnatifidis vel majoribus versus basin pinnatis segmentis (vel pinnulis III. ord.) parum obliquis, lateribus parallelis apice truncato rectangularibus, 1–1.5 cm longis 0.5–0.7 mm latis ubique dentatis (dentibus brevibus, deltoideis, non aristatis), majoribus plus minusve profunde serrulato-laciniatis, laciniis subquadratis apice dentatis. Rachi, costis costulisque paleis tenuissimis parvis, lanceolatis, pallide luteo-brunneis sat sparse vestito. Venis in lobis pinnatis, plerisque furcatis, adscendentibus. Soris costularibus, sat magnis, globosis, indusiis non repertis.'

'This new species differs from the many African relatives by its large size, the broad, rectangular ultimate segments with many small teeth and in being (apparently) exindusiate. Small, early falling indusia may possibly be found in quite young sori, but in every case very different from the large indusia of *D. schimperiana* (Hochst.) C. Chr., which comes nearest to our species, especially in scale-characters.'

Holotype: Herbarium Filicum Carl Christensen 5112, 22 Juli 1930, Mission H. Humbert-Plantes de l'Afrique Equatoriale – 1929, no. 8825 ter., '*Dryopteris ruwenzoriensis* nsp.' [Christensen scripsit]. Massif du Ruwenzori, versant Ouest (Congo Belge, Ituri), Altitude vers 2000 m, Date de la récolte: Juillet (BM!). Paratypes: ditto nos. 8849 (P! BM!); 8900 bis (BM!); Mission Ch. Alluud Afrique Orientale 1908–1909, no. 303, Ruwenzori (Est), hte. Vall. du Mobuku, montée du Col de Buamba, 3300–3400 m, Janv. 1909 (BM!).

The above diagnosis and comments are typed on a sheet in a capsule mounted with the type specimen at the BM. From the lamina morphology alone it seemed to me that this was a good species, and this was confirmed on examining the spores, which are up to *c.* 42  $\mu$ m long. These have a remarkable surface of somewhat dense blunt spines, unlike any other *Dryopteris* examined, and do not have clear wings of perispore. In *Dryopteris schimperiana*, which is close to *D. ruwenzoriensis*, the spores are smaller, and have short, more or less clear wings of perispore. The other major difference is the more prominent teeth at the apices of the segments in *D. ruwenzoriensis*, and the often somewhat reddish-brown stipe-base scales; the pinnule-apices are also slightly more obtuse than in many specimens of *D. schimperiana*, and the lamina is laxer. The indusium can be small in *D. schimperiana* on occasions, but is always either small or absent in *D. ruwenzoriensis*. The stipe contains a circle of about six or seven separate vascular strands.

So far *D. ruwenzoriensis* is known only from the Ruwenzori (Mountains of the Moon, Uganda and Zaïre), but it may well occur elsewhere in Africa, and a search in other herbaria may reveal it, identified most probably as *D. schimperiana*.

Other specimens examined: Uganda, Western Province, Toro District, Ruwenzori, Namwamba valley, 3200 m, in heath forest, 6 Jan. 1935, *G. Taylor* 2954 (BM!), on rocks in river, 3170 m, 7 Jan. 1935, *G. Taylor* 2990 (BM!), under *Podocarpus* trees, 2900 m, 11 Jan. 1935, *G. Taylor* 3079a (BM!); Uganda, Western Province, Bigo, River Bujuku, riverside, 3450 m, 23 July 1952, *H. A. Osmaston* 1687 (BM!).



Fig. 4 *Dryopteris ruwenzoriensis* C. Chr. Holotype (Humbert 8825) (BM).

## Hybrids

A list of 89 naturally occurring *Dryopteris* hybrids (excluding hybrid-derived apomictic or polyploid species), as known to the author, is given below in alphabetical order by regions. However, it should be noted that apart from North America, Europe (in the wide sense) and Japan, search for hybrids has been non-existent or only preliminary; see Fraser-Jenkins (1984: 39–40) for information about the identification of hybrids from spores, etc. The Japanese hybrids are taken from Nakaike (1970, 1975) and Hirabayashi (1974). A useful list of hybrids, though also containing polyploid species, is that of Knobloch (1976), and North American hybrids are taken from this source, and also from Wagner (1970) and Widén, Britton, Wagner & Wagner (1975). Knobloch's list was intended to bring together all the available literature records and did not set out to decide the validity of the hybridity or nomenclature. It has been revised recently by Knobloch, Gibby & Fraser-Jenkins (1984). European hybrids are those verified by the present author after detailed long-term study; thus there are some modifications from published lists and the list here is believed to be definitive for the present. Where the hybrids have not yet been given binomials they are listed after the first parental species, the normal convention of placing the parents in alphabetical order being followed.

