Morphology and anatomy of the rhizome and frond in the African species of *Polystichum* (Pteropsida: Dryopteridaceae)

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ABSTRACT

The generic circumscription of the polystichoid ferns within the Dryopteridaceae and their relationships has been and still is much debated. Although floristic accounts for *Polystichum* are available for many parts of the world, its morphology and evolutionary trends within the genus are still poorly understood. In this study, primarily based on the *Polystichum* species from Africa and neighbouring islands, the morphology and anatomy of the rhizome and frond are addressed. Several species from other genera within the Dryopteridaceae are used for comparison, to gain a better understanding of generic affinities and evolution in this family.

INTRODUCTION

Polystichum Roth is a cosmopolitan genus comprising 180 to 200 species. Although floristic accounts of the genus exist for many parts of the world, a comprehensive modern taxonomic account for the genus as a whole has never been undertaken. The circumscription and definition of species within the genus are still weak. Reasons for the group's inadequate taxonomic status include the occurrence of common and widespread allopolyploid taxa (D.H. Wagner 1979), sterile F1 hybrids, apomictic taxa, substantial phenotypic variation within populations and in most cases, a lack of critical morphological studies.

The morphology and anatomy of *Polystichum* representatives from the Indian subcontinent was studied by Chandra & Nayar (1982) and those of western North America by D.H. Wagner (1979). *Polystichum*, *Arachniodes* Blume, *Cyrtomium* C.Presl, *Dryopteris* Adans. and *Phanerophlebia* C.Presl form a closely related group of genera within the tribe Dryopterideae and are here referred to as the polystichoid ferns. *Cyrtomium* and/or *Phanerophlebia* are often included in *Polystichum* (Tryon & Tryon 1982; Kramer 1990). Yatskievych (1996), however, treated *Cyrtomium* and *Phanerophlebia* as distinct genera and showed that both have a closer affinity with *Polystichum* than with each other, a hypotheses first proposed by Christensen (1930). The genera *Arachniodes*, *Dryopteris* and *Polystichum* are not always clearly separable, as each include species that display characters generally associated with the other genera. The proposed close affinity of these genera is also supported by the occurrence of a natural hybrid between *Dryopteris* and *Polystichum* (W.H. Wagner 1985). Widén *et al.* (1981) showed that phloroglucinols widespread in *Dryopteris* also occur in *Arachniodes* but are rare in *Polystichum*. Indusia, when present, are peltate in *Polystichum* and reniform in *Arachniodes* and *Dryopteris*. All these genera, however, also contain species that are exindusiate.

This study is primarily based on *Polystichum* species from Africa, Macaronesia, the Madagascan region and the Marion Island groups, but observations on species from outside of this region are also considered. For comparative purposes several species from other genera within the Dryopterideae were included in the study. The aim is to gain a better understanding of generic affinities within the Dryopterideae and to speculate on possible evolutionary trends within the group.

MATERIALS AND METHODS

Material used in the anatomical study was obtained from the wild and from cultivated plants (Table 1). Voucher specimens are housed at the Compton Herbarium (NBG). Fresh material was fixed in FAA for at least 24 hours. For rhizomes, serial sections were cut by hand, stained with alcian blue for one minute, rinsed in water and temporarily mounted in glycerine. Camera lucida drawings were prepared at × 7.5, × 15 or × 31.25 magnifications using a Wild 'Heerbrugg' microscope. The stelar structure of the rhizome was reconstructed using these sections.

Roots, stipes, rachises, secondary rachises and laminae were sectioned 45 µm thick using a Reichert-Jung Hn 40 freeze microtome. Sections were stained with safranin and alcian blue for one minute, rinsed in water and dehydrated in a series of 50% ETOH, 40% ETOH:60% toluene, 20% ETOH:80% toluene and 100% toluene, after which they were permanently mounted in Entellan (Art. 7961, E. Merck, Darmstadt).

For describing the vasculature of the stipe and lamina fresh material was used; freehand serial sections were made at 2.5 or 5 mm intervals along the entire length of the axis, noting where bundles divide or fuse and where pinnae and pinnules originate.

Epidermal features were studied using pinna or pinnule fragments removed from selected specimens, and

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TABLE 1.—Material examined in the study of the rhizome and frond stelar structure

Taxon	Voucher	Origin
Rhizome		
Arachniodes webbiana (A.Br.) Schelpe subsp. *foliosa* (C.Chr.) Gibby *et al.*	*Roux 2573*	NORTHERN PROVINCE.—2329 (Pietersburg): Louis Trichardt, Hanglip Forest Station, (–BB).
Polystichum		
dracomontanum Schelpe & N.C.Anthony	*Roux 2715*	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, Tugela Gorge, (–DB).
incongruum J.P.Roux	*Roux 2678*	EASTERN CAPE.—3227 (Stutterheim): Amabele, (–DA).
incongruum J.P.Roux	*Roux 2695*	EASTERN CAPE.—3226 (Fort Beaufort): Hogsback Forest Station, (–DB).
incongruum J.P.Roux	*Roux 2713*	WESTERN CAPE.—3322 (Oudtshoorn): Knysna, Touws River, (–DC).
macleae (Baker) Diels	*Roux 2561*	MPUMALANGA.—2530 (Lydenburg): Sabie, (–BB).
monticola N.C.Anthony & Schelpe	*Roux 2513*	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
transkeiense W.B.G.Jacobsen	*Roux 2540*	KWAZULU-NATAL—2731 (Louwsburg): Ngome Forest Reserve.
transvaalense N.C.Anthony	*Roux 2510a*	KWAZULU-NATAL—2828 (Bethlehem): Royal Natal National Park, (–DB).
wilsonii H.Christ	*Roux 2521*	FREE STATE.—2829 (Harrismith): Harrismith, Platberg, (–AC).
Frond		
Cyrtomium caryotideum (Wall. ex Hook. & Grev.) C.Presl var. *micropterum* (Kunze) C.Chr.	*Roux 501*	EASTERN CAPE.—3325 (Port Elizabeth): Settler's Park, (–DC).
Dryopteris		
antarctica (Baker) C.Chr.	*Roux 2632*	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, (–AC).
athamantica (Kunze) Kuntze	*Roux 348*	GAUTENG.—2627 (Potchefstroom): Roodepoort, Strubens Valley, (–BB).
dracomontana Schelpe & N.C.Anthony	*Roux 2764*	LESOTHO.—2928 (Marakabeis): Semonkong, LeBihan, (–CC).
inaequalis (Schltdl.) Kuntze	*Roux 1975*	EASTERN CAPE.—3129 (Port St Johns): Port St Johns, (–DA).
inaequalis (Schltdl.) Kuntze	*Roux 1933*	KWAZULU-NATAL.—2831 (Nkandla): Nkandla Forest, (–CA).
pentheri (Krasser) C.Chr.	*Roux 1984*	EASTERN CAPE.—3227 (Stutterheim): Isidinge Forest, (–CA).
pentheri (Krasser) C.Chr.	*Roux 1989*	EASTERN CAPE.—3227 (Stutterheim): Evelyn Valley Forest, (–CA).
pentheri (Krasser) C.Chr.	*Roux 1892*	FREE STATE.—2829 (Harrismith): Farm Metz, (–CA).
Polystichum		
dracomontanum Schelpe & N.C.Anthony	*Roux 2715*	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
incongruum J.P.Roux	*Roux 2678*	EASTERN CAPE.—3227 (Stutterheim): Amabele, (–DA).
luctuosum (Kunze) T.Moore	*Roux 2709*	EASTERN CAPE.—3227 (Stutterheim): Pirie Forest, (–CB).
macleae (Baker) Diels	*Roux 2548*	MPUMALANGA.—2430 (Pilgrim's Rest): Graskop, (–DD).
monticola N.C.Anthony & Schelpe	*Roux 2520*	KWAZULU-NATAL.—2829 (Harrismith): forest south of Seheletwane, (–AC).
pungens (Kaulf.) C.Presl	*Roux 2370*	WESTERN CAPE.—3318 (Cape Town): Table Mountain, (–CD).
setiferum (Forssk.) T.Moore ex Woyn.	*Sine coll. s.n.*	Madeira.
transkeiense W.B.G.Jacobsen	*Roux 2498*	EASTERN CAPE.—3029 (Kokstad): Weza Forest, (–DA).
transvaalense N.C.Anthony	*Roux 2516*	KWAZULU-NATAL.—2829 (Harrismith): forest south of Seheletwane, (–AC).

