

The status of *Protasparagus* and *Myrsiphyllum* in the *Asparagaceae*

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Summary. The generic limits within the *Asparagaceae* are revised. Only the genus *Asparagus* is now recognised, with two subgenera: *Myrsiphyllum* and *Asparagus*. Seed testa morphology is examined in detail and a key to the morphotypes is provided. One new combination in the genus *Asparagus* is made. A key to the two subgenera is provided.

INTRODUCTION

The genus *Asparagus* was included in the *Species Plantarum* of Linnaeus (1753) with 12 species listed. Jussieu (1759) proposed the family *Asparagaceae* in which he recognised 16 genera, including *Asparagus*. The remaining 15 genera are regarded by Dahlgren *et al.* (1985) as belonging to other families. The first formal division of the genus occurred when Willdenow (1808) described the genus *Myrsiphyllum*, based on *Medeola asparagoides* L. (which is regarded here as *Asparagus asparagoides* (L.) Wight). *Myrsiphyllum* included all known bisexual *Asparagus* species with flattened cladodes and axillary flowers.

Roemer and Schultes (1829) chose to treat *Asparagus* as a single genus. Kunth (1850), however, while retaining *Asparagus* within the *Liliaceae*, further subdivided *Asparagus s.l.* into the three separate genera: *Myrsiphyllum* Willd., *Asparagus* L. with unisexual flowers and *Asparagopsis* Kunth with bisexual flowers, linear to filiform cladodes and flowers arranged in fascicles or racemes. Unknown to Kunth, the name *Asparagopsis* had been used previously by Montagne (1840) for a genus of Rhodophyceae and was therefore, in Kunth's usage, an illegitimate later homonym.

In the most recent monograph on the genus, Baker (1875) recognised only one genus *Asparagus*, but subdivided it into three subgenera, *Euasparagus* Baker (= *Asparagus*), *Asparagopsis* (Kunth) Baker and *Myrsiphyllum* (Willd.) Baker.

This treatment of the genus was followed by all subsequent taxonomists until Dahlgren & Clifford (1982), after Huber (1969, 1977), revived the idea of three separate genera. At the same time they transferred *Asparagus s.l.* from *Liliaceae* to *Asparagaceae*, in which they included the six genera *Asparagus*, *Asparagopsis*, *Myrsiphyllum*, *Ruscus*, *Danäe* and *Semele*. Obermeyer (1983) restricted her studies to the South African species included in *Asparagus s.l.* and followed Huber (1969, 1977), publishing the generic name *Protasparagus* Oberm. to replace the homonym *Asparagopsis* Kunth. She also published 38 new combinations in *Protasparagus*. In

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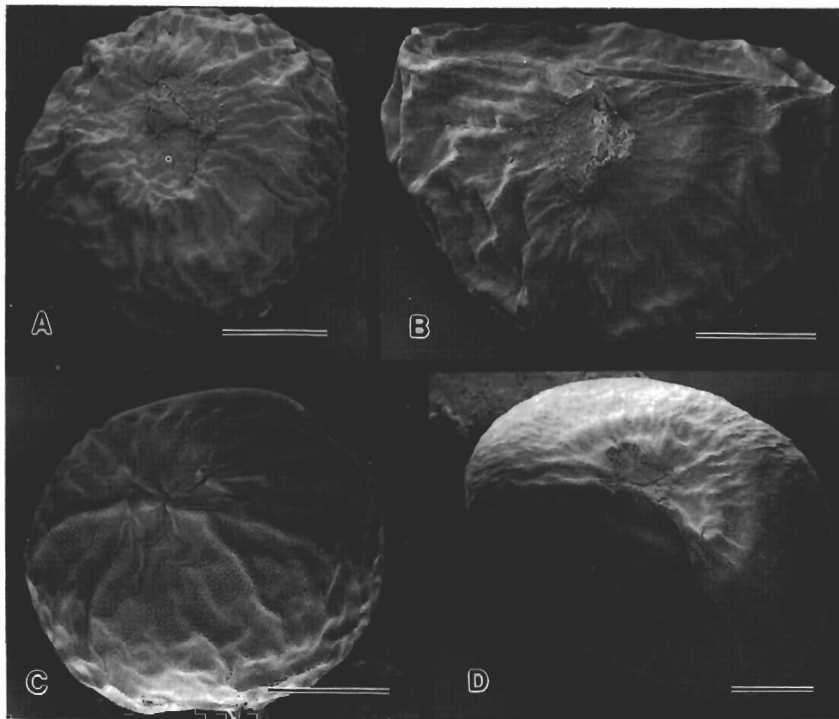


FIG. 1. Seed shape. *Asparagus tenuifolius* (Schneider 89). **A** globose seed from a single seeded berry $\times 22.6$ (SEM); **B** ventrally angular seed from a 6 seeded berry $\times 27.2$ (SEM). **C** *Asparagus officinalis* (Schneider 678) globose seed from a single seeded berry $\times 27.6$ (SEM). **D** *Asparagus officinalis* (Carnidia s.n.) ventrally angular seed from a 5-seeded berry $\times 18.8$ (SEM). Scale line = 1 mm.

a revision of the genus *Myrsiphyllum* Willd., Obermeyer (1984) published one new species and eight new combinations and also discussed the differences between *Protasparagus* and *Myrsiphyllum*. Dahlgren *et al.* (1985) transferred the three genera *Ruscus*, *Danäe* and *Semele* into the separate family *Ruscaceae* on the grounds of phytochemistry, leaf morphology and floral morphology, leaving only the three genera *Asparagus*, *Protasparagus* and *Myrsiphyllum* in the family *Asparagaceae*. However, the authors suggested that '...*Protasparagus* and *Myrsiphyllum* are perhaps best treated as subgenera of *Asparagus*'. Mathew (1989) followed Dahlgren *et al.* (1985) in recognising the three genera, circumscribed as follows:

Asparagus. Spines present or absent; flowers unisexual; erect or pendent; solitary, in fascicles or racemes; ovary locules each containing 2 ovules; seeds dorsally rounded with a pointed hilum; perianth segments free or connate at the base forming a short tube, spreading in the upper part; filaments spreading.