### Europe (including western Asia, Macaronesia, and north-west Africa) (23):

*D.* × *ambroseae* Fraser-Jenkins & Jermy (= *D. dilatata* × *D. expansa*); *D.* × *asturiensis* ined. (= *D. affinis* subsp. *affinis* × *D. corleyi*); *D.* × *brathaica* Fraser-Jenkins & Reichst. (= *D. carthusiana* × *D. filix-mas*); *D.* × *cedroensis* Gibby & Widén (= *D. guanchica* × *D. oligodonta*); *D.* × *complexa* Fraser-Jenkins in press, and nothosubspecies (= *D. affinis* subsp. × *D. filix-mas*); *D.* × *deweveri* (J. Jansen) J. Jansen & Wachter (= *D. carthusiana* × *D. dilatata*); *D. expansa* × *D. filix-mas*; *D.* × *euxinensis* Fraser-Jenkins & Corley (= *D. caucasica* × *D. filix-mas*); *D.* × *fraser-jenkinsii* Gibby & Widén (= *D. affinis* subsp. *affinis* × *D. guanchica*); *D.* × *gomerica* Gibby & Widén (= *D. aemula* × *D. guanchica*); *D.* × *graeca* Fraser-Jenkins & Gibby (= *D. pallida* subsp. *pallida* × *D. submontana*); *D.* × *initialis* Fraser-Jenkins & Corley (= *D. caucasica* × *D. oreades*); *D.* × *madalena* Fraser-Jenkins (= *D. azorica* × *D. crispifolia*); *D.* × *mantoniae* Fraser-Jenkins & Corley (= *D. filix-mas* × *D. oreades*); *D.* × *martinsiae* Fraser-Jenkins (= *D. aemula* × *D. crispifolia*); *D.* × *picoensis* Fraser-Jenkins (= *D. affinis* subsp. *affinis* × *D. azorica*); *D.* × *pseudoabbreviata* Jermy (= *D. aemula* × *D. oreades*); *D.* × *sardoa* Fraser-Jenkins & Reichst. (= *D. oreades* × *D. tyrrhena*); *D.* × *sarvelae* Fraser-Jenkins & Jermy (= *D. carthusiana* × *D. expansa*); *D.* × *sjoegrenii* Fraser-Jenkins (= *D. azorica* × *D. dilatata*); *D.* × *telesii* Fraser-Jenkins (= *D. crispifolia* × *D. dilatata*); *D.* × *uliginosa* (A. Braun ex Doell) Kuntze ex Druce (= *D. carthusiana* × *D. cristata*); *D.* × *vidae* Fraser-Jenkins & Gibby (= *D. pallida* subsp. *pallida* × *D. villarii*).

### North America (31):

*D.* × *algonquinensis* D. Britton (= *D. fragrans* × *D. marginalis*); *D.* × *atropalustris* Small (= *D. celsa* × *D. cristata*); *D.* × *australis* (Wherry) Small (= *D. celsa* × *D. ludoviciana*); *D.* × *benedictii* Wherry (= *D. carthusiana* × *D. clintoniana*); *D.* × *bootii* (Tuckerman) L. Underw. (= *D. cristata* × *D. intermedia*); *D.* × *burgessii* B. Boivin (= *D. clintoniana* × *D. marginalis*); *D. campyloptera* × *D. expansa*; *D. campyloptera* × *D. intermedia*; *D. campyloptera* × *D. marginalis*; ? *D. carthusiana* × *D. celsa*; *D. carthusiana* × *D. goldiana*; *D. celsa* × *D. clintoniana*; *D. celsa* × *D. goldiana*; *D. clintoniana* × *D. cristata*; *D. clintoniana* × *D. goldiana*; ? *D. cristata* × *D. goldiana*; *D.* × *dowellii* (Farw.) Wherry (= *D. clintoniana* × *D. intermedia*); *D. expansa* × *D. intermedia*; *D. expansa* × *D. marginalis*; *D. filix-mas* × *D. goldiana*; *D. filix-mas* × *D. marginalis*; ? *D. fragrans* × *D. intermedia*; *D. goldiana* × *D. intermedia*; *D. intermedia* × *D. marginalis*; *D.* × *leedsii* Wherry (= *D. celsa* × *D. marginalis*); *D.* × *neo-wherryi* W. Wagner (= *D. goldiana* × *D. marginalis*); *D.* × *pittsfordensis* Slosson (= *D. carthusiana* × *D. marginalis*); *D.* × *separabilis* (W. Palmer) Small (= *D. celsa* × *D. intermedia*); *D.* × *slossoniae* Wherry ex Lellinger (= *D. cristata* × *D. marginalis*); *D.* × *triploidea* Wherry (= *D. carthusiana* × *D. intermedia*); *D.* × *uliginosa* (A. Braun ex Doell) Kuntze ex Druce (= *D. carthusiana* × *D. cristata*).