cleared using household bleach. Once cleared the material was repeatedly rinsed in clean water and semi-permanently mounted in either glycerine or glycerine jelly. Cover slips were sealed with Entellan.

RESULTS AND DISCUSSION

MORPHOLOGY

Rhizome

Detailed studies of the rhizome of *Polystichum* are scant and its morphology remains poorly known. The rhizome anatomy of *Cyrtomium falcatum* was studied by Gibson *et al.* (1984) and found to be basically identical to that of *Polystichum*. Rhizomes are rarely represented in herbarium collections, hence in modern floristic accounts they are often not mentioned. In many species the rhizome is bulky and this may explain why most collectors are deterred from collecting them. The *Polystichum* species studied by Chandra & Nayar (1982) in India, all have short, stout, and erect rhizomes that are mostly unbranched. In African species two distinct rhizome types, namely, erect and decumbent occur. The erect rhizome type is short and generally unbranched with a large number of fronds crowded in the apical region (Figure 1A). Up to seven leaf gaps overlap at any given time. This rhizome type is sheathed by a mass of wiry roots, with

FIGURE 1.—Rhizome and lamina morphology. A–D, *Polystichum*: A, erect rhizome type in *P. transvaalense*, *Roux 2585*. B, C, *P. incongruum*: B, decumbent rhizome type, *Roux 2377*; C, acroscopic proximal pinnules, basiscopic pinnule shows free venation, *Roux 2385*. D, *P. macleae*, *Roux 2242*, acroscopic pinna, section shows free venation. E, L, M, *Arachniodes webbiana* subsp. *foliosa*, *Roux 1001*: E, basiscopic proximal pinnule; L, rachis section showing confluent nature of axes sulci; M, pinnule segment showing venation. F, *Dryopteris inaequalis*, *Taylor 4264*, basiscopic proximal pinnule and acroscopic pinnule with free venation; G, *Cyrtomium caryotideum* var. *micropterum*, *Roux 1913*, section of pinna outline with reticulate venation; H, *Phanerophlebia auriculata*, pinna outline with section showing venation, after Yatskievych (1996). I, J, *P. transkeiense*, *Roux 2493*: I, proximal part of rachis showing non-confluent nature of axes sulci; J, distal part of rachis showing confluent nature of axes sulci; K, *C. falcatum ex hort.*, non-confluent nature of sulci. All vouchers housed in NBG. Scale bars: A, B, 2 mm; C, I–M, 5 mm; D–F, 10 mm; G, H, 20 mm.
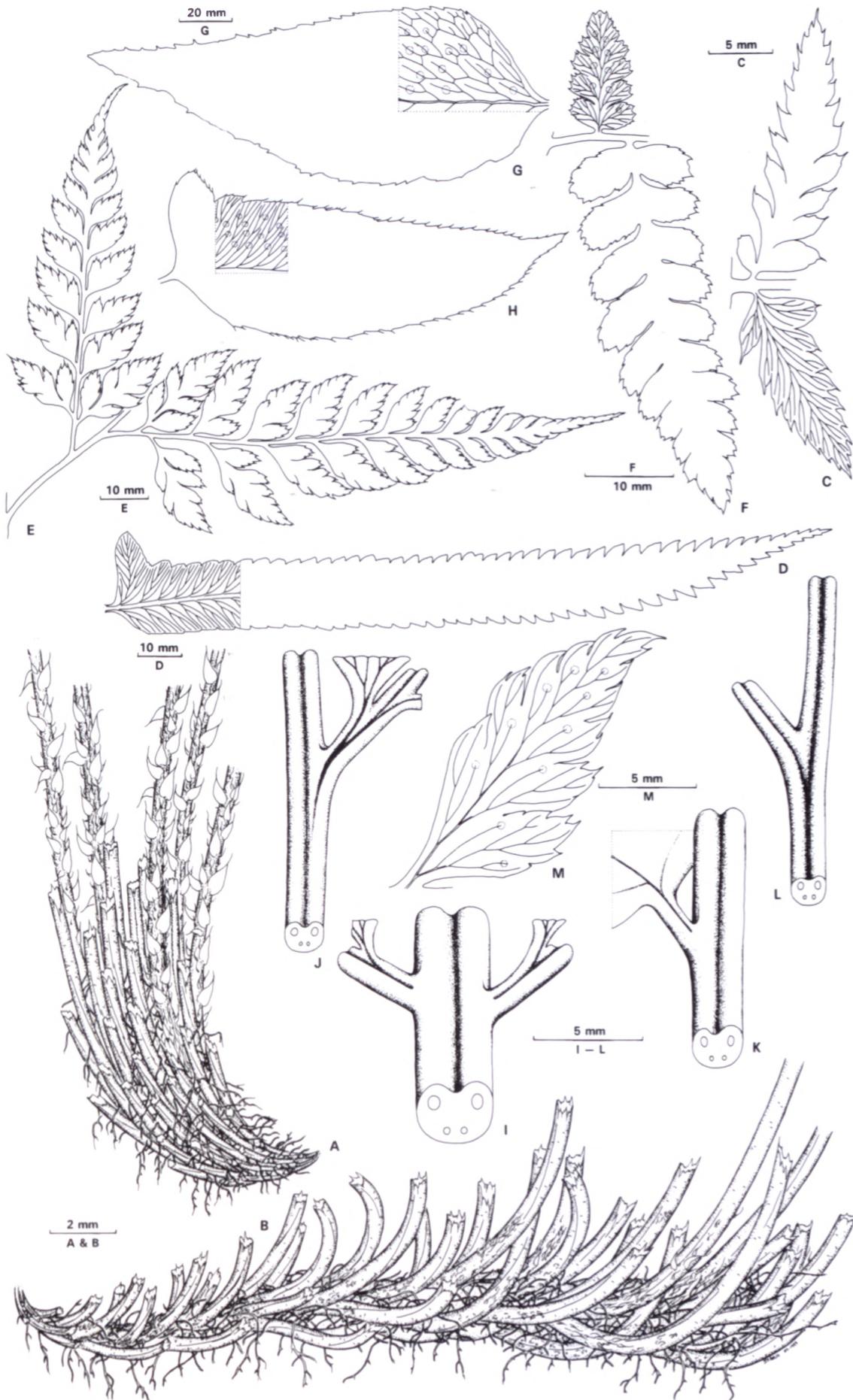
helically arranged persistent stipe bases several layers deep and, at least in the younger parts, also with paleae, giving greater bulk to the rhizome; the highly dissected stellar structure suggests that it is derived. The decumbent rhizome type is usually long and branched, terete to slightly laterally or dorsoventrally flattened; up to five leaf gaps overlap at a time; the fronds are generally more widely spaced, often exposing the rhizome internodes (Figure 1B). In both rhizome types paleae form a dense covering especially over the apical region.

