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OVULAR FEATURES OF AFRICAN ARUNDINOID GRASSES

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ABSTRACT

Pre-fertilisational ovules of 34 species in 12 genera of African arundinoid grasses were examined, and found to possess a number of peculiar features. Most strikingly, haustorial synergids, reported earlier by Philipson (1977) and Philipson and Connor (1984) for a number of Australasian and South American arundinoids were found in at least 19 African taxa. This character, and an expanded micropyle, are used to recognise a monophyletic danthonioid group, that includes species of *Chaetobromus*, *Cortaderia*, *Karroochloa*, *Merxmuellera*, *Pentameris*, *Pentaschistis*, *Pseudopentameris*, *Schismus*, *Tribolium* and *Urochlaena*, as well as *Chionochloa*, *Danthonia*, *Erythanthera*, *Lamprothyrsus*, *Pyrrhanthera*, *Rytidosperma* and *Sieglingia*. The full extent of this group remains indeterminate, however, since several smaller arundinoid genera remain embryologically unstudied. Significantly, the genera *Centropodia*, *Dregeochloa*, *Arundo* and *Phragmites* do not appear to belong in this group, despite their present association with its members.

INTRODUCTION

Most recent classifications of the Poaceae treat the family as comprising five major subfamilies, the Panicoideae, the Pooideae, the Bambusoideae, the Chloridoideae, and the Arundinoideae (e.g. Renvoize 1981; Campbell 1985; Dahlgren *et al.* 1985; Watson *et al.* 1985; Clayton and Renvoize 1986; Gibbs-Russell *et al.* 1990). In a recent cladistic analysis of the grasses, Kellogg and Campbell (1986) were able to show that the first three of these subfamilies, and possibly the fourth, behave as good monophyletic groups. However, unable to find any apomorphies uniting the members of the Arundinoideae, or even a large subset of it, they concluded that this subfamily is clearly polyphyletic, and that it does not contain any large monophyletic group.

The lack of cohesion displayed by the arundinoid grasses has long been recognised by agrostologists (Watson and Clifford 1976; Renvoize 1981; Campbell 1985; Tomlinson 1985; Clayton and Renvoize 1986; Conert 1986) and the group has been retained primarily on the grounds that its members show 'slightly more overall similarity with each other than with members of any other groups' (Watson and Clifford 1976). The delimitation, and subdivision of the arundinoids, therefore, remains problematic, and the relationships between its constituent taxa are unclear (Clayton and Renvoize 1986).

Clayton (1981), attempting to explain the confusion that identifies the arundinoids, suggested that the extant genera are dismembered fragments of a group whose core has gone extinct, while Tomlinson (1985) proposed that the difficulties posed by arundinoid taxonomy may be a reflection of extensive convergence and parallelism within the group. Support for Clayton's view comes from the general perception that the arundinoids are rather primitive, and are plesiomorphic for most characters (Stebbins 1956; Kellogg and Campbell 1986).

Renvoize (1981) identified, as the 'core genera' of the Arundinoideae, a group of taxa corresponding roughly with the traditional tribe Danthonieae, a group whose centre of distribution lies in the southern hemisphere (Conert 1971). Originally placed in the Aveneae and Festuceae (e.g. see Hubbard 1934) on the basis of

TABLE 1. The genera of the Arundineae (Arundinoideae: Poaceae) following Clayton and Renvoize (1986). Taxa marked with an asterisk have not yet been embryologically studied.

Tribolium
Urochlaena
**Elytrophorus*
**[1]Prionanthium*
**Spartochloa*
**Notochloa*
**Zenkeria*
**Piptophyllum*
**Styppeiochloa*
Chionochloa
Danthonia
Chaetobromus
**Plinthanthesis*
Pentaschistis
Pentameris
**Poagrostis*
Pseudopentameris
Rytidosperma
**Phaenanthoecium*
**Alloeochaete*
**Monachather*
Pyrrhanthera
Dregeochloa
Centropodia
**Danthonidium*
**Anisopogon*
**Diplopogon*
**Amphipogon*
**Crinipes*
**Nematopoa*
**Leptagrostis*
**Dichaetaria*
Cortaderia
Lamprothyrsus
Arundo
**Hakonechloa*
**Molinia*
Phragmites
**Gynerium*

1. Investigated in present study, but study material immature.

superficial similarities in spikelet morphology, the members of this tribe were moved to the neighbourhood of the Arundineae by De Wet (1954, 1956, 1960) who used mainly anatomical and cytological features. Subsequently, Renvoize (1981) and Clayton and Renvoize (1986) sank the group into the Arundineae (Table 1) claiming that the separation of the two tribes is unjustified. Recently, however, Conert (1986) revived the tribe, although in a modified form.