### Mainland China and Korea (4):

*D.* × *daliensis* Z. R. Wang in press (= *D. woodsii* × *D. zinongii*); unnamed hybrid of *D. fangii*; ? *D.* × *saxifragi-varia* Nakai (? = *D. bissetiana* × *D. varia*); *D.* × *shuichangensis* Chiu & Yao ex Ching (pro sp.) (= *D. crassirhizoma* subsp. *whangshangensis* × *D. dickinsii*).

**Japan (23):**

Many of the Japanese hybrids have not been reported clearly enough or with sufficient detail of spores, etc., to ascertain that they are hybrids in the sense of this account; this list could, perhaps, contain some which are apomictic species. *D. × fujipedis* Kurata (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. lacera*); *D. × gotenbaensis* Nakaike (= *D. hondoensis* × *D. uniformis*); *D. × haganecola* Kurata (= *D. cycadina* × *D. uniformis*); *D. × hakonecola* Kurata (= *D. dickinsii* × *D. uniformis*); *D. × hisatsuana* Kurata (= *D. handeliana* × *D. lacera*); *D. × kidoana* Kurata nom. nud. (= ? *D. commixta* × *D. sp.*); *D. × kominatoensis* Tag. (= *D. monticola* × *D. tokyoensis*); *D. × mayebarae* Tag. (= *D. commixta* × *D. uniformis*); *D. × mituii* Seriz. (= *D. lacera* × *D. uniformis*); *D. × otomasui* Kurata (= *D. commixta* × ? *D. polylepis* or ? *D. uniformis*); *D. × pseudo-commixta* Kurata (= *D. commixta* × *D. dickinsii*); *D. × rarissima* Kurata (= *D. commixta* × *D. sparsa*); ? *D. × shibisanensis* Kurata (= *D. commixta* × *D. cycadina*); *D. × sugino-takaoi* Kurata (= *D. lacera* × *D. polylepis*); *D. × tetsu-yamanakae* Kurata (= *D. commixta* × *D. sieboldii*); *D. × tokudai* Sugim. (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. polylepis*); *D. × toyamae* Tag. (= *D. sieboldii* × ? *D. lacera*); *D. × watanabei* Kurata (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. uniformis*); *D. × yamashitae* Kurata (= *D. sparsa* × *D. subexaltata*). According to Hirabayashi (pers. comm. 1982) a few other hybrids recently found in Japan are soon to be described, and Nakaike (1982) lists *D. × kousaii* Akas., *D. × tonensis* Kurata, *D. × wakui* Kurata, and *D. × yasuhikoana* Kurata.

**Indian subcontinent (9):**

*D. × flemingii* Fraser-Jenkins in press (= *D. chrysocoma* × *D. juxtaposita*); *D. × ghatakii* Fraser-Jenkins in press (= *D. austro-indica* × *D. cochleata*); *D. × liddarensis* Fraser-Jenkins in press (= *D. barbiger* subsp. *barbiger* × *D. serrato-dentata*); *D. × loyalii* Fraser-Jenkins in press (= *D. caroli-hopei* × *D. marginata*); *D. × macdonellii* Fraser-Jenkins in press (= *D. filix-mas* × *D. ramosa*); *D. sparsa* (2×) × *D. sparsa* (4×); *D. × vidyae* Fraser-Jenkins in press (= *D. sparsa* × *D. splendens*); *D. × wechteriana* Fraser-Jenkins in press (= *D. chrysocoma* × *D. nigropaleacea*); *D. × zygo-parentalis* Fraser-Jenkins in press (= *D. darjeelingensis* × *D. scottii*).

**List of synonyms**

The following is a list of synonyms within the genus *Dryopteris*. The species to which the synonyms are referred may be found listed after each section or in the index. In Christensen's *Index filicum* and supplements (1905–1934), Pichi Sermolli (1965), and Jarrett *et al.* (1985) many more species are placed in Christensen's subgenus *Dryopteris* than in the modern genus *Dryopteris* as he included *Ctenitis* and other closely related genera such as *Nothoperanema*, as well as many thelypteroid ferns, and many that are synonyms of *Dryopteris* species. It is hoped that the present list is nearly complete and will complement the *Index filicum* as far as *Dryopteris* (in the modern sense) is concerned. All the names in *Index filicum* and supplements have been checked and any not appearing in the present list have been excluded from *Dryopteris*.

