

## Miscellaneous notes

VARIOUS AUTHORS

### POACEAE

#### APOMIXIS IN THE GENUS *PENTASCHISTIS* (ARUNDINOIDEAE)

Apomixis is defined as asexual reproduction by seeds (Nogler 1984) and usually leads to offspring, which are genetically identical to the mother plant. Apomixis is also defined as the initiation of an individual from a single cell or a zygote equivalent, in which the nucleus is not formed by syngamy (Mogie 1992). A plant can also reproduce asexually by vegetative propagation. Apomixis is common in the flowering plants (Brown & Emery 1958) and known in 300 species, representing 35 plant families (Hanna & Bashaw 1987). It occurs at a high frequency among perennial forage grasses and has been reported in 125 species, representing most of the tribes (Bashaw & Hanna 1990).

Two different classes of unreduced (apomictic) embryo sacs are formed, namely aposporous and diplosporous. The aposporic embryo sac is derived from a somatic cell surrounding the ovule. This cell is usually located close to the chalazal pole of the megaspore. Two types of aposporous embryo sac development can be recognised, namely the *Hieracium* and *Panicum* types. Diplosporic embryo sacs develop from an unreduced archesporium cell.

Aposporous embryo sacs usually have only four nuclei at maturity, whereas sexual embryo sacs usually have eight nuclei. The four nuclei are the egg and either two synergids and one polar, or one synergid and two polar nuclei (Brown & Emery 1958). Antipodal cells are completely absent.

The term apospory alone does not imply apomixis unless followed by parthenogenesis or apogamy. Furthermore, the development of aposporous embryo sacs may vary from occasional to regular in plants and ovules (Narayan 1951; Johnston 1953; Narayanaswami 1954, 1955).

The genus *Pentaschistis* (Nees) Spach consists of 68 species (Linder & Ellis 1990) of which 57 are indigenous and 40 endemic to South Africa (Gibbs Russell *et al.* 1990). The mature ovule and megagametophyte of eleven *Pentaschistis* species were previously investigated (Verboom *et al.* 1994). Some species possess weakly to undeveloped haustorial synergids. Fine-grained or no starch is found in most species, with the exception of *P. chippendalliae*. The inner integument of all the species, except *P. pungens*, is discontinuous at the micropylar end. The outer integument is typically highly reduced, forming a basal collar or restricted to the chalazal half of the ovule (Verboom *et al.* 1994).

*Polygonum*-type embryo sac development has been reported for three *Pentaschistis* species (namely *P. palli-*

*da*, *P. patula* and *P. tomentella*) (Labuschagne 1990). The aim of this study is to determine the type of embryo sac development in order to infer the mode of reproduction and the possibility of hybridisation in the different species.

#### MATERIALS AND METHODS

The material used in the cytological study was collected in the field throughout the distribution areas of the different *Pentaschistis* species. Voucher herbarium specimens are housed in the Geo Potts Herbarium, Bloemfontein (BLFU) and/or in the National Herbarium, Pretoria (PRE). Inflorescences of different developmental stages were fixed in Carnoy's fixative (Carnoy 1886) and serially dehydrated with ethanol and tertiary butanol. The wax penetration was achieved overnight at 60°C, followed by embedding in pastulated synthetic paraffin wax. Seven-micron sections were made and affixed to pre-treated slides (Jensen 1962).

The cytological material was stained using a modified double staining method (Spies & Du Plessis 1986) of safranin (Johansen 1940) and fast green (Sass 1951) and mounted with Eukitt. A minimum of twenty embryo sacs per plant, representing different developmental stages, were studied for each specimen.

#### RESULTS

All studied specimens (Table 1), except the six *P. erios-toma* specimens, formed eight-nucleate embryo sacs. Embryo sac development as observed during this study, was unaffected by the different ploidy levels (Klopper *et al.* 1998). In most of the species the megaspore mother cell divided meiotically to form a linear tetrad of four haploid megaspores. The chalazal megaspore developed into the female gametophyte (Figure 1B–H) and the other three megaspores degenerated (Figure 1A). The nucleus of the functional megaspore divided mitotically to form an eight-nucleate embryo sac (Figure 1B–H).