Branching of the rhizome takes place through the formation of lateral buds at regular or irregular intervals along the main stem. Branching in *Polystichum transkeiense* W.B.G.Jacobsen is regular. In certain habitats, *P. incongruum* J.P.Roux, *P. monticola* N.C.Anthony & Schelpe and *P. pungens* (Kaulf.) C.Presl also show regular branching. In *P. dracomontanum* Schelpe & N.C.Anthony and *P. marionense* Alston & Schelpe, lateral buds initiate the formation of long stoloniferous outgrowths. As a result, large clonal stands are formed by these species. Fronds are initially widely spaced along these stolons but marked primary thickening takes place distally, and the fronds become more closely spaced. Roots are irregularly formed over the entire length of the stolons. Since the thinner stoloniferous branches can rot away more readily, individual rhizomes may become isolated thus serving as a means of clonal propagation.

Branching and stolon formation is here viewed as an adaptation for plants occurring in environments not always conducive to sexual reproduction. Species with this type of rhizome often occur in more exposed, often dryish habitats that may also be subjected to periodic fires. It is therefore also possible that the clonal habit might be an adaptation to periodic burning. The short, suberect to erect rhizome type is, however, much more common in the genus. In contrast to the decumbent rhizome type, the erect rhizome of the African species mostly remains unbranched resulting in these species occurring as individuals rather than as clonal clusters. Plants with this rhizome type are also adapted to a wide range of habitat conditions, but tend to be more site-specific. The erect rhizome is generally well seated in the substrate, whereas the decumbent rhizome type mostly grows epigeally, although the stolons of *P. dracomontanum* are subterranean. Occasionally the rhizome in *P. transkeiense* may also be subterranean.

Species in the genera *Arachniodes*, *Cyrtomium*, *Dryopteris* and *Phanerophlebia* have either erect or decumbent rhizomes. If the cyatheoid ferns are accepted as an ancestor of the dryopteroid ferns, as suggested by Bower (1928); Ching (1940); Copeland (1947); Nayar (1970, 1979) and Holttum (1973), then the short erect rhizome should be viewed as the primitive state and the decumbent rhizome as derived. However, a dennstaedtioid origin as proposed by Holttum (1947) and Pichi Sermolli (1977) would suggest the reverse. Hasebe *et al.* (1995) and Pryer *et al.* (1995) presented strong morphological and molecular evidence that Dennstaedtiaceae branched off the tree below the Dryopteridaceae, with Cyatheaceae considerably below that. The evolutionary transformation of the rhizome habit thus remains open to debate.

Roots

An abundance of wiry adventitious roots occurs irregularly over the entire surface of the rhizome, often forming a dense fibrous mass. Roots appear to be long-lived but they are, however, only initiated at or near the growing apex of the rhizome. Young roots are whitish to pale brown and mostly simple, whereas older roots are dark brown to black and frequently monopodially branched. Golden brown root hairs form a dense covering a short distance behind the root apex. They do, however, lose their function on the older parts of the roots and become abraded. In the erect rhizome type, roots also provide good anchorage.

Fronds

All the *Polystichum* species within the study area are evergreen; the fronds remain alive for at least two annual cycles. The fronds are persistent and are shed through decay or mechanical damage only. A type of frond re-orientation as described by Noodén & W.H. Wagner (1997), occurs in *P. wilsonii* H.Christ. In this high altitude species, which frequently grows in exposed sites, a large percentage of the fronds may collapse during the cold winter months. The plants are, however, never entirely deciduous. Frond length varies considerably among species and in *P. incongruum* it can attain a length of 1.8 m. There is a strong correlation between the rhizome type and the number of fronds borne by a plant. Species with an erect rhizome always bear more fronds than those with a decumbent rhizome. In *P. transvaalense* N.C.Anthony, up to 27 fronds are borne by each plant, whereas in species with a decumbent rhizome, the number of fronds rarely exceeds seven. Fronds in the *Polystichum* species studied are monomorphic, with no evident differentiation between the sterile and fertile fronds. The fronds are differentiated into a distinct stipe and lamina. Vernation of the fronds is initially circinate, but as the stipe and lamina elongate, the juvenile fronds become hook-shaped in species such as *P. dracomontanum*, *P. luctuosum* (Kunze) T.Moore, *P. transvaalense* and *P. wilsonii*. Monomorphic fronds are most common in the Dryopterideae, but in *Dryopteris*, e.g. *D. dracomontanum* Schelpe & N.C.Anthony, they are dimorphic.

Stipe

The use of stipe characters in fern taxonomy has been studied by Lin & De Vol (1977, 1978). They clearly illustrate that stipe characters, especially anatomy, are more useful at the generic and family level than at the species level. The stipe in all the studied species of *Polystichum* is firm. In species with erect rhizomes the stipes grow directly upwards, whereas in species with a decumbent rhizome, they are initially strongly curved upwards. Stipe length and diameter are variable but may be up to 930 mm long in *P. incongruum* and up to 10 mm diam. in *P. volkensii* (Hieron.) C.Chr. In most species the stipe base is variously rounded adaxially and abaxially, but distally they all become shallowly to deeply sulcate adaxially. In most taxa the basal part of the stipe is castaneous (brownish) to ebeneous (black) and often lustrous (nitid), becoming paler distally in dried material. In

live plants, however, the distal part of the stipe generally remains green. The stipe bases of the African *Polystichum* species appear not to be modified into distinct trophopods as described by W.H. Wagner & Johnson (1983). Trophopods have been reported for all the *Phanerophlebia* species with the exception of *P. macrosora* (Baker) Underw. (Yatskievych 1996). In most species the dorsolateral aerophore line is conspicuous throughout the length of the stipe, generally being somewhat paler in colour than the surrounding tissue. In *P. luctuosum* the aerophore line is often green, thus contrasting strongly with the generally castaneous to ebeneous stipe. The stipe is always clothed with paleae, the density of which shows considerable variation amongst the species.