Protasparagus. Spines usually present; flowers bisexual; erect; in fascicles or racemes, rarely solitary; ovary locules each containing 4–many ovules; seeds \pm globose; perianth segments free, spreading from the base; filaments spreading.



FIG. 2. Testa morphotypes. **A** morphotype A. Seed testa of *Protasparagus minutiflorus* (Gerstner 22951) \times 710 (SEM). **B** morphotype B. Seed testa of *Myrsiphyllum asparagoides* (Keighery 7871) \times 686 (SEM). **C** morphotype C. Seed testa of *Asparagus tenuifolius* (Schneider 89) \times 705 (SEM). **D** morphotype D. Seed testa of *Asparagus saundersiae* (Venter 1946) \times 720 (SEM). **E** morphotype E. Seed testa of *Protasparagus longicladus* (Brown NR248) \times 720 (SEM). **F** morphotype F. Seed testa of *Protasparagus schroederi* (Morton A3270) \times 710 (SEM). Scale line = 50 μ m.

Myrsiphyllum. Spines absent; flowers bisexual; pendent; solitary or rarely in small fascicles of 3; ovary locules each containing 4–many ovules; seeds \pm globose; perianth segments connivent at the base forming a short tube spreading in the upper part; filaments connivent, forming a tube around the ovary.

During the preparation of the account of *Asparagaceae* for the Flora of Ethiopia (Sebsebe, in prep.) it has become evident that the generic delimitation within the family as proposed by Obermeyer (1983, 1984), Dahlgren *et al.* (1985) and Mathew (1989) appeared to break down in certain species. The present study has involved the examination of 10 species of *Myrsiphyllum*, 29 species of *Protasparagus* and 51 species of *Asparagus* and has aimed to elucidate the relationships between these genera.

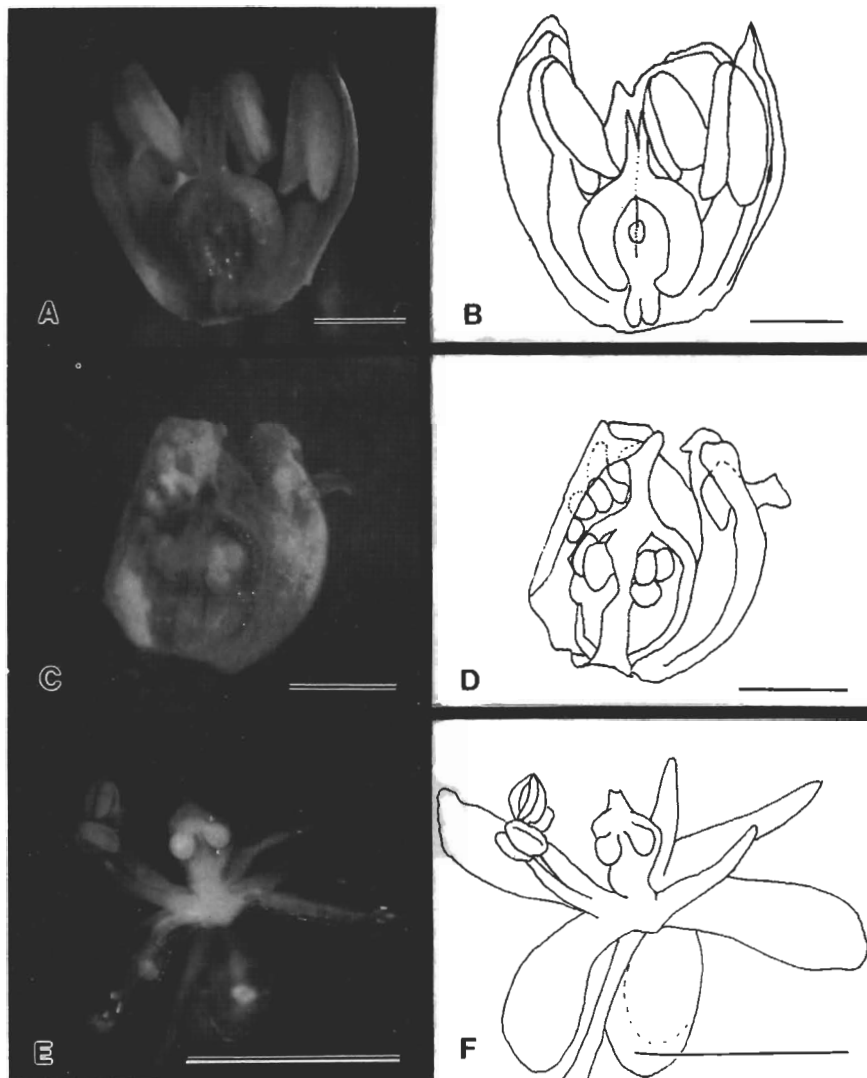


FIG. 3. Sexuality of flowers and the number of ovules per locule. *Asparagus aphyllus* (Davis 18166), **A** Photograph and **B** interpretation of the bisexual flower, dissected to reveal 2 ovules per locule $\times 6$ (LM). *Protasparagus cooperi* (Smook 4670), **C** Photograph and **D** interpretation of the bisexual flower, dissected to reveal 2 ovules in the left hand locule, and 3 ovules in the right hand locule $\times 7$ (LM). *Asparagus vaginellatus* (Willing 55), **E** Photograph and **F** interpretation of the bisexual flower. The ovary is dissected to reveal the single ovule per locule $\times 14$ (LM). Scale line = 2 mm.