*Pentaschistis airoides* (Nees) Stapf subsp. *airoides*, *P. pallida* (Thunb.) Linder, *P. tomentella* Stapf, *P. viscidula* (Nees) Stapf and *P. curvifolia* (Schrud.) Stapf had an eight-nucleate embryo sac. In one ovule of a *P. pallida* specimen (Spies 3563) and in one ovule of *P. setifolia* (Spies 2475), two eight-nucleate embryo sacs (Figures 2, 3) were seen per ovule.

In *P. erios-toma* the embryo sac developed from a nucellus cell (Figures 3, 4). The cell's nucleus divided mitotically to form a four-nucleate embryo sac. All the

TABLE 1.—Embryo sac development in some specimens of the genus *Pentastichis*

Species	Voucher specimen	Polygonum-type	Panicum-type
Group 1			
<i>P. airoides</i> subsp. <i>airoides</i>	Spies 2926, 3807	•	
<i>P. pallida</i>	Spies 3239, 3484, 3493, 3494, 3495, 3552, 3563, 3570, 3653, 3805, 3822, 3840	•	
<i>P. setifolia</i>	Spies 2475	•	
<i>P. tomentella</i>	Spies 2996, 3008	•	
Group 2			
<i>P. viscidula</i>	Spies 3520	•	
Group 3			
<i>P. calcicola</i>	Spies 3587, 3588	•	
<i>P. tortuosa</i>	Spies 3521	•	
Group 4			
<i>P. curvifolia</i>	Spies 3659	•	
Group 6			
<i>P. eriostoma</i>	Spies 3144, 3526, 3528, 3536, 3555, 3686		•

nuclei of the embryo sac were unreduced. More than one embryo sac per ovule was observed.

#### DISCUSSION

The development of an eight-nucleate embryo sac (*Polygonum*-type embryo sac) is characteristic of most angiosperms (Mogie 1992). It typifies the embryo sac development of the grasses (Greenham & Chapman 1990).

Twenty-eight specimens, representing nine species, were examined (Table 1). Eight of the species (*P. airoides* subsp. *airoides*, *P. calcicola*, *P. curvifolia*, *P. pallida*, *P. setifolia*, *P. tomentella*, *P. tortuosa* and *P. vis-*

*cidula*) had monosporic, eight-nucleate embryo sac development (Figures 1, 2). All these species showed *Polygonum*-type embryo sacs, thus an indication of sexual reproduction. The morphology of the embryo sac corresponded in all specimens and even at different ploidy levels. In most of the specimens only one anatropous ovule per flower was observed (Figure 1). In Spies 3563 and 2475, two embryo sacs per anatropous ovule were observed per flower (Figures 2, 3). The haploid chromosome numbers of these two specimens are not available and therefore no assumption, in respect to the influence of the ploidy levels, can be made.

In one species, *P. eriostoma*, aposporic embryo sac development was observed in all the specimens exam-