Lamina

Most *Polystichum* species in the study area have 2-pinnate pinnatifid to 3-pinnate laminae, with 1-pinnate laminae recorded in *P. falcinellum* (Sw.) C.Presl, *P. kalambatitrense* Tardieu, *P. macleae* (Baker) Diels and *P. maevaranense* Tardieu only. *P. macleae* has laminae ranging from 1-pinnate to 2-pinnate. Lamina length varies considerably between species with the longest laminae, up to 925 mm, having been recorded in *P. volkensii* (Hieron.) C.Chr. Lamina outline also shows variation between species, but within a species the degree of variation is fairly restricted.

Pinnae and pinnules are borne subopposite to alternate on the rachis and secondary rachis. Proximally the pinnae and pinnules are usually short-stalked but distally they become sessile and eventually adnate. They are mostly herbaceous in texture, but in *P. dracomontanum* and *P. marionense*, both of which grow in harsh conditions, the pinnules are usually coriaceous. The lamina is always discolorous with the adaxial surface darker in colour. Adaxially the pinnules are pale to dark green in colour, but in *P. dracomontanum* and *P. incongruum* at Hogsback in the Eastern Cape, exposed and older fronds generally turn bronze.

Polystichum is characterised by a largely acroscopic pinna development (Figure 1C, D), but basiscopically developed laminae are often present in *P. vestitum* (G.Forst.) C.Presl and *P. whiteleggei* Watts. The degree to which the proximal acroscopic pinnules are developed shows considerable inter- and infraspecific variation. Interspecific variation is exemplified especially in *P. drepanum* (Sw.) C.Presl, *P. incongruum* and *P. macleae*.

In *Arachniodes* and *Dryopteris* the laminae are mostly basiscopically developed (Figure 1E, F). In *Arachniodes* and in *Cyrtomium* and *Phanerophlebia*, where most species have 1-pinnate laminae, the pinnae are also acroscopically developed and often conspicuously auricled (Figure 1G, H, M).

In *Polystichum* the pinnae are mostly oblong-acuminate to narrowly oblong-acuminate in outline, but in some species they may be ovate, narrowly triangular, or in *P. marionense* often deltoid. In some species the proximal pinnae are reduced towards the base of the frond,

and often also strongly conduplicate and deflexed. In most species the proximal pinnae are usually widely spaced with no or little overlap with the more distal ones. Towards the lamina apex, however, the pinnae frequently become imbricate. The number of stalked pinnae per lamina ranges from 12 to 15 in *P. maevaranense*, but up to 45 in *P. setiferum* (Forssk.) T.Moore ex Woyn. Pinna length in most species falls within the 100 to 200 mm range, but in *P. marionense* the pinnae may reach a maximum length of only 36 mm, whereas in *P. drepanum* the proximal pinnae may be up to 450 mm long.

Pinnules are always inaequilateral, asymmetric and variously ovate, trullate or rhomboid in outline, with an acroscopic auricle. The base is mostly truncate acroscopically whilst basiscopically it is mostly narrowly to broadly cuneate. Margins may be lobate, serrate, doubly serrate or dentate with the teeth being obtuse, pungent or aristate. Pichi Sermolli (1972), in describing *P. kilimanjaricum* Pic.Serm., emphasized the number and direction of the pinnule awns, but we found them to be extremely variable and of no taxonomic value. In *P. marionense* the pinnule margins of plants growing in exposed conditions are often revolute. The number of short-stalked pinnules per pinna ranges from five in *P. marionense* to 27 in *P. zambesiacum* Schelpe. Pinnules are mostly small, but in *P. drepanum* the proximal acroscopic pinnule can be up to 83 × 15 mm. Indumenta occur on both the adaxial and abaxial lamina surfaces of most species with the abaxial surface generally more densely set.

Rachis

Chromatically the rachis does not differ significantly from the stipe, being green throughout, but in older fronds it may become dark brown proximally. The aerophore line that extends from the stipe is generally visible with the naked eye and may be paler or darker in colour than the surrounding tissue. The rachis is mostly straight throughout its length but distally it may become slightly flexuose in some species. Adaxially the rachis forms a V-shaped sulcus along its entire length. In *P. luctuosum* the sulcus is shallow and not very prominent. Holttum (1959) stressed the importance of the external shape of the rachis in defining related groups: in the *Dryopteris*-group of ferns, to which *Polystichum* belongs, the rachis has a median sulcus that opens adaxially to admit the sulcus of the secondary rachises; the raised edges of the secondary rachis sulcus join the sides of the costa sulcus with the edge of the pinnule-lamina decurrent on the secondary rachis as a lateral wing.