Over the last fifty years, particularly, the danthonioid arundinoids have received a great deal of attention from various workers (e.g. Zotov 1963; Conert 1966, 1971; Conert and Tuerpe 1969; Blake 1972; Nicora 1973; Connor and Edgar 1974, 1979; Veldkamp 1980; Jacobs 1982; Connor 1983). During this period, the taxonomy of the group has changed considerably with the genus *Danthonia*, initially the largest genus, gradually being trimmed down in size, and several segregate genera being split off. In Africa, *Danthonia* gave birth, among others, to the genera *Dregeochloa*, *Karroochloa*, *Merxmuellera*, and *Pseudopentameris* (Conert 1966, 1971; Conert and Tuerpe 1969), while in Australasia and South America, it gave rise to a range of genera such as *Chionochloa*, *Notodanthonia* (*Rytidosperma*), *Erythranthera*, *Pyrrhanthera* and *Plinthanthesis* as well as a host of *Cortaderia* species (Conert 1961; Zotov 1963; Connor and Edgar 1971, 1979; Blake 1972; Nicora 1973). Much of the present classification of the Danthonieae is based on spikelet and floret morphology, and caryopsis data, from work done, particularly, by Conert (1961, 1971, 1986). As various workers have pointed out, however, spikelet structure is 'subject to a good deal of parallel evolution' and so, may produce unreliable results (Clayton 1981). Kellogg (1990) recently pointed out, in a study on florets of *Poa*, that this parallelism is to some extent a product of the differential development and growth rates in different species of grasses.

De Wet (1954, 1956, 1960) initiated the first serious non-morphological analysis of relationships in the danthonioid grasses, thereby breaking away from traditional, strictly-morphological methods, and his discussions of the group concentrate on cytological and anatomical characters. His results established a high level of character heterogeneity for these traits across the danthonioids. Recently, Ellis produced a series of papers describing, in some depth, the leaf anatomy of a range of African arundinoid-danthonioid genera including *Merxmuellera*, *Pentameris*, *Dregeochloa*, *Pseudopentameris*, and *Chaetobromus* (Ellis 1977-1988), and this was followed up by a study of *Pentaschistis* leaf anatomy by Ellis and Linder (1992). These authors found that in some instances, the leaf anatomy of some *Pentaschistis* species is more similar to that of neighbouring genera, than it is to other members of the same genus, and they therefore hinted that a realignment of danthonioid genera may be necessary. The groupings obtained in these anatomical works were found to be congruent with the morphological groupings obtained earlier by the same authors (Linder and Ellis 1990) in a revision of the genus *Pentaschistis*. In another recent study, Hilu and Esen (1990) examined the prolamins in a range of arundinoid and non-arundinoid grasses. Using both cladistic and phenetic methods, they showed that the arundinoids examined formed a tight cluster, but that the individual genera themselves were intermingled and not easily separable. They suggested that a high degree of prolamin homogeneity indicated a monophyletic origin for this group of arundinoids. In a separate phenetic analysis of the grasses, Hilu and Wright (1982) obtained similar results, thus providing support for this idea.

The use of embryology in taxonomy is nothing new. Recently, Kapil and Bhatnagar (1991) argued that the use of embryological characters in taxonomy is justified for a number of reasons; among other things, they argued that embryological characters are well correlated with taxonomic groups, and that they are not easily affected by selective pressures. Kellogg and Campbell (1986) suggested that embryo characters are of prime importance in elucidating relationships among grass taxa. Certainly, in allied plant groups, they have been found to provide extremely significant systematic information (Hamann 1975; Campbell and Kellogg 1986; Kircher 1986; Rudall and Linder 1988). Although, some systematic work has been done using the characters of the mature post-fertilisational embryos of grasses (e.g. Reeder 1953), character variation in pre-fertilisational ovules in the Poaceae is relatively unexplored. Some work has been done, however, to establish the general nature of the ovule in grasses (Anton and Cocucci 1984, De Triquell 1986) and this provides a good base for comparative studies.