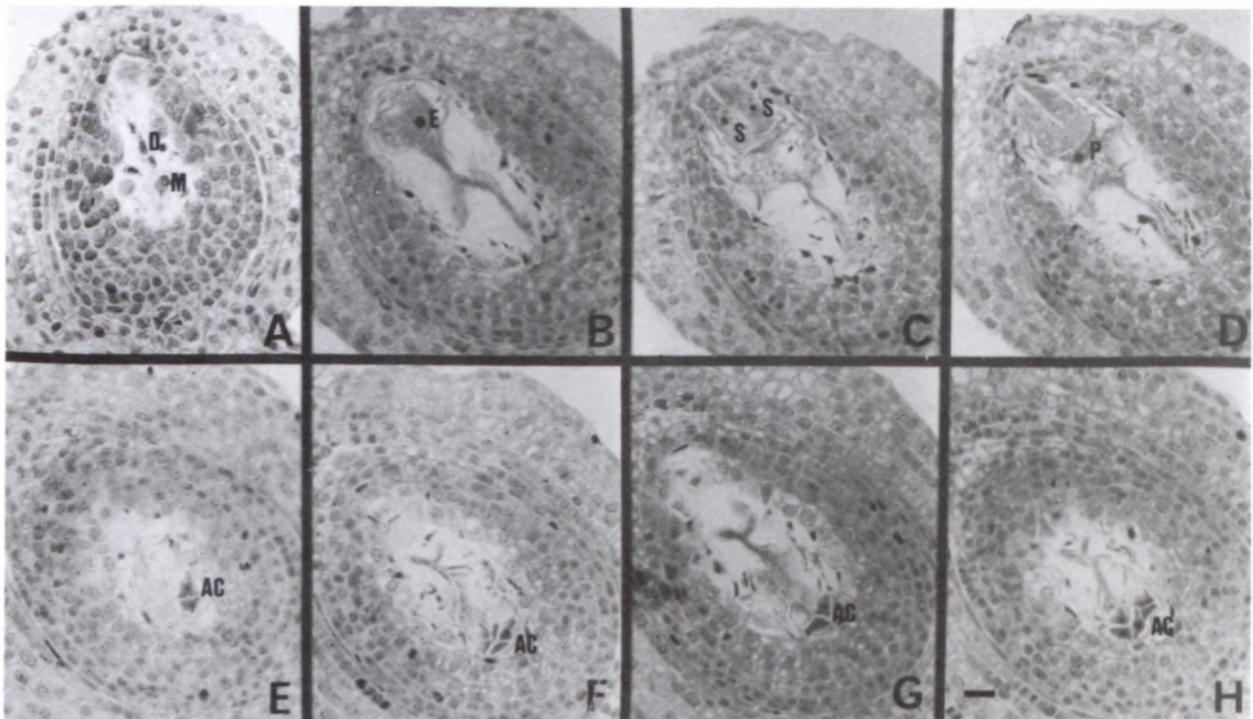


FIGURE 1.—Megasporogenesis and embryo sac development in the genus *Pentastichis*. A, four macrospores, chalazal macrospore developing and other three degenerating in *P. pallida*, Spies 3805. B–H, *P. tomentella*, Spies 3008: B, egg cell; C, two synergids; D, one polar nucleus; E–G, antipodal complex with two antipodal cells visible; H, antipodal complex with five antipodal cells visible. AC, antipodal complex; D, degenerating macropores; E, egg cell; M, chalazal macrospore; P, polar nucleus; S, synergid. Scale bar: 20.8  $\mu$ m.