Our observations on live *Polystichum*, *Cyrtomium* and *Dryopteris* material show that the rachis sulcus does not always open to admit the secondary rachis sulcus, as the pinna stalk is often terete, especially in the lower part of the lamina (Figure 1I, J, K). In *Arachniodes*, however, the sulci of the rachis and that of the lower order axes are confluent (Figure 1L). Paleae similar to those occurring on the stipe extend to the rachis. Palea density on the rachis is, however, determined by the species and to a lesser degree also by the prevailing environmental conditions.
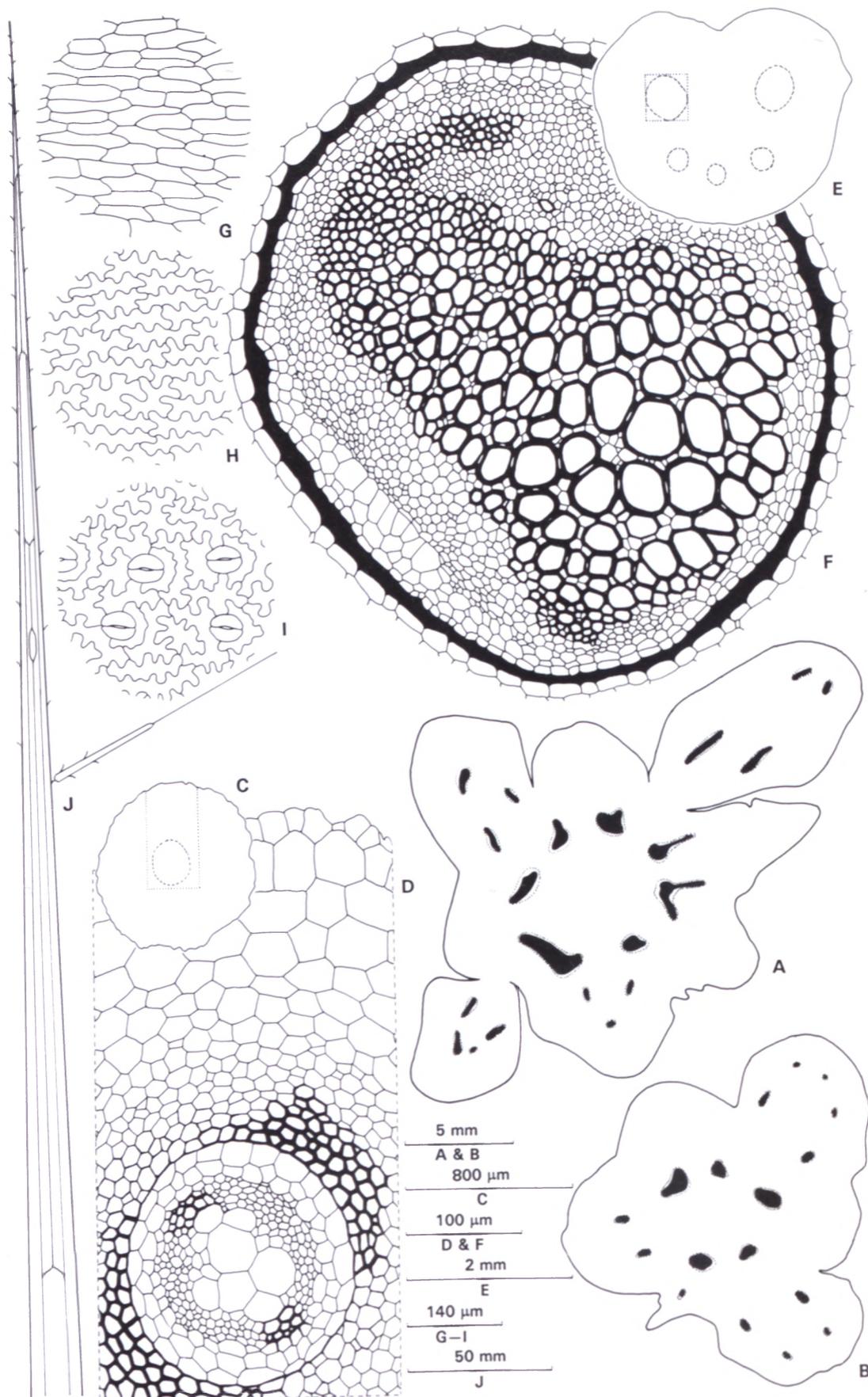
FIGURE 2.—Rhizome, root and frond anatomy in *Polystichum*. A, B, t/s rhizomes showing distribution of vascular tissue: A, *P. transvaalense, Roux 2510A* (NBG); B, *P. dracomontanum*. C, t/s root; D, t/s root showing vascular and non-vascular tissue. E, t/s rachis; F, t/s dorsal vascular bundle of rachis. G, *P. crinulosum, sine coll. s.n.* (P), adaxial epidermis; H, I, *P. aculeatum, Maire s.n.* (RAB), adaxial and abaxial epidermal cells; J, *P. transkeiense, Roux 2498* (NBG), schematic presentation of frond vasculature showing branching and fusion of vascular bundles along axes. B–D, *Roux 2715* (NBG); E, F, *Roux 2377* (NBG). Scale bars: A, B, 5 mm; C, 800 µm; D, F, 100 µm; E, 2 mm; G–I, 140 µm; J, 50 mm.

Bulbils

Bulbils are here defined as buds or outgrowths capable of developing into an independent plant. Although external stimuli may contribute to the formation of bulbils, this ability largely appears to be fixed genetically. In the polystichoid ferns the ability to produce gemmae appears to be restricted to *Polystichum*, *Dryopteris* and *Phanerophlebia juglandifolia* (Willd.) J.Sm. Within *Polystichum* a diverse group of species is capable of producing bulbils. They have been recorded in sections *Lasiopolystichum* Daigobo, *Metapolystichum* Tagawa, *Macropolystichum* Daigobo, *Cyrtomiopsis* Tagawa, *Stenopolystichum* Daigobo and *Haplopolystichum* Tagawa emend. Daigobo. Bulbils in *Polystichum* are borne either at the retuse apex of a terminal pinna, at the apex of an extended glabrous rachis or, as in the case of the species within the study area, adaxially on the rachis near the frond apex in or near the pinna 'axils'. One to three bulbils per frond appear to be the norm, but in *P. pauciaculeatum* Bonap. up to five bulbils are borne by a frond. Paleated bulbils may also occur near the pinna apices in *P. tsaratananense* Tardieu and occasionally on the stipe of *P. setiferum* (Moore 1855). African and Madagascan species bearing gemmae include *P. crinulosum*, *P. kilimanjaricum*, *P. maevaranense*, *P. magnificum* F.Ballard, *P. pauciaculeatum*, *P. tsaratananense* and *P. volkensii* and total 27% of the species within the defined area. Within the Madagascan region 62% of the species are bulbiliferous compared with the 64% of species occurring in the West Indies (Mickel 1997).

Most taxa which produce bulbils seem to occur in moist or tropical conditions where this form of vegetative reproduction may contribute to more rapid colonisation in areas of fierce competition. Bulbil formation in the ferns, its distribution and ecological implications, requires further study. The fact that bulbil formation occurs in clearly unrelated taxa suggests that it originated independently in these groups.

Venation

Venation patterns in the genera of the Dryopterideae are diverse. This is the principle character commonly used to segregate *Cyrtomium* and *Phanerophlebia* from *Polystichum*. In *Polystichum* the veins of all the species in the study area are always free and anadromous (Figure 1C, D), but in the circumboreal *P. braunii* (Spenn.) Fée, at least some of the veins are catadromous (Kramer 1987). Most veins run into the teeth where they always terminate near the lamina margin. In *P. volkensii* the veins show a slight enlargement towards their apices.

In the fertile pinnules of 2-pinnate species of *Polystichum*, the veins mostly terminate in the soral receptacle midway between the costa and the margin. This feature is also found in several *Arachniodes* and *Dryopteris* species. Variations, however, do occur with the fertile vein often extending for a short distance beyond the sorus. However, in 1-pinnate *Polystichum* and free-veined *Phanerophlebia* species, the venation of the fertile pinnae shows no or little differentiation from that of the sterile pinnae, in that the veins bearing sori are

not conspicuously shortened, thus extending well beyond the sorus (Figure 1H). Also in most *Dryopteris* species the sori-bearing veins are not shortened and extend to the margin (Figure 1F).

Cyrtomium and some *Phanerophlebia* species have reticulate venation (Figure 1G). Studies showed that reticulation in these genera have different origins (Mitsuta 1977). In *Cyrtomium* the reticulations have either a costal or a discal origin, whereas in *Phanerophlebia* they are exclusively marginal (W.H. Wagner 1979). The areolae formed by the reticulations in *Cyrtomium* all have one or two (often three) free excurrent veinlets on which the sori are borne. In *Phanerophlebia* the areolae have no included veinlets.

ANATOMY

Rhizome: stelar structure

The stelar structure of the *Polystichum* rhizome can best be classified as a dictyostele as defined by Schmid (1982). By this definition, two or more perforations (leaf, root or branch gaps) overlap along the vascular cylinder. In those *Polystichum* species with the erect rhizome type, the number of vascular bundles or meristeles (leaf, root and branch traces excluded) may number as many as eight (Figure 2A). In the decumbent rhizome type, however, the number is typically lower at four or five (Figure 2B), but in *P. monticola* up to seven vascular bundles may occur. These bundles are variable in size and shape and are situated approximately in a medial ring.