*abbreviata* (DC.) Newman ex Manton, non (Schrader) Kuntze = *affinis* subsp. *affinis*  
*abbreviata* auct., non (DC.) Newman ex Manton, nec (Schrader) Kuntze = *oreades*  
*acutidens* Ching in Ching & Wang, non C. Chr. = *purpurella*  
*adenorachis* C. Chr. = *fructuosa*  
*adiantoides* T. Suzuki = *hasseltii*  
*affinis* (Fischer & C. Meyer) Newman ex C. Chr., comb. inval. (in syn.) = *caucasica*  
*alexeenkoana* Fomin = *dilatata*  
*alpicola* Ching & Z. R. Wang, in press = *chrysocoma*  
*ambigens* (Franchet & P. A. L. Savat.) Koidz. = *uniformis*  
*ambigens* ('Nakai) Koidz. = *uniformis*  
*ambigua* Druce, nom. nud. = × *deweveri*  
*ambigua* Sledge = *deparioides* subsp. *ambigua* (Sledge) Fraser-Jenkins, in press  
*americana* (Fischer ex Kunze) Clute, nom. provis. (inval.) = *campyloptera*  
*amoena* Ching = *kwanzanensis*  
*amurensis* (Milde) Takeda, non Christ = *amurensis*  
*aneitensis* (Hook.) C. Chr. = ? *hasseltii*  
*angustipinna* Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*  
*aperta* (Fée) C. Chr. = *patula*  
*apicifixa* Ching, Boufford & Shing = *fructuosa*  
*apicisora* Ching & Y. T. Hsieh = *peninsulæ*

- aquilonaris* Maxon = *fragrans*  
*aristata* (Villars) Druce, non (G. Forster) Kuntze = *expansa*  
*assimilis* S. Walker = *expansa*  
*athyrioides* (M. Martens & Galeotti) Kuntze = *cinnamomea*  
*atrata* (Kunze) Ching = *hirtipes* subsp. *atrata* (Kunze) Fraser-Jenkins, in press  
*australis* (Ten.) Guadagno = *pallida*  
*austriaca* auct., non (Jacq.) Woyнар ex Schinz & Thell. = *dilatata*  
*balearica* (Litard.) Nardi = *pallida* subsp. *balearica* (Litard.) Fraser-Jenkins  
*barbellata* Fomin = *sichotensis*  
*basiaurita* Ching = *dickinsii*  
*bernieri* Tard. = *bojeri*  
*bipinnata* C. Chr. in A. L veill , non Copel. = *fuscipes*  
*blepharolepis* C. Chr. = *sublacera*  
*blinii* A. L veill  = *marginata*  
 × *bohemica* Domin, nom. inval. = *felix-mas*  
 × *borbasii* Litard. = *remota*  
*borreri* (Newman) Newman ex Tavel = *affinis* subsp. *borreri* (Newman) Fraser-Jenkins  
 × *boydii* (Stansf.) C. Morton = *remota*  
*bullatipaleacea* Ching = *championii*  
*bulligera* Ching = *erythrosora*  
 × *burnatii* Christ & Wilczek = *villarii*  
*buschiana* Fomin = *crassirhizoma* subsp. *crassirhizoma*  
*callolepis* C. Chr. = *antarctica*  
*canaliculata* Ching = *pulcherrima*  
*canaliculatis* Ching ex Fraser-Jenkins, nom. nud. = *pulcherrima*  
*caudifrons* Ching in Ching & Wang = *integriloba*  
*caudipinna* Nakai = ? *erythrosora*  
*cavalerii* A. L veill , non (Christ) C. Chr. = *fructuosa*  
 × *cebennae* Fraser-Jenkins = *tyrrhena*  
*centro-chinensis* Ching = *rosthornii*  
*changii* Ching, non *zhangii* Ching = *championii*  
*changtounensis* Ching ex Fraser-Jenkins, nom. nud. = *pulcherrima*  
*chapaensis* C. Chr. & Ching ex Ching = *polita*  
*chichisimensis* Nakai ex H. It  = *insularis*  
*chingii* Nair = *pulcherrima*  
*cochin-chinensis* Ching, nom. nud. = *integriloba*  
*confertipinna* Ching & Shing = *fuscipes*  
*constantissima* Hayata = *formosana*  
*cordipinnula* C. Chr. = *remotipinnulata*  
*coreano-montana* Nakai = *sichotensis*  
*cyrtolepis* Hayata = *wallichiana*  
*decurrentiloba* Ching & C. F. Zhang, in press = *uniformis*  
*dehuaensis* Ching & Shing = *bissetiana*  
*dentipalea* Nakai = *uniformis*  
*discreta* Ching & S. K. Wu = *pulcherrima*  
*dispar* Ching & C. F. Zhang, in press = *fuscipes*  
 × *doeppii* Rothm. = *remota*  
*doiana* Tag. = *wallichiana*  
 × *doluchanovii* A. Askerov = *remota*  
*doniana* (Spreng.) Ching = *wallichiana*  
*doshunglaensis* Ching & S. K. Wu, nom. nud. = *alpestris*  
*elongata* (Aiton) T. Sim, non (J. Smith) Kuntze = *aitoniana*  
*elongata* '(Sw.) Chev.' = *aitoniana*  
*emigrans* Copel. = *deparioides* subsp. *concinna* C. Chr.  
*enneaphylla* (Baker) C. Chr. = *sieboldii*  
*espinosai* Hicken = *karwinskyana*  
*euspinulosa* (Asch.) Fomin, nom. inval. = *carthusiana*  
*extremiorientalis* V. Vassiljev, nom. nud. = *expansa*