MATERIALS AND METHODS

Herbarium specimens in the collections of the Royal Botanic Gardens, Kew were used for this investigation. A complete list of the specimens examined is given in Appendix I. Flowers were dissected, drawn and photographed under a Wild M7 dissecting microscope with a $\times 0.8$ polaroid back and material was illuminated using a Schott KL 1500 cold light.

Seeds were prepared for examination under the Scanning Electron Microscope by ultrasonic cleaning in 50% acetone for 15 minutes, with any residual pericarp being removed using fine forceps, as suggested by Cutler (pers. comm.). The samples were then placed in a desiccator for 48 hours before being attached to the SEM stubs using 'Araldite' adhesive. After a further 24 hours in the desiccator the seeds were coated with platinum using a Balzer SCD 030 sputter coater before being examined with a Cambridge Stereoscan 240 scanning electron microscope.

RESULTS

The character states listed in Table 1 are discussed below and their taxonomic value assessed. Particular attention is drawn to cases where the character state does not comply with the classification of Obermeyer (1983, 1984), Dahlgren *et al.* (1985) and Mathew (1989). The characters are numbered according to Table 1.

TABLE 1. Character states of species with the *Asparagaceae*

The family is subdivided into three genera as accepted by Obermeyer (1983, 1984), Dahlgren *et al.* and Mathew (1989).

- 1 = Presence (Y) or absence (N) of spines; B = modified branches giving a spiny appearance.
- 2 = Seed shape; g = globose, a = angular.
- 3 = Testa surface structure, (see text p. 71).
- 4 = Perianth segments, spreading (N) or connivent (Y).
- 5 = Filaments spreading (N) or connivent (Y).
- 6 = Flowers; bisexual (B), unisexual (U).
- 7 = The numbers of ovules per ovary locule.
- 8 = Chromosome number ($2n$ = sporophyte number, n = gametophyte number).
- 9 = Flowers borne singly (1), up to 3 together (2), in fascicles (3) or in racemes.
- * = material not available.

	1	2	3	4	5	6	7	8	9
<i>Myrsiphyllum</i>									
<i>alopecurum</i> Oberm.	N	*	*	Y	Y	B	6	*	1
<i>asparagoides</i> (L.) Wight	N	g	B	Y	Y	B	6-10	$2n = 20^i$	1
<i>declinatum</i> (L.) Oberm	N	g	B	Y	Y	B	4	*	1
<i>fasciculatum</i> (Thunb.) Oberm.	N	g	B	Y	Y	B	7	$2n = 20^i$	1
<i>krausianum</i> Kunth	N	*	*	Y	Y	B	10	*	1
<i>ovatum</i> (Salter) Oberm.	N	g	B	Y	Y	B	8-10	*	1
<i>ramosissimum</i> (Baker) Oberm.	N	*	*	N	N	B	5	*	1
<i>scandens</i> (Thunb.) Oberm.	N	g	C	N	N	B	4	*	1
<i>undulatum</i> Schlecht. ex. Kunth	N	*	*	Y	Y	B	10	*	1
<i>volubile</i> (Thunb.) Oberm.	N	g	C	*	*	*	*	*	*

TABLE 1. Continued

	1	2	3	4	5	6	7	8	9
<i>Protasparagus</i>									
<i>aethiopicus</i> (L.) Oberm.	Y	g	D	N	N	B	>4	*	4
<i>africanus</i> (Lam.) Oberm.	Y	g	C	N	N	B	>5	2n = 20 ^a	3
<i>angusticladus</i> (Jessop) Oberm.	Y	*	*	N	N	B	>4	*	4
<i>aspergillus</i> (Jessop) Oberm.	Y	*	*	N	N	B	6	*	4
<i>buchananii</i> (Baker) Oberm.	Y	g	C	N	N	B	4	*	4
<i>capensis</i> (L.) Oberm.	Y	g	C	N	N	B	5	2n = 40 ⁱ	3
<i>cooperi</i> (Baker) Oberm.	Y	g	*	N	N	B	2	2n = 40 ^{jl}	1-2
<i>crassicladus</i> (Jessop) Oberm.	Y	g	E	*	*	*	*	*	*
<i>densiflorus</i> (Kunth) Oberm.	Y	g	C	N	N	B	6-7	2n = 60 ⁱ	4
<i>denudatus</i> (Kunth) Oberm.	Y	g	C	N	N	B	6	*	3
<i>exuvialis</i> (Burch.) Oberm.	Y	g	C	N	N	B	6	*	3
<i>falcatus</i> (L.) Oberm.	Y	g/a	C	N	N	B	4	2n = 40 ^j	4
<i>glaucus</i> (Kies) Oberm.	Y	g	C	N	N	B	10	*	3
<i>humilis</i> (Engl.) B. Mathew	N	g	C	N	N	B	4	*	4
<i>krebsianus</i> (Kunth) Oberm.	Y	g	D	N	N	B	4	2n = 20 ⁱ	4
<i>larcinus</i> (Burch.) Oberm.	Y	*	*	N	N	B	7	2n = 20 ^o	3
<i>longicladus</i> (N. E. Brown)									
B. Mathew	Y	g	E	N	N	B	4	*	3
<i>macowanii</i> (Baker) Oberm.	N	g	*	N	N	B	4	*	3
<i>minutiflorus</i> (Kunth) Oberm.	Y	g	A	N	N	B	4	*	4
<i>nelsii</i> (Schinz) Oberm.	Y	*	*	N	N	B	>4	*	4
<i>oxycanthus</i> (Baker) Oberm.	Y	*	*	N	N	B	4	*	4
<i>racemosus</i> (Willd.) Oberm.	Y	g	C	N	N	B	4-6	2n = 20 ^{ijkl}	4
<i>retrofractus</i> (L.) Oberm.	Y	*	*	N	N	B	6	*	1
<i>rigidus</i> (Jessop) Oberm.	N	g	D	N	N	B	4	*	4
<i>rubicundus</i> (Berg.) Oberm.	Y	*	*	N	N	B	6	*	1-2
<i>schroederi</i> (Engl.) Oberm.	Y	g	F	N	N	B	4	*	3
<i>stipulaceus</i> (Lam.) Oberm.	Y	*	*	N	N	B	4	2n = 80 ⁱ	3
<i>subulatus</i> (Thunb.) Oberm.	Y	*	*	N	N	B	4	*	3
<i>virgatus</i> (Baker) Oberm.	N	g	C	N	N	B	6	n = 20 ^m	1
<i>Asparagus</i> L. (or unspecified in the literature)									
<i>acerosus</i> Roxb.	Y	g	C	N	N	B	5	*	4
<i>acutifolius</i> L.	N	g	C	N	N	U	2	2n = 40 ^d	1
<i>adscendens</i> Roxb.	Y	g	*	N	N	B	4	*	4
<i>albus</i> L.	Y	g	A	N	N	B	5	2n = 20 ^b	3
<i>altissimus</i> Munby	Y	*	*	N	N	B	4	*	3
<i>angolensis</i> Baker	Y	*	*	N	N	B	5	*	3
<i>aphyllus</i> L.	B	a/g	C	N	N	B	2	2n = 40 ^d	1
<i>benguellensis</i> Baker	N	*	*	N	N	U	2	*	1
<i>brachyphyllus</i> Turcz.	N	*	*	Y	N	U	2	2n = 40 ^s	1
<i>curillus</i> Buch.-Ham. ex Roxb.	Y	*	*	N	N	B	4	n = 10 ⁿ	4
<i>davuricus</i> Fisch. ex Link	N	*	*	N	N	U	2	*	1
<i>drepanophyllus</i> Welw. ex Baker	Y	g	*	N	N	B	4	*	4
<i>filicinus</i> Buch.-Ham. ex D. Don	N	g	C	N	N	B	2-3	2n = 20 ^p	1
<i>filifolius</i> Bertol.	Y	*	*	Y	N	B	2	*	1
<i>flagellaris</i> Baker	Y	g	*	N	N	B	1-2	*	1
<i>fysonii</i> Macbride	Y	*	*	N	N	B	1-2	*	1
<i>gilletii</i> Chiov.	Y	g	C	*	*	*	*	*	*
<i>gonocladus</i> Baker	Y	*	*	N	N	B	6	*	4
<i>gracilis</i> Royle	N	g	C	N	N	B	4	n = 10 ^a	1-2