The rhizome of *Cyrtomium falcatum* is a radially symmetrical dictyostele but here only three traces vascularise each frond; the lowest one diverging into the abaxial region of the frond axis and the other two traces into the adaxial region of the frond axis (Gibson *et al.* 1984).

The rhizome branch trace in *P. transkeiense* is a strand that originates laterally from one of the larger vascular bundles of the main axis. This trace is dorsoventral and haplostelic as defined by Schmid (1982). The first frond borne by this rhizome branch is not associated with a leaf gap. However, when the second and third fronds develop, non-overlapping leaf gaps are formed. At this stage the stele is still dorsoventral. A true dictyostele is established later.

Root traces branch at irregular distances off the dorsal or lateral surfaces of the main axis vascular bundles and are not associated with root gaps. Chandra & Nayar (1982) claim that they originate from the base of the leaf trace as well, but we were unable to confirm this. The stele in the roots of most species is circular in cross section, whereas in *P. luctuosum* it is often conspicuously elliptic with the protoxylem centres forming the distal poles. In all the *Polystichum* species studied the roots were found to be consistently diarch and exarch (Figure 2C, D). In *Cyrtomium caryotideum* var. *micropterum*, a taxon often included in *Polystichum* (Kramer 1990), the roots were found to be triarch.

Frond: stelar structure of the axes

The stelar structure of the stipe base is characterised by four to five (rarely seven) vascular bundles arranged in a U-shape towards the adaxial surface. Khullar & Gupta (1979) reported up to nine vascular bundles in *P. biaristatum* (Blume) T.Moore, whereas smaller species like *P. obliquum* (D.Don) T.Moore merely have two. In *Polystichum* the arc is a broken line with the larger vascular bundles located in a dorsolateral position at either end and the smaller ones between (Figure 2E). The smaller vascular bundles are the first to branch from the lateral ends of two adjacent rhizome meristeles and the larger ones are the last to branch from the rhizome meristeles. A reduction in the number of vascular bundles usually takes place along the length of the stipe as some of the smaller bundles merge. An increase often occurs as a bundle may also split to fuse again after a short distance. The xylem strand in the larger meristeles is curved and hooked adaxially, the so-called hippocampus shape when viewed in cross section (Lin & De Vol 1977) (Figure 2F). Xylem bundles in the smaller meristeles are circular to broadly elliptic in cross section. In *Dryopteris* we observed a consistently larger number of vascular bundles (up to 12) in the stipe.

Xylem tissue in the vascular bundles is composed of helical and scalariform tracheids with thin plates of xylem parenchyma irregularly dispersed between them. Protoxylem of the smaller and larger vascular bundles has an endarch arrangement. The phloem, which forms a sheath around the xylem, is more prominent in the outer dorsolateral and ventral sides of the xylem. The pericycle consists of large parenchymatous cells two to four cell layers deep. The endodermis is characterised by inner and radial walls that are secondarily thickened and in which numerous simple and branched pits of variable sizes are scattered. Pit apertures are always elliptic in outline.

In all the species of the Dryopterideae studied the arrangement of the vascular tissue in the rachis is essentially the same as that of the stipe. In the rachis, however, there is a further reduction in the number of vascular bundles towards the lamina apex. Also here the smaller bundles initially merge with one another at irregular intervals and often also divide as in the stipe. The final small bundle eventually merges with one of the larger dorsolateral bundles some distance from the lamina apex. The two dorsolateral meristeles eventually fuse and continue as a single vascular bundle to the lamina apex (Figure 2J).

The vascular tissue serving each pinna, branches as a single dorsolateral trace from one of the two larger vascular bundles. This trace soon divides and the two (rarely three) bundles that are formed run parallel to one another for most of the pinna length before they finally merge near the pinna apex. This condition holds true for 1-pinnate species and those with more compound laminae suggesting the costa of 1-pinnate species to be analogous with the secondary rachis of species with more compound laminae. Costules and veins branch from one of the two pinna meristeles or the terminal bundle of the pinna apex and remain single-stranded.

Rhizome: non-vascular tissue

In most of the species investigated the non-vascular tissue of the rhizome is distinctly differentiated into parenchymatous ground tissue and sclerenchyma. Histologically the cortex and pith are identical, consisting of small isodiametric parenchyma cells. Towards the epidermis, however, the cells become compressed with the anticlinal walls somewhat sinuate. A narrow sheath of sclerenchyma several cell layers deep is situated beneath the epidermis. In the outer cortical layer this sclerenchyma usually extends to the root trace. In *P. transkeiense* a small sclerotic cap is formed on the outer periphery of the root trace only, whereas in *P. dracomontanum* and *P. incongruum* a sclerotic sheath often forms around the entire root trace. Chandra & Nayar (1982) also found sclerenchyma bundles associated with the departing leaf trace bundles. Small to large groups of partially to moderately thick-walled sclerenchymatous cells occur at random throughout the ground tissue of most species and often extend to the stipe bases. Their abundance appears to be determined by age and the environment with more cell aggregates present in older parts of the rhizome as well as in plants occurring in exposed habitats. In older rhizomes they appear to be concentrated near the larger meristeles. Considering the abundance and distribution of sclereid clusters in the ground tissue of the rhizome, Chandra & Nayar (1982) suggested some evolutionary trends and species relationships within *Polystichum*. D.H. Wagner (1979) also found the presence of sclereid clusters in the rhizome of *P. munitum* (Kaulf.) C.Presl diagnostic in separating it from *P. imbricans* (D.C.Eaton) D.H.Wagner where they are mostly absent. However, because of their variability, we consider them to be of no taxonomic value for the species we studied. The deposition of phenolic substances in the sclerenchymatic clusters in especially the older parts of the rhizome may act as a preservative against decay, thus promoting longevity.

The cortex of *Polystichum* roots is composed of a dense inner sclerenchymatic sheath and parenchymatous outer cortex. In old roots the outer non-sclerotic cortical layer decomposes. Sclerenchyma cells opposite the protoxylem poles are generally not as strongly lignified as the rest of the sheath (Figure 2D). Schneider (1996) terms these non-sclerotic cells opposite the protoxylem poles passage cells, a feature that characterises the *Davallia* type of root.

Frond: non-vascular tissue

In cross section the stipe base is usually circular, tetragonal or transversely broadly ovate in outline. In the upper part of the stipe, however, the adaxial surface is usually variously sulcate, as is the rachis. In cross section the epidermal cells are small and isodiametric in outline and their walls generally densely lignified, similar to the underlying band of sclerenchyma. In young material this layer is interrupted dorsolaterally by the aerophore lines studied by Davies (1991). In younger fronds the lateral aerophore lines are composed of parenchymatous cells with large intercellular spaces and are usually not very rich in phenolic substances. With age, however, this tis-

sue also becomes sclerified. Stomata occurring on the stipe and rachis are confined to the aerophore line and may be raised but are mostly flush with the epidermis. A tanniferous sclerenchyma layer is deposited on the inner tangential and radial walls of the cell layer adjoining the endodermis. The density of this layer is determined by age with that in older fronds being more prominent.