- falconeri* (Hook.) Kuntze = *barbigera* subsp. *barbigera*  
*fatuhivensis* E. Brown = ? *hirtipes* subsp. *hirtipes*  
*fenyangshanensis* Ching & C. F. Zhang, in press = *cycadina*  
*fibrillosa* (C. B. Clarke) Hand.-Mazz., non (Baker) C. Chr. = *pulcherrima*  
*fibrillosissima* Ching = *pulcherrima*  
*floridana* (Hook.) Kuntze = *ludoviciana*  
*fournieri* (Baker) C. Chr. = *mexicana*  
*fuliginosa* C. Chr. = *cognata*  
*gamblei* (C. Hope) C. Chr. = *stenolepis*  
*gillespiei* Copel. = *aneitensis*  
*giraldii* (Christ) C. Chr. [lectotype: 'Nephrod. non elongatum, sed var. giraldii n. var. Christ, Alla meta del monte Si-Ku-Tzui-San, J. Giraldi, [18] Juglio 1894' (P!)] = *sericea*  
*gongboensis* Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press  
*gracillima* Ching = *deparioides* subsp. *gracillima* (Ching) Fraser-Jenkins, in press  
*grandissima* Tag. = *marginata*  
*grossa* (Christ) C. Chr. = *scottii*  
*gushanica* Ching & Shing = *bissetiana*  
*gushiangensis* ['*gushaigensis*'] Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press  
*gutishanensis* Ching & C. F. Zhang, in press = *championii*  
*harae* H. Itô = *pulvinulifera*  
*hatusimae* H. Itô = *hasseltii*  
*hayatae* Tag. = *subexaltata*  
*heleopteroides* Christ = *cochleata*  
× *hercynica* Rothm., nom. nud. = *carthusiana*  
*heterolepia* Alderw. = *chaerophyllifolia*  
*heteroneura* (Tag.) Ching = *pseudosieboldii*  
*hirtosparsa* Y. C. Wu, non Christ = *integriloba*  
*hololepis* (Hayata) Tag. = *varia*  
*hopei* Fraser-Jenkins ex Rush, nom. nud. = *caroli-hopei*  
*huangangshanensis* Ching = *rosthornii*  
*hunanica* Ching = *kinkiensis* [juvenile]  
*hupehensis* Ching = *rosthornii*  
*hwangii* Ching = *integriloba*  
*hypophlebia* Hayata = *fructuosa*  
*immixta* Ching = *bissetiana*  
*indecora* (Liebm.) C. Chr. = *cinnamomea*  
*indusiata* (Makino) Makino & Yamamoto ex Yamamoto = *tenuicula*  
*infrahrtella* Ching & Z. Y. Liu, in press = *championii*  
*infrapuberula* Ching, Boufford & Shing = *namegatae*  
*integripinnula* Ching = *cordipinna*  
*inuyamensis* H. Itô = *fuscipes*  
*jiulongshanensis* Chiu & Yao ex Ching = *purpurella*  
*julaodongensis* Ching & Z. R. Wang in Z. R. Wang & Z. X. Zhang, nom. nud. = *rosthornii*  
*junlianensis* Kung = *lepidopoda*  
*kaihuaensis* Ching & C. F. Zhang, in press = *fuscipes*  
*kemulariae* Mikheladze = *remota*  
*kobayashii* Kitagawa = *sacrosancta*  
*kodamae* Hayata = *formosana*  
*komarovii* Kossinsky = *barbigera* subsp. *komarovii* (Kossinsky) Fraser-Jenkins, in press  
*kongboensis* Ching ex Fraser-Jenkins, nom. nud. = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press  
*kooshiangensis* Ching ex Fraser-Jenkins, nom. nud. = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press  
*koraiensis* Tag. = *gymnophylla*  
*kuratae* Nakaike, nom. nud. = ? *hangchowensis*  
*labordei* (Christ) C. Chr. = *gymnosora*  
*laeta* (V. Komarov) C. Chr., non (Sw.) C. Chr. = *goeringiana*