TABLE 1. Continued

	1	2	3	4	5	6	7	8	9
<i>greveanus</i> H. Perrier	Y	*	*	N	N	B	>4	*	1-2
<i>laevisimus</i> Steud. ex Baker	Y	*	*	N	N	B	5	*	4
<i>longipes</i> Baker	N	*	*	Y	N	U	2	*	1-2
<i>lownei</i> Baker	N	*	*	N	N	U	2	*	1
<i>lucidus</i> Lindl.	Y	*	*	N	N	U	2	n = 10 ^h	1-2
<i>maritimus</i> (L.) Miller	N	a/g	C	N	N	U	2	*	1-2
<i>meiocladius</i> Leveille	N	g	C	N	N	U	2	*	1
<i>microraphis</i> Baker	Y	*	*	N	N	B	6	*	1-2
<i>monophyllus</i> Baker	Y	*	*	N	N	U	2	*	1
<i>mucronatus</i> Jessop	Y	g	B	N	N	B	5	*	1-2
<i>officinalis</i> L.	N	a/g	C	Y	N	U	2	2n = 20-40 ^{df}	1-2
<i>oligoclonos</i> Maxim.	N	*	*	N	N	U	2	*	1
<i>palaestinus</i> Baker	N	a	C	N	N	U	2	*	1
<i>persicus</i> Baker	N	a	C	N	N	U	2	2n = 60 ^f	1
<i>petersianus</i> Kunth	Y	g	C	*	*	*	*	*	*
<i>psilurus</i> Welw. ex Baker	N	*	*	N	N	B	4	*	1
<i>rogersii</i> R. E. Fries	Y	*	*	N	N	B	4	*	4
<i>saundersiae</i> Baker	Y	g	D	N	N	B	4	*	4
<i>schoberiodes</i> Kunth	N	g	C	N	N	B	4	2n = 20 ^g	1-2
<i>schumanianus</i> Schlechter ex H. Perrier	Y	g	C	N	N	B	4	*	3
<i>scoparius</i> Lowe	Y	*	*	N	N	B	4	2n = 20 ^c	3
<i>simulans</i> Baker	N	g	B	N	N	B	4	*	1-2
<i>somalensis</i> Chiov.	Y	*	*	N	N	B	6	*	3
<i>stipularis</i> Forsk.	B	a/g	C	N	N	B	2	2n = 20 ^{de}	1
<i>striatus</i> Thunb.	B	*	*	N	N	B	6-7	*	3
<i>tenuifolius</i> Lam.	N	a/g	C	N	N	U	2	2n = 20 ^d	1
<i>thunbergianus</i> Schult. f.	Y	g	*	N	N	B	6-7	*	1-2
<i>trichophyllus</i> Bunge	Y	*	*	Y	N	U	2	2n = 20 ^g	1
<i>turkestanicus</i> Popov	N	g	C	N	N	U	2	2n = 20 ^d	*
<i>umbellulatus</i> Bresler	N	*	*	N	N	B	5	*	3
<i>vaginellatus</i> Boj. ex Baker	Y	g	C	N	N	B	1-2	*	1-2
<i>verticillatus</i> L.	Y	*	*	N	N	U	2	2n = 20 ^f	1

Sources of chromosome numbers

- ^a = Baguar & Abid Askari, 1970.
- ^b = Barros Neves, 1973.
- ^c = Borgen, 1969.
- ^d = Bozzini, 1959.
- ^e = Bramwell *et al.*, 1976.
- ^f = Davies & Willis, 1959.
- ^g = Hong & Zhu, 1987.
- ^h = Hsu, 1971.
- ⁱ = Jessop, 1966.
- ^j = Kar, 1985.