The lamina anatomy of species with 1-pinnate fronds differs slightly from those species with more compound laminae. In cross section the pinnules are flat with a shallow V-shaped sulcus adaxially along the costa that has slightly raised margins. The costa and veins that are situated equidistant between the adaxial and abaxial surfaces are enveloped by a narrow layer of parenchymatous tissue, a bundle sheath, that stretches from the adaxial to the abaxial epidermis. This tissue becomes lignified as the frond ages. In *P. macleae*, a 1-pinnate species, the pinna structure is similar except that the costa is significantly enlarged abaxially. This enlarged costa is composed of parenchymatous mesophyll in which the two vascular strands that run parallel to each other occur.

Epidermal cells

Epidermal cells can provide many characters of taxonomic value (Stace 1984), such as cell size, shape, orientation and anticlinal wall undulation. Cell size, however, may be influenced by ploidy level and environmental factors (Metcalfe & Chalk 1950).

Epidermal cell size in *Polystichum* has been studied by Chandra (1977), who concluded that *Polystichum* has a closer affinity with *Cyrtomium* than it has with *Arachniodes* and *Dryopteris*. Epidermal cells in all the species of this investigation are elongated parallel to the veins and are irregular in shape. Cell size of the adaxial

and abaxial epidermis differ, those of the abaxial epidermis usually being larger. The anticlinal walls of the epidermal cells are generally sinuous to deeply lobed (Figure 2H), but in *P. crinulosum* (Desv.) J.P.Roux the cells walls are almost straight (Figure 2G). Epidermal cells occurring abaxially along the veins are generally narrow and their anticlinal walls are not as deeply sinuate as those of the intercostal cells. Cell size varies considerably between species, with the smallest cells in *P. ammifolium* and the largest in *P. wilsonii* (Table 2).

Stomata

Stomatal ontogeny in pteridophytes has been studied by Mickel & Lersten (1967), Pant & Khare (1969), Sen & Hennipman (1981) and Mehra & Soni (1983) to name a few. The most comprehensive studies on the morphology of the mature stomatal complex are those of Van Cotthem (1970), Sen & Hennipman (1981) and Mehra & Soni (1983).

Stomata in *Polystichum* are confined to the abaxial surface of the lamina and are positioned in the same plane as the epidermal cells, oriented with their longitudinal axis parallel to the lateral veins (Figure 2I). Anomocytic, eupolocytic, copolocytic and staurocytic stomata have been reported for *Polystichum* (Van Cotthem 1970; Chandra 1977; Mehra & Soni 1983). In the species dealt with here, we found eupolocytic stomata to be the most common type, followed by the anomocytic state. A few copolocytic stomata were noted in *P. aculeatum* (L.) Roth, *P. dracomontanum*, *P. falcinellum*, *P. incongruum* and *P. kalambatitrense*. Guard cell length is fairly variable: the smallest stomata were recorded in *P. crinulosum* and the largest in *P. falcinellum* (Table 3). In *P. setiferum* stoma initials often abort during early development. Stoma size appears to be related to ploidy level (Table 3).

TABLE 2.—Adaxial epidermal cell length in *Polystichum*

Taxon	Range and mean (μm)	SD	N
aculeatum (L.) Roth	78–(116.33)–230	25.93	60
ammifolium (Poir.) C.Chr.	36–(69.88)–108	16.08	100
crinulosum (Desv.) J.P.Roux	62–(86.90)–108	15.62	10
dracomontanum Schelpe & N.C.Anthony	40–(90.04)–200	31.20	100
drepanum (Sw.) C.Presl	64–(90.77)–166	17.81	90
falcinellum (Sw.) C.Presl	70–(135.17)–210	25.26	70
incongruum J.P.Roux	56–(103.2)–206	27.50	100
kalambatitrense Tardieu	82–(134)–176	29.01	20
kilimanjaricum Pic.Serm.	92–(134)–244	30.86	30
luctuosum (Kunze) T.Moore	68–(110.9)–162	19.36	100
macleae (Baker) Diels	40–(85.48)–136	18.65	100
maevaranense Tardieu	102–(136)–176	20.24	10
magnificum F.Ballard	82–(127.34)–196	26.08	70
marionense Alston & Schelpe	44–(90.63)–166	26.80	60
monticola N.C.Anthony & Schelpe	62–(117.02)–196	28.99	100
pauciaculeatum Bonap.	56–(95.5)–170	23.31	100
pungens (Kaulf.) C.Presl	62–(111.7)–204	29.88	100
setiferum (Forssk.) T.Moore ex Woyn.	50–(88.57)–124	16.52	100
transkeiense W.B.G.Jacobsen	50–(87.3)–138	17.44	100
transvaalense N.C.Anthony	82–(138.85)–226	27.01	100
tsaratananense Tardieu	62–(105.46)–154	23.91	30
volkensii (Hieron.) C.Chr.	64–(113.06)–176	23.63	60
wilsonii H.Christ	76–(147.38)–284	39.82	100
zambesiacum Schelpe	44–(78.16)–196	20.85	100
× *maderense* J.Y.Johnson	52–(124)–210	41.86	40
× *saltum* J.P.Roux	128–(173.44)–248	31.56	50

SD, standard deviation; N, number of observations.

TABLE 3.—Guard cell length in *Polystichum*

Taxon	Range and mean (µm)	SD	N	Ploidy
aculeatum (L.) Roth	40–(51.48)–62	4.54	400	tetraploid
ammifolium (Poir.) C.Chr.	32–(40.94)–50	3.44	500	–
crinulosum (Desv.) J.P.Roux	30–(38.36)–44	3.17	50	–
dracomontanum Schelpe & N.C.Anthony	34–(49.54)–65	5.41	500	–
drepanum (Sw.) C.Presl	36–(45.16)–56	3.46	500	tetraploid
falcinellum (Sw.) C.Presl	42–(61.76)–76	5.06	500	octoploid
incongruum J.P.Roux	34–(47.46)–76	6.90	500	tetraploid
kalambatitrense Tardieu	50–(56.8)–70	3.41	100	–
kilimanjaricum Pic.Serm.	40–(53.96)–70	5.75	150	–
luctuosum (Kunze) T.Moore	34–(42)–52	3.76	500	triploid
macleae (Baker) Diels	32–(46.03)–60	5.49	500	tetraploid
maevaranense Tardieu	46–(52.76)–60	3.07	50	–
magnificum F.Ballard	50–(56.1)–64	3.13	100	–
marionense Alston & Schelpe	22–(46.82)–64	5.62	300	–
monticola N.C.Anthony & Schelpe	30–(54.08)–70	6.36	1000	hexaploid
pauciaculeatum Bonap.	30–(43)–54	4.54	500	–
pungens (Kaulf.) C.Presl	38–(50.33)–68	5.62	500	octoploid
setiferum (Forssk.) T.Moore ex Woyn.	20–(39.37)–52	3.63	300	diploid
transkeiense W.B.G.Jacobsen	32–(42.94)–54	3.86	500	tetraploid
transvaalense N.C.Anthony	22–(48.93)–62	3.96	500	tetraploid
tsaratananense Tardieu	28–(39.38)–46	3.07	100	–
volkensii (Hieron.) C.Chr.	36–(48.79)–56	4.08	200	–
wilsonii H.Christ	38–(56.46)–74	5.83	500	tetraploid
zambesiacum Schelpe	28–(43.88)–56	3.69	500	–
× *maderense* J.Y.Johnson	46–(57.92)–66	3.46	100	pentaploid
× *saltum* J.P.Roux	54–(59.68)–66	3.24	50	tetraploid

SD, standard deviation; N, number of observations.