- lanceolato-cristata* (Hoffm.) Alston = *carthusiana*  
*lancifrons* Hayata ex Fraser-Jenkins, nom. nud. = *fructuosa*  
*lancipinnula* Ching, nom. nud. = *subimpressa*  
 × *laschii* E. Walter = × *uliginosa*  
*laserpitiifolia* (Scortech. ex Beddome) C. Chr., non (Mett.) Kuntze = *hasseltii*  
*lastii* (Baker) C. Chr. = *kilemensis*  
*latibasis* Ching = *lepidopoda*  
*laurisilvicola* T. Suzuki = *polita*  
 × *lawalreei* Janchen = *remota*  
*layardii* (Baker) C. Chr. = *aneitensis*  
*lepidorachis* C. Chr. = *championii*  
*lepinei* (Kuhn) Kuntze = *dicksonioides*  
*leveillei* Nakai, non Christ = *marginata*  
*libanotica* (Rosenstock) C. Chr. = *pallida* subsp. *libanotica* (Rosenstock) Nardi  
*likiangensis* Ching, non *lichiangensis* (C. H. Wright) C. Chr. = *montigena*  
*liliana* Golitsin [Golitsin] = *aemula*  
*linganensis* Ching & C. F. Zhang, in press = *championii*  
*lingtzeensis* Ching ex Fraser-Jenkins, nom. nud. = *sublacera*  
*linyingensis* Ching & C. F. Zhang, in press = *erythrosora*  
 × *litardierei* Rothm. = *oreades*  
*lividis* Ching & C. H. Wang = *polita*  
*liyangensis* Ching & Lan = ? *erythrosora*  
*longistipes* Ching = *lepidopoda*  
*ludens* (Baker) C. Chr. = *arborescens*  
*macaronesica* Romariz = *aitoniana*  
*macrocarpa* R. Stewart = *chrysocoma*  
 × *madeniana* Kunkel, nom. nud. = *oligodonta*  
*maderensis* Milde ex Alston = *intermedia* subsp. *maderensis* (Milde ex Alston) Fraser-Jenkins  
*makinoi* Koidz. = *fuscipes*  
*manshurica* Ching ex Wang et al. = *expansa*  
*matsuzoana* Koidz. = *varia*  
*maxima* (Baker) C. Chr. = *arborescens*  
*medioxima* Koidz. = *fuscipes*  
*mediterranea* Fomin = *wallichiana*  
*mehrae* Khullar, nom. nud. = *blanfordii* subsp. *blanfordii*  
*melanocarpa* Hayata = *platypus*  
*melanolepis* (Alderw.) Alderw., comb. inval. (in syn.) = *scottii*  
*metafuscipes* Ching & C. F. Zhang, in press = *erythrosora*  
*metcalfii* Ching = *marginata*  
*mimetica* Ching & C. F. Zhang, in press = *cordipinna*  
*mingetsensis* Hayata ex Fraser-Jenkins, nom. nud., non *mingetsuensis* Hayata = *fructuosa*  
*mingetsuensis* Hayata = *reflexosquamata*  
*minimisora* Nakai = *expansa*  
*minjiangensis* Kung = *sublacera*  
 × *mixta* Rothm., nom. nud., non Rosenstock = × *mantoniae*  
*monticola* (Makino) C. Chr. = *goldiana* subsp. *monticola* (Makino) Fraser-Jenkins  
*morrisonensis* (Hayata) Hayata = *expansa*  
*multijugata* Ching & Shing ex Ching & C. F. Zhang, in press = *fuscipes*  
*nakanensis* Ching = *microlepis*  
*nanchuanensis* Ching & Liu, in press = *tenuicula*  
 × *neglecta* Domin, non Brade & Rosenstock = ? × *deweveri*  
*neoassamensis* Ching = *assamensis*  
*neochrysocoma* Ching = *woodsiiisora*  
*neolacera* Ching = *peninsulae*  
*neolepidopoda* Ching & S. K. Wu = *lepidopoda*  
*neopodophylla* Ching = *podophylla*  
*nigra* Ching = *lepidopoda*  
*nigrisquama* Hayata = *scottii*