Philipson (1977) and Philipson and Connor (1984) reported the occurrence of an unusual embryological feature, namely haustorial synergids, for a number of danthonioids from New Zealand and the Americas. The ultrastructure and possible function of these structures was investigated by Philipson (1981), who suggested that they may be involved in the uptake of nutrients for the embryosac, as well as the secretion of substances to guide pollen tube growth. Philipson and Connor (1984) suggested that the absence of these structures from other grasses, is indicative of their derived (apomorphic) nature, and therefore might be of some use in revealing a monophyletic group within the arundinoids.

In this study, the ovule characters of a number of species in 12 genera of African arundinoid-danthonioid grasses are examined, taking into consideration only the features of the ovule at the mature embryosac stage (ontogenetic embryosac development will essentially be ignored).

The aims of the study, briefly, are as follows:

(1) To produce a record of embryological character data for the taxa under study.

(2) To identify those embryological characters which appear unusual or derived (synapomorphies) and which may therefore be of use in the revelation of monophyletic groups.

(3) To identify patterns in the embryological character data across the range of taxa examined.

A longer-term objective of the study is also to provide new data for use in the development of a complete phylogenetic revision of the African arundinoids.

MATERIALS AND METHODS

Ovule characters were examined for 34 species in 12 genera of African arundinoids (present generic delimitation) (Table 2). In addition, the ovular features of eight other taxa were also investigated for comparative purposes. These include two non-African arundinoids, two bambusoids, two panicoids, and two chloridoids. Ovules selected for study were specifically taken from florets undergoing, or about to undergo, anthesis (i.e. pre-fertilisation), to ensure embryosac maturity and ontogenetic homogeneity across the range of material studied. Study material was taken from plant material collected in the field between July 1991 and January 1992. This plant material had, subsequent to collection, been fixed in FAA for at least 24 hours and stored in 70% ethanol. Two separate procedures were employed in the preparation and examination of ovular material:

(1) **DIC.** Approximately 12-15 ovaries of each species were dissected out of suitably mature florets using fine forceps. Ovules were then separated from the ovary wall in a drop of Herr's (1971) clearing fluid (lactic acid: chloral hydrate: phenol: clove oil: xylene, 2: 2: 2: 2: 1 by weight) under a Zeiss Stemi SR dissecting microscope with below-stage lighting (magnifications used 8X, 12X, 20X, 32X and 50X) using size 00 insect pins. The free ovules were mounted on microscope slides following the method described by Herr (1971). Two cover slips were placed next to each other on a standard microscope slide with a drop of Herr's fluid, so that a narrow channel remained between them. This channel was then filled with Herr's fluid, and about 7-10 ovules placed inside. Finally, a third cover slip was carefully placed over the channel, again with a drop of Herr's fluid. The ovules were then allowed to clear completely for two days, and observed using differential interference contrast (DIC) optics on a Zeiss Axioskop microscope (magnifications used 200X, 400X and 1000X). The ovules of all but two species studied were prepared and examined in this way.

(2) **Sections.** The ovules of a number of the species investigated were also prepared for examination by an alternative method: serial sectioning and staining. This exercise was performed essentially to confirm the observations obtained by the first method. Whole ovaries, along with their styles, were dissected out (approximately 8

of each species examined) and then passed mechanically (Sukura tissue processor) through a dehydration series containing : 2 baths 70% ethanol, 2 baths 100% ethanol, 2 baths N-propanol, 2 baths N-butanol and 2 baths wax (6-8 hours each). The wax-soaked ovaries were retrieved, and embedded in wax. Wax blocks were trimmed and serially sectioned, on a Leitz Wetzlar rotary microtome, to a thickness of 10 microns. Sections were applied to microscope slides with Haupt's adhesive and then passed manually through a staining sequence comprising the following chemicals (Johansen 1940): xylene (2 baths, 5 minutes each), 2-methoxy-ethanol (1 bath, 2 minutes), 96% ethanol (2 baths, 2 minutes each), safranin (1 bath, 30 minutes), distilled water (brief rinse), 2-methoxy-ethanol (1 bath, 1-2 minutes), fast green (1 bath, 1 minute), 96% ethanol (brief rinse), n-butanol (2 baths, 1-2 minutes each), and xylene (2 baths, 5 minutes each). Finally, a large cover slip was laid over each slide with a few drops of DPX mountant. Slides were viewed using normal transmission optics on a Zeiss Axioscope microscope (magnifications used 200X, 400X and 1000X).

In each case, photographs were taken on the Zeiss Axioskop microscope, using Ilford 400 Delta film.

TABLE 2. A list of taxa examined for ovule characters, with vouchers. Supraspecific classification follows Clayton and Renvoize (1986) except that *Karroochloa* and *Merxmuellera* are separated from *Rytidosperma*.