- ^k = Kar & Sen, 1984.
- ^l = Kar & Sen, 1985.
- ^m = Mahabale & Inamder, 1975.
- ⁿ = Mehra & Dhawan, 1971.
- ^o = Nordenstam, 1982.
- ^p = Pandita, 1979.
- ^q = Renard *et al.*, 1983.
- ^r = Tamanyan & Pogolian, 1979.
- ^s = Zakharyeva & Makushenko, 1969.

1. Presence or absence of spines

Obermeyer (1983, 1984) used this character to separate *Myrsiphyllum*, where spines are absent, from *Protasparagus*, which is usually spiny. Our results show that only *Myrsiphyllum* consistently lacks spines; both *Protasparagus* and *Asparagus* have species with or without spines. Hence the character is of limited taxonomic value in subdividing the family at the generic level.

2. Seed shape

Obermeyer (1983, 1984) defined *Asparagus* as having seeds with a ventrally angular hilum in conjunction with a convex dorsal side, while *Protasparagus* and *Myrsiphyllum* both as having globose seeds. Our results indicate that, rather than being genetically fixed, seed shape depends on the packing arrangement in the berry. Regardless of the genus, when a berry is single-seeded, the resulting seed is normally globose. Obermeyer (1983, 1984) stated that globose seeds only occur in *Protasparagus* and *Myrsiphyllum*. However, *Asparagus aphyllus*, *A. officinalis* (Fig. 1C and 1D), *A. stipularis* and *A. tenuifolius* (Fig. 1A and 1B) which Obermeyer placed in *Asparagus s.s.*, may also have globose seeds in certain circumstances.

When the berry is multiple-seeded, the seed is normally angular. This is believed to depend on the packing configuration in the capsule (cf. Marais & Reilly 1978). Multiple-seeded berries predominate in *Asparagus*, but can also occur in *Protasparagus* (*P. falcatus*), where the resulting seeds are angular. *Myrsiphyllum* species show a slight modification of the model described above; whilst they possess multiple-seeded berries, in the majority of cases the seeds appear to develop in isolation and are thus globose. However, contact faces do form when the seeds touch during development, resulting again in angular seeds.

The unreliability of this character is further substantiated in the case of *A. maritimus*. A collection from France, Hot de Seven (Bureau s.n.) had two globose seeds and a single dorsally convex and ventrally angular seed in the same berry. This and the other examples suggest seed shape is unsuitable as a taxonomic character for the subdivision of the *Asparagaceae*.

3. Seed and testa morphological types

Whether the seed surface is smooth or undulate has been shown to be dependent on the dehydration experienced by the seed after collection. This character is therefore not included in the key below. However, the details of the fine structure of the seed surface have been shown to be consistent and have been used to form the basis of the key. The species examined show six basic testa types. This variation is, however, not considered significant enough to be used in the subdivision of the *Asparagaceae*.

Although the seed surfaces of members within the *Asparagaceae* have been examined previously (Jessop 1975; Obermeyer 1984), neither investigation noted the occurrence of a two layered testa, one layer of which, the epidermis, may or may not be detachable from the seed at maturity. Jessop (1975), in his survey of the seed surface characters in the *Liliaceae s.l.* of South Africa regarded the *Asparagus* seed type as totally distinct. However, as a result of this survey, we believe this to be incorrect. In the survey undertaken here, *Asparagus virgatus* was shown to possess testa morphotype C (defined below). In this particular morpho-

type the epidermal layer of testa is normally detached from the seed when it is removed from the berry. Thus the *A. virgatus* testa shown by Jessop (1975) was not homologous with the testa layers shown in the other members of the family he investigated, and a valid comparison cannot be drawn.

The distribution of the seed testa morphotypes described in the key below are shown in Table 1.

A KEY TO THE TESTA MORPHOTYPES FOUND IN THE *Asparagaceae*

1. Testa epidermis detached; only one layer of polygonal, angular, straight cells; cell boundaries channelled; periclinal walls convex, domed or flat topped; dome polygonal angular-ovoid or circular.....2
 Testa epidermis attached; often two layers of cells (the testa epidermis and the phytomelan-carrying subepidermic testa cells) totally or at least partially visible; rarely only the flat, slightly elongate-isodiametric testa epidermal cells visible.....4
2. Relief around the central dome small or absent, giving testa cells a colliculate appearance, cell size c. 15–30 μm (see Fig. 2a)..... Group A
 Relief around the central dome pronounced and formed in the periclinal wall..... 3
3. Periclinal wall of dome sinuous, periclinal wall with micropapillate secondary sculpturing, cell size c. 15–40 μm (see Fig. 2b)..... Group B
 Periclinal wall of dome not sinuous, periclinal wall with smooth-reticulate or micropapillate secondary sculpturing; cell size c. 12–42 μm (see Fig. 2c)..... Group C
4. Testa epidermis very thin with testa cells beneath clearly visible; testa cells polygonal, angular to circular, commonly isodiametric, cell boundaries channelled, anticlinal walls straight, periclinal walls convex, domed; periclinal walls with reticulate or micropapillate secondary sculpturing; cell size of epidermis c. 15–120 μm , testa, c. 10–20 μm (see Fig. 2d) . . Group D
 Testa epidermis thick, totally or partially obscuring the testa cells beneath . . 5
5. Periclinal wall concave, randomly alveolate, cell boundaries rigid, testa cells when visible commonly isodiametric; cell size of epidermis c. 30–150 μm , testa, c. 10–20 μm (see Fig. 2e)..... Group E
 Periclinal wall flat or slightly concave; cell boundaries channelled, epidermal cell size c. 40–150 μm (see Fig. 2f)..... Group F

4. *The presence or absence of connivent perianth segments* & 5. *The presence or absence of connivent filaments*

The presence of both a connivent perianth and connivent filaments in *Myrsiphyllum* was used by Obermeyer (1984) to distinguish the genus from *Protasparagus*. However, our results show *Myrsiphyllum ramosissimum* and *M. scandens* to have both spreading filaments and spreading perianth segments, suggesting an error by Obermeyer (1984). Connivent perianth segments are also found in *Asparagus brachyphyllus*, *A. filifolius*, *A. longipes*, *A. officinalis* and *A. trichophyllus*, and thus cannot be used as a diagnostic character at the generic level. The results do show, after *Myrsiphyllum ramosissimum* and *M. scandens* have been removed, that connivent filaments are a constant feature of *Myrsiphyllum*.