- nigrosquamosa* Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press  
*nilamoensis* Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*  
*nipponensis* Koidz. = *cystolepidota*  
*nyalamensis* ['nyalamense'] Ching & S. K. Wu = *pulcherrima*  
*nyingchiensis* Ching = *sublacera*  
*obovata* (Baker) C. Chr. = *hasseltii*  
*obtusissima* (Makino) Makino, non (Mett. ex Kuhn) Christ = *fuscipes*  
*obtusissima* (Mett. ex Kuhn) Christ, non (Makino) Makino = *macrochlamys*  
*odontophora* Copel. = *aneitensis*  
*ogawae* ['ogawai'] H. Itô = *varia*  
*okushirensis* Miyabe & Kudô = *dickinsii*  
*omeicola* Ching = *rosthornii*  
*oxyodon* (Franchet) Kitagawa, non *oxyodus* (Baker) C. Chr. = *goeringiana*  
*pachyphylla* Hayata = *wallichiana*  
*paleacea* Hand.-Mazz., non (Lagasca ex Sw.) C. Chr., nec (T. Moore) Fomin = *wallichiana*  
*paleacea* (Lagasca ex Sw.) C. Chr., non Hand.-Mazz., nec (T. Moore) Fomin = *wallichiana*  
*paleacea* (T. Moore) Fomin, non (Lagasca ex Sw.) C. Chr., nec Hand.-Mazz. = *wallichiana*  
*paleacea* '(Don) Druce' = *wallichiana*  
*paleacea* '(Don) Hand.-Mazz.' = *wallichiana*  
*paleacea* '(Sw.) Hand.-Mazz.', comb. inval. = *wallichiana*  
*pallida* '(Bory) Fomin' = *pallida*  
*pandurata* Ching ex Fraser-Jenkins, nom. nud. = *basisora*  
*para-chrysocoma* Ching & Z. R. Wang = ? *chrysocoma*  
*parallelogramma* (Kunze) Alston = *wallichiana*  
*parasparsa* Ching & S. K. Wu = *sparsa*  
*patagonica* Diem = *felix-mas*  
*patentissima* (Wallich ex Kunze) Nair = *wallichiana*  
*patentissima* '(Franch.) Nair' = *wallichiana*  
*persimilis* Ching & C. F. Zhang, in press = *fuscipes*  
*petelotii* C. Chr. = *polita*  
*phaeocoma* Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *lepidopoda*  
*phaeolepis* Hayata = *formosana*  
*platylepis* Rosenstock = *kilemensis*  
*poilanei* Tard. = *bodinieri*  
 × *poyseri* Wherry = *clintoniana*  
*pseudatrata* Ching = *cycadina*  
*pseudoerythrosora* Ching & C. F. Zhang, in press, non Kodama = *erythrosora*  
*pseudo-erythrosora* Kodama, non Ching & C. F. Zhang = *championii*  
*pseudodontoloma* Ching = *lachoongensis*  
*pseudofibrillosa* Ching = *redactopinnata*  
*pseudo-felix-mas* Nakai & Kodama, nom. nud., non (Fée) Rothm. = *crassirhizoma* subsp. *crassirhizoma*  
*pseudo-lunanensis* Tag. = *dickinsii*  
*pseudomarginata* Ching, nom. nud. = *caroli-hopei*  
*pseudomas* (Wollaston) Holub & Pouzar = *affinis* subsp. *affinis*  
*pseudo-sabae* ['pseudo-sabaei'] Hayata = *fructuosa*  
*pseudo-sikkimensis* Ching & S. K. Wu = *sikkimensis*  
*pseudosparsa* Ching = *purpurella*  
*pseudouniformis* Ching = *uniformis*  
*pseudovaria* (Christ) C. Chr. = *fructuosa*  
*psilosora* Tag. = *hasseltii*  
*pudouensis* Ching, in press = *pacifica*  
*qamdoensis* Ching = *pulcherrima*  
*quatanensis* Ching = *wallichiana*  
*raddeana* (Fomin) Fomin = *pallida* subsp. *raddeana* (Fomin) Nardi  
*raynalii* Tard. = *manniana*  
*reflexipinna* Hayata = *diffracta*  
*reholtumii* M. Price, nom. nud. = *pulvinulifera*