BAMBUSOIDEAE
  Bambuseae
    Arundiniinae
      Arundinaria
        sp., *No voucher*
  Ehrharteae
      Ehrharta
        pusilla Nees *ex* Trin., *Linder 5417*

ARUNDINOIDEAE
  Arundineae
      Tribolium
        hispidum (Thunb.) Renvoize, *Linder 5403*
        obliterum (Hemsl.) Renvoize, *Linder 5453*
      Urochlaena
        pusilla Nees, *Linder 5358*
      Prionanthium
        dentatum (L.f.) Henr., *Linder 5430*
      Chaetobromus
        dregeanus Nees, *Linder 5404*
        involucratus (Schrad.) Nees, *Linder 5416*
      Pentaschistis
        ampla (Nees) McClean, *No voucher*
        argentea Stapf, *Linder 5013*
        aristidoides (Thunb.) Stapf, *Linder 5357*
        aristifolia Schweick., *Linder 5425*
        chippendalliae Linder, *Linder 4711*
        eriostoma (Nees) Stapf, *Linder 5454*
        holciformis (Nees) Linder, *Linder 5526*
        pallescens (Schrad.) Stapf, *No voucher*
        patula (Nees) Stapf, *Linder 5434*
        pungens Linder, *Linder 5443*
        tomentella Stapf, *Linder 5419*
        velutina Linder, *Linder 5446*
      Pentameris
        macrocalycina (Steud.) Schweick., *Linder 4418*
        thuarii Beauv., *Linder 5456*
      Karroochloa
        purpurea (L.f) Conert & Tuerpe, *Linder 5449*
        schismoides (Stapf *ex* Conert) Conert & Tuerpe, *Linder 5411*
        tenella (Nees) Conert & Tuerpe, *Linder 5360*

TABLE 2. Continued

- ARUNDINOIDEAE
  - Arundineae
    - *Merxmuellera*
      - *arundinacea* (Berg.) Conert, *Linder 5442*
      - *disticha* (Nees) Conert, *Barker 1010*
      - *dura* (Stapf) Conert, *Linder 5421*
      - *lanata* (?), *Linder 4769*
      - *rufa* (Nees) Conert, *Linder 5397*
      - *stricta* (Schrad.) Conert, *Linder 5448*
    - *Pseudopentameris*
      - *macrantha* (Schrad.) Conert, *No voucher*
    - *Schismus*
      - *barbatus* (Loefl. *ex* L.) Thell., *Linder 5359*
    - *Dregeochloa*
      - *pumila* (Nees) Conert, *Linder 5408*
    - *Centropodia*
      - *glauca* (Nees) T.A.Cope, *Linder 5410*
    - *Cortaderia*
      - *selloana* (Schult.) Aschers & Graebn., *No voucher*
    - *Arundo*
      - *donax* L., *No voucher*

- CHLORIDOIDEAE
  - Pappophoreae
    - *Schmidtia*
      - *pappophoroides* Steud., *No voucher*
  - Eragrostideae
    - Uniolinae
      - *Fingerhuthia*
        - *africana* Lehm., *No voucher*

- PANICOIDEAE
  - Paniceae
    - Setariinae
      - *Panicum*
        - *maximum* Jacq., *No voucher*
      - *Urochloa*
        - *oligotricha* (Fig. & De Not.) Henr., *No voucher*

RESULTS

The species descriptions are ordered as in Table 2, following the classification of Clayton and Renvoize (1986). Although new terminology has been kept to a minimum, a few terms have been introduced here and require explanation. The extent to which the integuments cover the ovule is rather variable, and determines whether they are termed complete, incomplete, partial or collar-like (Fig. 1). Where an integument covers an ovule entirely, such that its edges meet closely at the micropyle (Fig. 1*a*), it is termed complete, and the micropyle constricted. If this is not the case, then the integument is termed incomplete, partial or collar-like, depending on the level of integumentary development (Fig. 1*b*-*d*). When neither integument is complete, the micropyle is enlarged, and is termed expanded. The presence of haustorial synergids growing through the micropyle may preclude the integuments from being complete, resulting in an expanded micropyle.