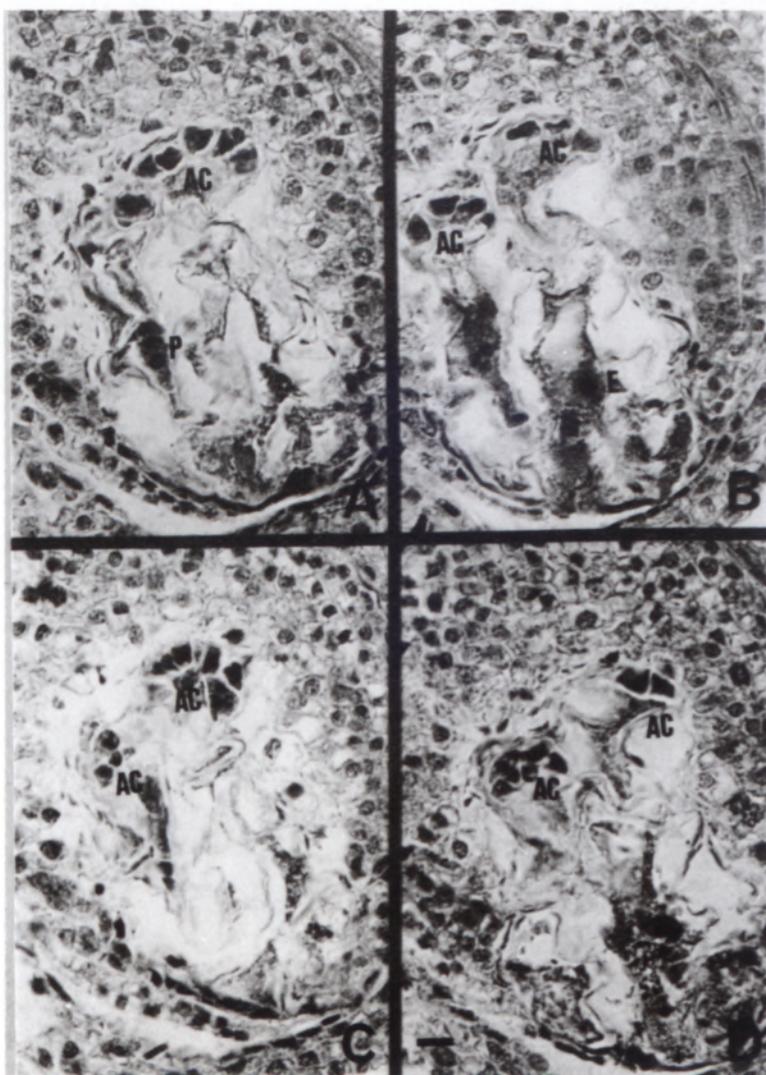


FIGURE 2.—Development of two eight nucleate embryo sacs in *Pentaschistis pallida*, Spies 3563. A, two polar nuclei visible in one embryo sac and antipodal complex with six antipodal cells in other; B, egg cell and three antipodal cells of antipodal complex visible in one embryo sac and four antipodal cells of antipodal complex in other; C, in both embryo sacs antipodal complexes visible with three antipodal cells in one and six in other; D, in both embryo sacs antipodal complexes visible with six antipodal cells in one and two in other. AC, antipodal complex; E, egg cell; P, polar nuclei. Scale bar: 12.8  $\mu$ m.

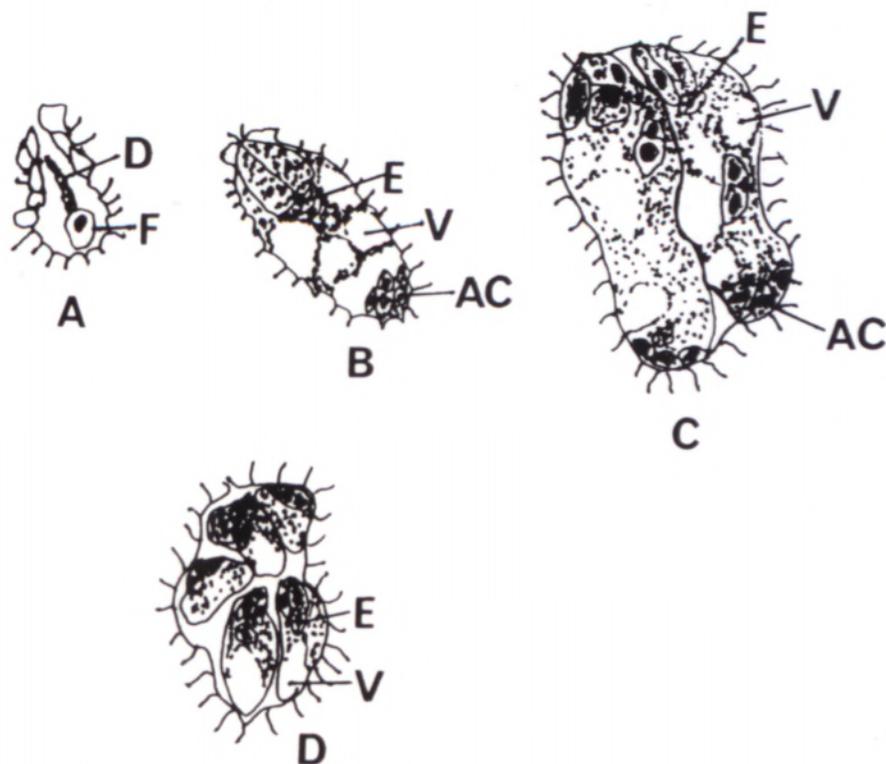


FIGURE 3.—Schematic representation of embryo sac development in the genus *Pentaschistis*, sketched by combining data from different serial sections. A, linear tetrad of macrospores with chalazal macrospore functional; B, mature *Polygonum*-type embryo sac; C, two mature *Polygonum*-type embryo sacs in one ovule; D, five aposporous embryo sacs in one ovule; three mature *Panicum*-type and two two-nucleate embryo sacs, *Pentaschistis eriostoma*. AC, antipodal complex; D, degenerating macrospores; E, egg cell; F, functional macrospore.