- remota* '(A. Br.) Hayek' = *remota* (A. Braun ex Doell) Druce, non Hayata  
*remotipinnata* Ching & C. F. Zhang, in press = *fuscipes*  
*remotissima* (Christ ex Matsum.) Koidz. = *sabae*  
*resendeana* Rezende-Pinto = *affinis* subsp. *affinis*  
*retroso-paleacea* Ching & C. F. Zhang, in press = *cordipinna*  
*rhomboideo-ovata* H. Itô = *hondoensis*  
*rigida* (Sw.) A. Gray = *villarii*  
*rigida* '(Hoffm. ex Sw.) Gray' = *villarii*  
*rigida* '(Sw.) Underw.' = *villarii*  
*rossii* (C. Chr.) C. Chr. = ? *glandulifera*  
*rubristipes* Ching & Z. Y. Liu, in press = *purpurella*  
*saamingensis* Ching = *tokyoensis*  
*sakurii* (Rosenstock) Tag. = *gymnophylla*  
 × *satumana* Kurata = × *pseudo-commixta*  
*schneideriana* Hand.-Mazz. = *sublacera*  
 × *schorapanensis* A. Askerov = *affinis* subsp. *persica* Fraser-Jenkins  
*semipinnata* Ching = *lunanensis*  
*setosa* (Christ) Kudô, non (Thunb.) Akas., nec (Blume) Kuntze, nec (C. Presl) C. Chr. = *sichotensis*  
*setosa* (Thunb.) Akas., non (Blume) Kuntze, nec (C. Presl) C. Chr., nec (Christ) Kudô = *bissetiana*  
*shensicola* Ching & Y. T. Hsieh = *peninsulae*  
*silaensis* Ching = *acuto-dentata*  
*simulans* Ching, non (Baker) Kuntze = *sri-lankensis*  
*sinoerythrosora* Ching & Shing = *erythrosora*  
*sinoefibrillosa* Ching = *pulcherrima*  
*sinosparsa* Ching & Shing = *viridescens*  
*siranensis* Nakai = *expansa*  
*spinulosa* (Roth) Kuntze = *carthusiana*  
*spinulosa* '(Müll. ex Roth) O. Ktze.' = *carthusiana*  
*squamifera* ['*squamigera*'] Ching & S. K. Wu = *pulcherrima*  
 × *subalpina* (Borbás) Domin, non Alderw. = *remota*  
*subassamensis* Ching = *subtriangularis*  
*subatrata* Tag. = *cycadina*  
 × *subaustriaca* Rothm. = *remota*  
*subbarbigera* Ching = *barbigera* subsp. *komarovii* (Kossinsky) Fraser-Jenkins, in press  
*subdecipiens* Hayata = *scottii*  
*subintegriloba* Seriz. = *integriloba*  
*sublaeta* Ching & Y. P. Hsu = *goeringiana*  
*submarginalis* Ching, Boufford & Shing = *crassirhizoma* subsp. *whangshangensis* (Ching) Fraser-Jenkins  
*submarginata* Loyal, non Rosenstock = *subimpressa*  
*submarginata* Rosenstock, non Loyal = *tenuicula*  
*submonticola* Nakai = *goldiana* subsp. *monticola* (Makino) Fraser-Jenkins  
*subodontoloma* Ching ex Loyal, nom. nud. = *subimpressa*  
*subopposita* Kodama ex Nakai, non Kuntze ex T. Mori = *expansa*  
*subramosa* Christ = *goeringiana*  
*sunnii* Ching = *pycnopteroides*  
*supraimpressa* Ching, Boufford & Shing = *porosa*  
*tabacicomma* Alderw. = *subarborea*  
*tahmingensis* Ching = *integriloba*  
*taitoensis* Tag., non *taitunensis* Koidz. = *polita*  
*taiwanicola* Tag. = *lepidopoda*  
*takesimensis* Kodama ex Nakai = *erythrosora*  
*takeuchiana* Koidz. = *formosana*  
*taquetii* Christ = *erythrosora*  
*tarningensis* Ching = *fuscipes*  
*tasiroi* Tag. = *handeliana*  
 × *tauschiei* (Čelak.) Domin = × *uliginosa*  
 × *tavelii* Rothm. = *affinis* subsp. *borreri*  
*tenuissima* Tag. = *woodsii* *sora*

- thibetica* (Franchet) C. Chr. = *dickinsii*  
*thwaitesii* (Baker) Kuntze, non (Hook.) C. Chr. = *deparioides* subsp. *concinna* C. Chr.  
*tieluensis* Ching & Y. P. Hsu = *basisora*  
*tienmohshangensis* Ching = *uniformis*  
*triangularifrons* Ching = *gymnosora*  
*tsangpoensis* Ching = *redactopinnata*  
*tsayüensis* Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*  
*tsutsuiana* Kurata = *namegatae*  
*undulata* (Beddome) Kuntze = *macrochlamys*  
*uropinna* M. Price = *subtriangularis*  
*ursipes* Hayata = *wallichiana*  
*venosa* Ching & S. K. Wu = *lachoongensis*  
*vescoi* (Drake) C. Chr. = *dicksonioides*  
*villarsii* auct. = *villarii*  
*viridis* Ching = *polita*  
*wenchuanensis* Kung = ? *habaensis*  
*whangshangensis* Ching = *crassirhizoma* subsp. *whangshangensis* (Ching) Fraser-Jenkins  
*wherryi* Crane = *celsa*  
*wladiwostokensis* B. Fedtsch. = *goeringiana*  
 × *woynarii* Rothm. = *remota*  
*wuyishanensis* Ching = *kinkiensis*  
*xanthomelas* (Christ) C. Chr. = *rosthornii*  
*yabei* Hayata = *varia*  
*yakusilvicola* Kurata = *cacaiana*  
*yandongensis* Ching & C. F. Zhang, in press = *kinkiensis*  
*yaoi* Ching = *tenuicula*  
*yikungensis* Ching ex Fraser-Jenkins, nom. nud. = *yigongensis*  
*yui* Ching = *bonatiana*  
*yungtzeensis* Ching = *dickinsii*  
 × *yuyamae* Kurata = × *hakonecola*  
*zayüensis* Ching & S. K. Wu = *pulcherrima*  
*zhangii* Ching, in press, non *changii* Ching = *tenuicula*

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Accepted names are given in roman and synonyms in *italic*; new names and principal page references are in **bold**. An asterisk (\*) denotes a figure. See pp 207–213 for a list of synonyms.

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