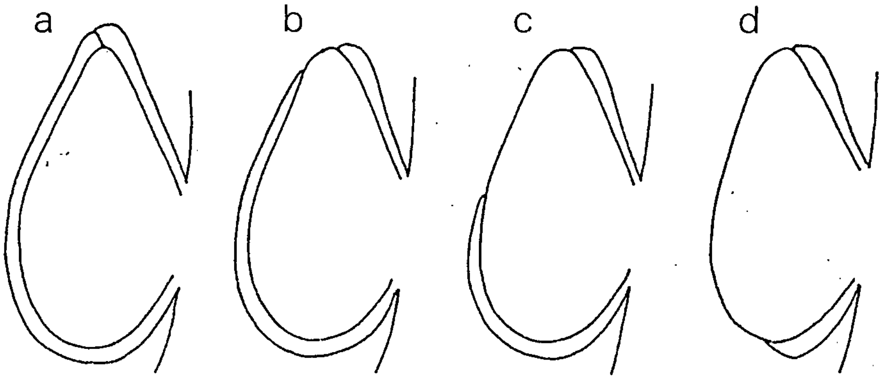

FIGURE 1. Schematic diagram showing variation in the development of the integuments, and the terminology used here to describe this variation: (a) complete, (b) incomplete, (c) partial, (d) collar-like.

Three other terms used are: (i) stylar wedge, this being a wedge-like thickening of the outer integument at the basal/ stylar end of the ovule, (ii) streamers, referring to an elongated structure usually extending from the polar nuclei to the antipodal complex, and (iii) synergid tails, these being tapering elongations of the synergids at their proximal end.

Species descriptions

ARUNDINARIA

Arundinaria sp.

PLATE 1a.

DIC. Ovule hemianatropous, very large (nearly 1mm in length). Outer integument incomplete, unthickened, probably having a stylar wedge. Inner integument complete, thickened about the micropyle. Nucellar cap complete, one cell thick. Micropyle endostomic, constricted. Embryosac small (relatively), about 1/3 length of ovule. Cellular features of embryosac rather unclear, but very different to that of the other grasses studied. Antipodals proliferative (numerous nuclei). One or two prominent nuclei in region of micropyle (identity uncertain), surrounded by large granules (starch?). Synergids non-haustorial.

(4 ovules examined)

Section. Ovule hemianatropous, very large. Outer integument incomplete, unthickened. Inner integument complete, thickened about micropyle. Nucellar cap complete, one cell thick. Micropyle endostomic, constricted. Embryosac roughly 1/3 length of ovule, cellular features unclear.

(2 ovules examined)

EHRHARTA

Ehrharta pusilla

Section. Ovule orientation unclear and some sections missing, casting doubt on accuracy and completeness of observations. Outer integument partial, unthickened, perhaps with a slight stylar wedge. Inner integument appears to be complete, with proliferative thickening in the region of the micropyle. Nucellar cap seems to be complete, 3-4 cells thick, cells flattened. Embryosac about 5/8 length of ovule. Antipodals proliferative. Synergids not clearly haustorial. Egg cell crescent-shaped, situated at base of synergids.

(2 ovules examined)

TRIBOLIUM

Tribolium hispidum

DIC. Material examined immature. Ovule hemianatropous, small. Outer integument partial, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap complete (young), 1-2 cells thick, cells cuboid. Embryosac poorly developed, features unclear. One ovule with megasporocyte or megaspore.

(5 ovules examined)

Tribolium obliterum

DIC. Ovule hemianatropous, small, adaxially indented at micropylar end. Outer integument probably collar-like to partial, perhaps slightly thickened in region of micropyle. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 3/4 length of ovule, features rather unclear. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Streamer from polar complex to antipodal region.

(5 ovules examined)

UROCHLAENA

Urochlaena pusilla

DIC. Ovule hemianatropous. Outer integument partial, unthickened, and apparently lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 5/8 length of ovule. Antipodals proliferative (up to 12 cells seen in one ovule), with large vacuoles. Polar nuclei medium. Synergids strongly haustorial, with large starch grains, protrude from the micropyle.

(12 ovules examined)

PRIONANTHIUM

Prionanthium dentatum

DIC. Material examined rather young. Ovule hemianatropous, small. Outer integument partial, unthickened, and possessing a slight stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete (complete only when very young, and then just one cell thick). Micropyle endostomic, expanded. Embryosac about 1/2-2/3 length of ovule, rather indiscrete, cellular features unclear. Antipodals proliferative (7 nuclei seen in one ovule). Synergids not clearly haustorial (too young?), but do possess fine-grained starch . Polar nuclei conspicuous. Paired streamers from polar cell to antipodal complex.