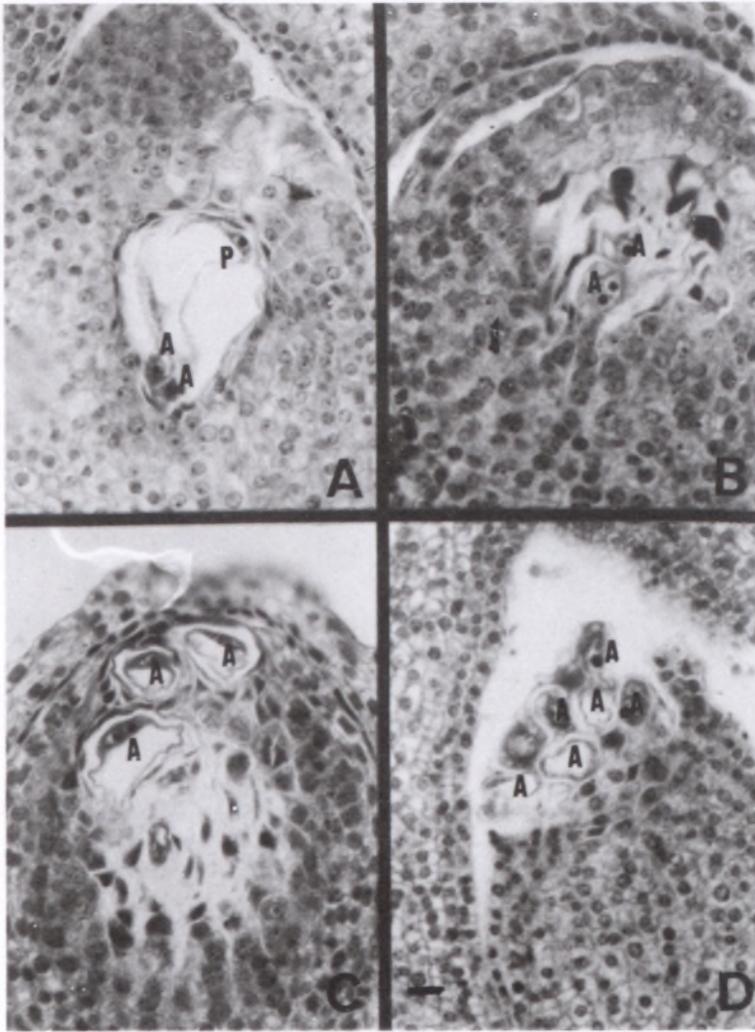


FIGURE 4.—Aposporic embryo sac development in *Pentaschistis eriostoma*. A, *Polygonum*-type embryo sac and two aposporic embryo sacs, Spies 3555; B, two aposporic embryo sacs, one with one nucleus and other with two nuclei, Spies 3536; C, three aposporic embryo sacs, two with one nucleus and one with two nuclei, Spies 3144; D, six aposporic embryo sacs, two with one nucleus each and other nuclei not visible in this section, Spies 3536. A, aposporic embryo sac; P, *Polygonum*-type embryo sac. Scale bar: 20.8  $\mu$ m.

ined (Figure 4). Thus, apomixis occurred in this species. In *P. eriostoma*, *Panicum*-type embryo sac development was observed. This is the first report of *Panicum*-type embryo sac development in a South African representative of the subfamily Arundoideae. Apomixis was previously reported in three genera of the tribe Arundineae, i.e. *Cortaderia* (Philipson 1978), *Danthonia* (Philipson 1986) and *Lamprothyrus* (Connor 1981).

*Pentaschistis eriostoma* is classified as a facultative apomict, because of the small degree of sexuality (only two *Polygonum*-type embryo sacs were observed in all the ovules studied). Most apomictic grasses are polyploid, heterozygous and generally derived from hybridisation. Therefore, many of the apomictic grasses are meiotically irregular and embryo sacs derived by syngamy are subject to a high frequency of abortion (Bashaw & Hanna 1990). Meiotic irregularities are frequent in *P. eriostoma* (Klopper *et al.* 1998) and this could support the hypothesis that *P. eriostoma* was derived from hybridisation.