6. Sexuality of the flowers & 7. The number of ovules per locule

These characters have been used in conjunction in recent classifications to separate *Asparagus*, with unisexual flowers and two ovules per locule, from *Protasparagus* and *Myrsiphyllum* with bisexual flowers and four or more ovules per locule. The results show that while most taxa conform, some do not. While unisexual species always have 2 ovules per locule, there are also bisexual species, *Asparagus aphyllus* (Fig. 3a), *Protasparagus cooperi* (Fig. 3b), *Asparagus filicinus*, *A. filifolius* and *A. stipularis* which have two ovules per locule. *Asparagus flagellaris*, a widespread species from East and West Africa, and *A. vaginellatus* (Fig. 3c) from Madagascar, both with bisexual flowers and one ovule per locule, cannot be placed to genus using the present classification. Thus, the number of ovules per locule cannot be used satisfactorily to divide the *Asparagaceae*. All of the unisexual taxa recorded in this investigation were dioecious. Sexuality as a taxonomic character is discussed below.

8. Chromosome number

The results indicate a base number (x) = 10 for the family. Diploids ($2n = 20$), triploids ($2n = 30$), tetraploids ($2n = 40$), hexaploids ($2n = 60$) and octoploids ($2n = 80$) all occur. There is thus no evidence to support the subdivision of the *Asparagaceae* on the basis of chromosome number. Literature references are given in Table 1.

9. Inflorescence structure

Obermeyer (1983, 1984) used inflorescence structure to distinguish between *Myrsiphyllum* and *Protasparagus*. In *Myrsiphyllum* the flowers are normally borne singly or in small fascicles of up to three flowers, whereas in *Protasparagus* the flowers are normally borne in larger fascicles of more than three flowers or in racemes. The results show that only *Myrsiphyllum* is consistent in its inflorescence structure. The apparently random distribution of this character otherwise does not support its use in the subdivision of the *Asparagaceae*.

CONCLUSIONS

The results show that the characters used to circumscribe the three presently accepted genera in the *Asparagaceae*, with the exception of flower sexuality and the presence of free or connivent filaments, are inconsistent. Only flower sexuality can reliably separate *Protasparagus* from *Asparagus*, but it seems scarcely tenable to separate these genera on flower sexuality when so many genera have both unisexual and bisexual species and when *Protasparagus* and *Asparagus* share so many other characters. Similarly only connivent filaments reliably distinguish *Myrsiphyllum* from the other members of the family. Thus, because of the high number of shared characters between the three genera, it is proposed that the family *Asparagaceae* be treated as containing a single genus, *Asparagus*. Connivent filaments distinguish *Myrsiphyllum* at a subgeneric level, while species with spreading filaments are placed in the second subgenus, *Asparagus*. As species traditionally placed in *Protasparagus* have free filaments they are here treated as members of the subgenus *Asparagus*.

A KEY TO THE SUBGENERA OF *Asparagus*

1. Flowers bisexual, pendulous, borne singly or in small fascicles of up to 3 flowers; perianth segments free but connivent at the base, spreading in the upper part; filaments connivent, forming a tube around the ovary; ovules 4–10 per locule; seeds angular to globose; testa morphology, only types B and C recorded; spines absent; cladodes often flattened, narrowly ovate-acuminate to cordate and leaflike (as in *Asparagus asparagoides*, *A. krausianus*, *A. multituberosus*, *A. ovatus*, *A. undulatus* and *A. volubilis*), otherwise linear to filiform. 1. subgenus *Myrsiphyllum*
- Flowers unisexual or bisexual, pendulous or erect, either solitary, in fascicles or in racemes; perianth segments free, spreading or connivent at the base, forming a tube, spreading in the upper part; filaments free; ovules 1–10 per locule; seeds angular to globose; testa morphology, all types recorded; spines present or absent; cladodes linear to filiform . . . 2. subgenus *Asparagus*

A NEW COMBINATION IN *Asparagus*

Asparagus alopecurus (Oberm.) Malcomber & Sebsebe comb. nov.

Myrsiphyllum alopecurum Oberm. in *Bothalia* 15: 85 (1984). Type: South Africa, Western Cape 2917 (Springbok), 22km W by S of Springbok (-DB), *Acocks* 19268 (holotype PRE; isotype K!).

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APPENDIX I. LIST OF SPECIMENS EXAMINED

AsparagusSubgenus **Myrsiphyllum**

- alopecurus* (Oberm.) Malcomber & Sebsebe
SOUTH AFRICA. *Acocks* 19268 (holotype K!).
- asparagoides* (L.) Wight
ATLANTIC ISLANDS. Tenerife, *Proby* 104. AUSTRALIA. *Keighery* 7871. KENYA. *Verdcourt & Greenway* 445. SOUTH AFRICA. *Jessop* 613; *Strey* 8723.
- declinatus* L.
SOUTH AFRICA. *Williams* 326; *Taylor* 8621.
- fasciculatus* Thunb.
SOUTH AFRICA. *Leistner* 3390; *Thompson* 1009.
- krausianus* (Kunth.) Jessop
SOUTH AFRICA. *Esterhuysen* 23454; *Acocks* 17992.
- ovatus* Salter
SOUTH AFRICA. *Salter* 8440; *Parker* 4485.
- undulatus* (L.f.) Thunb.
SOUTH AFRICA. *Wolley* 1351; *Leifroldt* 160.
- volubilis* Thunb.
SOUTH AFRICA. *Shode* A2771; *Jessop* 618.