CONCLUSIONS

This study illustrates our poor understanding of the genus. *Polystichum*, like other polystichoid ferns, is characterised by a set of features, most of which are also shared by other members within the assemblage, rather than a set of unique characters (Table 4). The genus can, however, be readily distinguished by an adaxially sulcate rachis with four to five (rarely seven) vascular bundles arranged in a U-shape, axes that are adaxially shallowly sulcate, the sulcus of the secondary axes confluent or not with that of the main axis, 1-pinnate to 3-pinnate fronds with (mostly) acroscopically developed pinnae and pinnules, anadromous free venation, indumentum composed of paleae (rarely also clavate glandular hairs), sori occurring dorsally on the veins or at a vein apex, and a peltate indusium (secondarily lost in a number of species).

In *Polystichum* the short, erect rhizome type is the most common, occurring in a wide range of taxa of which many are not considered related and is also widespread in the other polystichoid genera. Species belonging to this group are mostly forest dwelling and occur as individuals. Species in the second rhizome type can reproduce vegetatively and have the ability to grow in a wider range of habitats. This clone-forming group can consequently be found growing in forests, forest margins or open habitats. The sharing of resources by clone-forming plants (Hutchings 1997) may compensate for the fewer fronds produced by each rhizome branch.

Chandra & Nayar (1982) and D.H. Wagner (1979) consider the presence and distribution of sclerenchymatic cell aggregates in the cortex and pith of the rhizome of taxonomic value. Our observations, however, suggest their presence and number is influenced by age and habitat and we consequently consider them of no taxonomic value.

Root morphology and anatomy also appear to have little taxonomic value at the species or genus level. In *Polystichum* both the *Dennstaedtia* type and *Davallia* type of cortex occur (Schneider 1996). These root types are widespread within the Pteropsida occurring in several groups generally not considered related. The latter type, characterised by the presence of passage cells opposite the protoxylem poles, we observed in *P. luctuosum* only. All species had diarch roots apart from *Cyrtomium caryotideum* var. *micropterum*, where triarch roots were observed, a feature that requires further study.

Frond morphology in African *Polystichum*, as in most polystichoid ferns, is of the monomorphic type. Only in *Dryopteris*, however, do several species have dimorphic fronds. This derived feature is widespread and within the Pteropsida must have arisen independently on numerous occasions. The morphology and anatomy of the axes in polystichoid ferns also exhibit some important evolutionary trends. Holttum (1959) considered the external shape of the rachis and the way in which the shape is modified when a secondary rachis is attached to it, of significant evolutionary and taxonomic importance. He used this feature in separating fern groups with a similar habit and sori. Our observations in *Polystichum*, however, show that this feature exhibits intra- and interspecific variation in the pinnae stalks often being terete rather than sulcate. The pinna sulcus is thus not confluent with that of the rachis. The large number of small vascular bundles in the stipe and rachis of *Dryopteris* taxa we studied appears to be unique within the Dryopterideae, suggesting it to be of taxonomic value, but the evolutionary significance of this is not understood. The secondary rachis being homologous with the costa in 1-pinnate species of polystichoid ferns suggests frond simplification to be derived (Mitsuta 1977; Yatskievych 1989, 1996).

TABLE 4.—Summary of some morphological and anatomical character trends in the rhizome and frond of polystichoid ferns based on species studied and a literature survey

	Arachniodes	*Cyrtomium*	*Dryopteris*	*Phanerophlebia*	*Polystichum*
Rhizome	erect/decumbent	erect	erect/decumbent	erect	erect/decumbent
Roots	diarch	diarch/triarch	diarch	diarch	diarch
Lamina	1-pinnate to 3-pinnate	simple/1-pinnate	1-pinnate to 3-pinnate	simple to 1-pinnate	1-pinnate to 3-pinnate
Pinna symmetry	mostly basiscopic	mostly acroscopic	mostly basiscopic	mostly acroscopic	mostly acroscopic
Stipe vascular bundles	4–6	4–6	up to 12	4–6	2–9
Bulbils	?absent	absent	absent/present	absent/present	absent/present
Venation	free	reticulate	free/reticulate	free/reticulate	free*
Dromy	anadromous	anadromous	anadromous/catadromous	anadromous	anadromous
Frond morphism	monomorphic	monomorphic	monomorphic/dimorphic	monomorphic	monomorphic/dimorphic
Axes sulci	confluent/?not	not confluent	not confluent	not confluent	confluent/not
Stomata	mostly anomocytic	mostly eupolocytic	mostly eupolocytic	mostly eupolocytic	mostly eupolocytic

* Depending on the circumscription of the genus, for example *P. dubium* (Karst.) Diels has reticulations.

Within the polystichoid ferns as defined earlier, only certain *Polystichum* and *Dryopteris* species have the ability of producing bulbils on the laminae. In these genera one or more bulbils are mostly borne on the rachis behind the apical pinna. In the West Indies, however, most of the *Polystichum* species bear bulbils, either at a retuse apex of the terminal pinna or at the apex of an extended rachis. The ability to produce bulbils is here viewed as a derived feature. The distinct way in which the bulbils are borne suggest that this feature has also arisen independently on more than one occasion in *Polystichum*.

Ontogenetic studies show that monopodially branched free veins are ancestral and that reticulate venation within the polystichoid ferns is derived (Mitsuta 1977). It is widely accepted that reticulate veins are derived independently in *Cyrtomium* and *Phanerophlebia*. Yatskievych (1996) is also of the opinion that within *Phanerophlebia* it arose independently on two occasions. Sorus-bearing veins terminating near the lamina margin are here considered ancestral, whereas modified veins terminating in the sorus or extending for a short distance beyond the sorus are considered derived.

The epidermal cell anticlinal walls show considerable variation in the degree to which they are undulated and are here not considered to be of any taxonomic value. Polystichoid ferns are all hypostomatic, and the stomata are mostly of the anomocytic type. Our observations confirm that within closely related species ploidy level is reflected in the guard cell length as *P. pungens*, an octoploid (pers. obs.) has larger stomata than *P. incongruum* which is tetraploid (Table 3).

Judging by the information provided, more detailed studies on a wider range of species are required if a better understanding of *Polystichum*, and its affinity with the other genera in the Dryopterideae is to be formed. Further studies may reject or support some of the speculative evolutionary trends proposed here. The view of Yatskievych (1989) who suggested *Polystichum* to be polyphyletic, is supported here.

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