Although apomixis is rare in diploids (Stebbins 1971), apomixis and ploidy levels are not believed to be causally connected (Nogler 1984). Apomixis is present in diploid ( $2n = 2x = 26$ ) *P. eriostoma* specimens. Apomixis has been observed in a few diploids ( $2n = 2x$ ), *Ranunculus auricomus* (Nogler 1984), *Citrus* and *Potentilla* (Stebbins 1971) and *Tribolium* (Visser & Spies 1994). The reason for most apomicts being poly-

ploids is clear. Since apospory is caused by at least one copy of the wild-type gene and excess copies of the mutant gene (Mogie 1992), apospory can only be transmitted by reduced or unreduced ( $n = 2x$ ) gametes. Therefore, diploid apomicts can only be formed as dihaploids and not as hybrids.

*Pentaschistis eriostoma*, however, is believed to be a hybrid species (Du Plessis & Spies 1992). It is important to note that *P. eriostoma* has a secondary basic chromosome number ( $x = 6+7$  or  $x = 7+7-1$ ). However, if the hypothesis of hybridisation or polyploidisation and subsequent aneuploidy led to the existence of *P. eriostoma* is true, then *P. eriostoma* is a secondary diploid. Although apomixis occurs in *P. eriostoma*, a very low frequency of reduced embryo sacs (implying sexual reproduction) was also observed (Figure 4A). Further studies are thus necessary to determine the degree of sexuality and the role sexual reproduction plays in the propagation of *P. eriostoma*, to verify this hypothesis.

In conclusion, it can be stated for the first time that *Panicum*-type embryo sac development and apomixis has been observed in South African representatives of the subfamily Arundoideae. *Pentaschistis eriostoma* is an agamospecies [an apomictic population of common origin (Turesson 1929)]. The other *Pentaschistis* species reproduce sexually and have *Polygonum*-type embryo sac development.

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## PROGRESS WITH THE TRIAL PHASE FOR REGISTRATION OF NEW PLANT NAMES‡

‡ In a spirit of co-operation and to publicise this proposed innovation in plant nomenclature in southern Africa, this note has been submitted simultaneously to the following botanical journals: *South African Journal of Botany*, *Forum Botanicum* and *SABONET News*.

## INTRODUCTION

A number of far-reaching proposals aimed at the refinement and simplification of the *International Code of Botanical Nomenclature* were discussed in some detail at the Nomenclature Section of the XVth International Botanical Congress (IBC) held in August 1993 in Yokohama, Japan. Three of the main issues were the adoption of lists of *Names in current use* (Smith *et al.* 1993; Smith & Hawksworth 1994), the extended options of conserving and rejecting names (Greuter & Nicolson 1993), and the registration of all new plant names (Borgen *et al.* 1997; Greuter & Von Raab-Straube 1998). This paper deals with the last-named issue, namely the proposed system by means of which new names of plants and fungi would have to be dealt with from 1 January 2000 onwards.

Article 32.1 of the *International Code of Botanical Nomenclature* adopted at the 1993 IBC (Greuter *et al.* 1994) concludes with 'In addition, subject to the

approval of the XVI International Botanical Congress, names (autonyms excepted) published on or after 1 January 2000 must be registered.' Furthermore, Article 32.2 states that 'Registration is effected by sending the printed matter that includes the protologue(s) with the name(s) to be registered clearly identified, to any registering office designated by the International Association for Plant Taxonomy.'

To demonstrate the feasibility of a registration system, the International Association of Plant Taxonomy (IAPT) undertakes a non-mandatory trial of registration for a two-year period, starting 1 January 1998 (Borgen *et al.* 1997). Details of the proposed implementation of the registration requirement (Borgen *et al.* 1998) will be considered by the St Louis Congress in July 1999. Since May 1998, a searchable demonstration database containing all names trial-registered after January 1998 can be freely consulted on the Internet (<http://www.bgbm.fu-berlin.de/registration/QueryForm.htm>).