Subgenus **Asparagus**

- acerosus* Roxb.
INDIA. *Clarke* 11754; *Gamble* 1317. THAILAND. *Kerr* 2626. VIETNAM. *Thorel* 2123.
- acutifolius* L.
ITALY. *Prior* s.n. CYPRUS. *Atherton* 740; *Casey* 100.
- ascendens* Roxb.
AFGHANISTAN. *Griffith* 5855. INDIA. *Gamble* 22336; *Drummond* 14737.
- aethiopicus* L.
GHANA. *Morton* A3027. MOZAMBIQUE. *Mogg* 30866; *de Koning* 7660. SOUTH AFRICA. *Fourcade* 3477; *Cullett* 3575.
- africanus* Lam.
SENEGAL. *Tutin* 134. NIGERIA. *Gbile*, *Wit and Daranida* 1117. CAMEROON. *Sanford* 6250. ZAIRE. *Stauffer* 480. KENYA. *Mwangangi* 1575; *Mwangangi* 1953. SOUTH AFRICA. *Devenish* 1156; *Jessop* 603.
- albus* L.
CORSICA. *Wyatt* 65. SARDINIA. *Reverchon* 21.
- altissimus* Munby
MOROCCO. *Gattefosse* s.n.
- angusticladus* Jessop
GHANA. *Akpabla* 1265. MOZAMBIQUE. *de Koning* 8402.

- angolensis* Baker
TANZANIA. *Davies* E49.
- aphyllus* L.
GREECE. *Davis* 18166. TURKEY. *Khan, Prance & Radcliffe* 769; *Davis & Coode* 39169.
- aspergillus* Jessop
KENYA. *Gillett* 13590. ZIMBABWE. *Biegel* 1344.
- benguellensis* Baker
ANGOLA. *Welwitsch* 3872.
- brachyphyllus* Turcz.
NORTH CHINA. *Hancock* 137; *Licent* 1775; *Rock* 121272.
- buchananii* Baker
RWANDA. *Troupin* 4821. BURUNDI. *Van der Ben* 2214. TANZANIA. *Hedberg et al.* 240; *Richards & Arasululu* 26807; *Ruffo & Mmari* 1931.
- capensis* L.
SOUTH AFRICA. *Jessop* 703; *Weger* 496; *Boucher* 848; *Van Breda* 4294.
- cooperi* Baker
SOUTH AFRICA. *Smook* 4670; *Mauve* 5453.
- crassicladus* Jessop
SOUTH AFRICA. *Rogers* 25601; *Jessop* 627.
- curillus* Buch.-Ham. ex Roxb.
WEST HIMALAYAS. *Duthie* 24997.
- davuricus* Fisch. ex Link
NORTH CHINA. *Licent* 3532; *Licent* 7320; *Licent* s.n.
- densiflorus* (Kunth) Jessop
AUSTRALIA. *Rodd* NSW 136257. TANZANIA. *Semsei* 2706. MOZAMBIQUE. *Charneca* 38. SOUTH AFRICA. *Bruins Lich* s.n.
- drepanophyllus* Welw. ex Baker
CAMEROON. *Bretele* 748; *Letouzey* 3594.
- denudatus* (Kunth) Baker
SOUTH AFRICA. *Galpin* 13881; *de Winter* 3457.
- exuvialis* Burch.
KENYA. *Kimani* 224; *Kimani* 285. TANZANIA. *Leippert* 5423. BOTSWANA. *Wild & Drummond* 6974.
- falcatus* L.
SRI LANKA. *Hepper, Maxwell & Jayasuriya* 4460; *Davidse & Sumithraarachchi* 8689. NIGERIA. *Donald* 87. ZAIRE. *Jeluin* 9830. KENYA. *Milne-Redhead & Taylor* 7003. TANZANIA. *Cribb & Grey-Wilson* 10040; *Pács* 87007F.
- filicinus* Buch.-Ham. ex D. Don
CHINA. *Schneider* 1483; *Wilson* 943; *Wilson* 4684; *Henry* 9865; *Henry* 12181. THAILAND. *Kerr* 5434.
- filifolius* Bertol.
IRAQ. *Hamad* 53808 (2 sheets).
- flagellaris* Baker
MALI. *Hagerup* 31; BURKINA FASO. *Amshoff* 4323; CENTRAL AFRICAN REPUBLIC. *Fay* 6872. CAMEROON. *De Wilde & De Wilde-Duyffes* 2588; *Meurillon* 775.
- fysonii* Macbride
INDIA. *Wight* 2818; *Gamble* s.n.; *Gamble* 14413.
- gillettii* Chiov.
KENYA. *Bally* 12530.
- glaucus* Kies
SOUTH AFRICA. *Acocks* 8464; *Henrici* 4535.
- gonocladus* Baker
INDIA. *Meebold* 9448; *Jarrett, Saldanka & Ramamoorthy* HFP 839.
- gracilis* Royle
PAKISTAN. *Rodin* 5401. INDIA. *Parker* 3348.
- greveanus* H. Perrier
MADAGASCAR. *Phillipson* 1783; *Phillipson* 2421.
- humilis* Engl.
TANZANIA. *Mwasumbi* LBM 10550. MALAWI. *Blackmore & Patel* 302.
- krebsianus* (Kunth) Jessop
MALAWI. *Brass* 16171; *Robson* 1392; *Chapman* 6043. SOUTH AFRICA. *Rogers* 30094.
- laevissimus* Steud. ex Baker
INDIA. *Wight* 2816 (2 sheets); *Gamble* 20624.

- laricinus* Burch.
MALAWI. *Richards* 22640. SOUTH AFRICA. *Esterhuysen* 1275.
- longipes* Baker
GHANA. *Akpabla* 485. CULTIVATED. (ex Cameroon) *Sander* s.n. (holotype K!).
- longicladus* N. E. Brown
ZIMBABWE. *Robinson* 960; *Benson* NR248.
- lownei* Baker
SYRIA. *Lowne* s.n. (holotype K!). PALESTINE. *Meyers & Dinsmore* 344.
- lucidus* Lindl.
JAPAN. *Sinclair* 9435; *Furuse* 4644.
- macowanii* Baker
SOUTH AFRICA. *Dyer & Verdes* 5832; *Pooley* 861.
- maritimus* (L.) Miller
FRANCE. *Bureau* s.n. ITALY. *Mill* s.n. IRAN. *Wright & Bent* 427.
- meiocladus* Leveille
CHINA. *Forrest* 7997; *Cavalerie* 4468.
- microraphis* Baker
SOUTH AFRICA. *Symons* 38; *Killick & Vahrmeyer* 3809.
- minutiflorus* (Kunth) Baker
SOUTH AFRICA. *Gerstner* 22951; *Codd & Dyer* 4694.
- monophyllus* Baker
PAKISTAN (BALUCHISTAN). *Lace* 3316; *Lace* s.n.
- mucronatus* Jessop
SOUTH AFRICA. *Acocks* 2598; *Theron* 551.
- nelsii* Schinz
ZAMBIA. *Mutimushi* 3666. SOUTH AFRICA. *Stephens* 7083; *Codd* 4336.
- officinalis* L.
BRITISH ISLES. *Hubbard* s.n. EUROPE. *Carnidia* s.n. BULGARIA. *Schneider* 678. TURKEY. *Stainton* 8470. AUSTRALIA. *Durrington* 475.
- oligoclonos* Maxim.
SOVIET UNION. *Komarov* 396.
- oxycanthus* Baker
SOUTH AFRICA. *Dyer* 3375; *Story* 4531.
- palaestinus* Baker
JORDAN. *Townsend* 65/104; *Townsend* 65/270.
- persicus* Baker
SOVIET UNION. *Manakien* s.n. CENTRAL ASIA. *Vasak* s.n.
- peterianus* Kunth
TANZANIA. *Richards* 17892. MOZAMBIQUE. *Meller* s.n.
- psilurus* Welw. ex Baker
ANGOLA. *Wellman* 1805; *Richards* 17154.
- racemosus* Willd.
SOUTH EAST ARABIA. *Bent* 189. NEPAL. *Grey-Wilson & Phillips* 279. SRI LANKA. *Fosberg & Balakrishnan* 53574. ETHIOPIA. *De Wilde* 5995; *Gilbert & Sebsebe* 8789. SOUTH AFRICA. *Rodin* 1228; *Strey* 3719.
- ramosissimus* Baker
SOUTH AFRICA. *Killick* 1105; *Van der Schiff* 6333; *Moll* 2877.
- retrofractus* L.
SOUTH AFRICA. *Acocks* 1714; *Westhuizen* 183.
- rigidus* Jessop
SOUTH AFRICA. *Killick & Strey* 2380; *Schiff* 5589.
- rogersii* R. E. Fries
ZIMBABWE. *Sinaranda* 112; *Fanshawe* 7940.
- rubicundus* Berg
SOUTH AFRICA. *Orchard* 353; *Scharf* 2071.
- saundersiae* Baker
SOUTH AFRICA. *Scheepeis*, 1059; *Venter* 1946.
- scandens* Thunb.
SOUTH AFRICA. *Rodin* 3233; *Williams* 2628.
- schoberioides* Kunth
SOVIET UNION. *Komarov* 398. CHINA. *James* s.n.; *Taquet* 1574; *Taquet* 1575.

- schroederi* Engl.
GHANA. *Morton* A3270. NIGERIA. *Keay* 25794.
- schumannianus* Schlechter ex H. Perrier
MADAGASCAR. *Decary* 9659; *Phillipson* 2305.
- scoparius* Lowe
CAPE VERDE ISLANDS. *Newton* s.n.
- simulans* Baker
MADAGASCAR. *Humbert* 816; *Bernardi* 11116.
- somalensis* Chiov.
SOMALIA. *Gillett & Hemming* 24793.
- stipulaceus* Lam.
ZIMBABWE. *Wild* 3476. SOUTH AFRICA. *Salter* 8210.
- stipularis* Forsk.
SPAIN. *Ellman & Sandwich* 385. EGYPT. *Davis* 6346B. SAUDI ARABIA. *Collenette* 72-202; *Collenette* 2898.
- striatus* Thunb.
SOUTH AFRICA. *Acocks* 11892; *Acocks* 12158.
- subulatus* Thunb.
SOUTH AFRICA. *Jessop* 610; *Strey* 7457.
- tenuifolius* Lam.
YUGOSLAVIA. *Schneider* 89.
- thunbergianus* Schult. f.
SOUTH AFRICA. *Stephens & Glover* s.n.; *Bos* 1381.
- trichophyllus* Bunge
AFGHANISTAN. *Aitchison* 335; *Aitchison* 337. CHINA. *Purdom* 7362.
- turkestanicus* Popov
SOVIET UNION. *Anon* s.n.
- umbellulatus* Bresler
REUNION. *Coode* 4565. SEYCHELLES. *Merton* 70/30.
- vaginellatus* Boj. ex Baker
MADAGASCAR. *Baron* 5243; *Scott-Elliott* 2068; *Willing* 55.
- verticillatus* L.
BULGARIA. *Schneider* 309. IRAQ. *Omar, Al-Kaisi & Wedad* 49667.
- virgatus* Baker
TANZANIA. *Milne-Redhead & Taylor* 10420. ZAMBIA. *Richards* 22453.