(13 ovules examined)

Prionanthium ecklonii

DIC. Material examined immature. Ovule hemianatropous, small. Outer integument collar-like, perhaps slightly thickened near micropyle, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap complete, one cell thick. Micropyle endostomic, expanded. Embryosac not yet developed. One ovule seen with megaspore only.

(15 ovules examined)

CHAETOBROMUS

Chaetobromus dregeanus

Plate 1b,c.

DIC. Ovule hemianatropous. Outer integument collar-like, thickened in micropylar region (3-4 cells thick), and possessing a slight stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 2/3 length of ovule, rather indistinct, cellular features unclear. Antipodals apparently proliferative. Synergids strongly haustorial, with large starch grains, protrude from the micropyle, and possessing 'tails' proximally.

(10 ovules examined)

Section. Ovule hemianatropous, slightly flattened abaxially. Outer integument collar-like, thickened near micropyle, no stylar wedge seen. Inner integument and nucellar epidermis incomplete where haustorial synergids present; otherwise complete (young material?). Micropyle endostomic, expanded (constricted where synergid haustoria not present). Embryosac about 3/4 length of ovule, features unclear. Synergids seen to be haustorial in at least one ovule.
(3 ovules examined)

Chaetobromus involucratus

DIC. Ovule hemianatropous. Outer integument collar-like, slightly thickened at micropyle, and lacking a significant stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 5/8 length of ovule, fairly discrete. Antipodals proliferative, up to 12 seen per ovule, with large vacuoles. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei large.
(13 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, thickened at micropyle (3 cells thick). Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule, quite discrete. Antipodals proliferative. Synergids haustorial. Polar nuclei large.
(3 ovules examined)

PENTASCHISTIS

Pentaschistis ampla

DIC. Ovule hemianatropous, slight adaxial indentation at micropylar end. Outer integument collar-like to partial, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete or complete (complete nucellar cap, 1 cell thick, in most [younger?] ovules). Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule, features somewhat unclear.

Antipodals appear to be proliferative. Synergids with fine grained starch, apparently haustorial in some ovules.

(13 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis unclear, may be complete. Micropyle endostomic, expanded. Embryosac, about 2/3 length of ovule, poorly defined. Synergids possibly haustorial, unclear.

(1 ovule examined)

Pentaschistis argentea

Plate 1d-f.

DIC. Ovule hemianatropous, rather flattened/elongated. Outer integument partial, unthickened, and without a stylar wedge. Inner integument incomplete. Nucellar cap complete, 2-3 cells thick, cells cuboid to somewhat tangentially flattened. Micropyle endostomic, expanded. Embryosac approximately 1/2 length of ovule, rather indiscrete. Several nuclei present, identities and arrangement uncertain. Antipodals proliferative, up to 9 nuclei in one ovule. Synergids non-haustorial. Some fine granular material (starch?) in embryosac in usual position of egg apparatus. Almost certainly some apomictic embryosacs present

(11 ovules examined)

Section. Ovule hemianatropous. Outer integument partial, unthickened, and lacking a distinct stylar wedge. Inner integument incomplete. Nucellar cap complete, 2-3 cells thick, cells rather cuboid. Micropyle endostomic, expanded. Embryosac about 2/3 length of ovule. Antipodals proliferative. Synergids non-haustorial, but contain some starch (granular). Polar nuclei conspicuous. Additional, apomictic embryosacs.

(2 ovules examined)

Pentaschistis aristidoides

DIC. Ovule hemianatropous, small, rather slender. Outer integument collar-like to partial, not significantly thickened, and with no stylar wedge. Inner integument incomplete. Nucellar cap complete, 1 cell thick, cells cuboid, convex on outside. Micropyle endostomic, expanded. Embryosac roughly 5/8 length of ovule, quite discrete (sac well defined). Antipodals proliferative (up to 10 nuclei in one ovule). Synergids non-haustorial, although possibly possess some fine grained starch. Polar nuclei conspicuous.

(6 ovules examined)

Pentaschistis aristifolia

DIC. Ovule hemianatropous, small. Outer integument collar like, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap complete, 1 cell thick, cells roughly cuboid. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule, rather indistinct. Antipodals proliferative, up to 6 nuclei per ovule. Synergids not clearly haustorial (too young?), but possess fine-grained starch.

(13 ovules examined)

Pentaschistis chippendalliae

Plate 2a,b.

DIC. Material examined immature. Ovule hemianatropous. Outer integument collar-like, slightly thickened (2-3 cells thick here) in the region of the micropyle, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap complete to incomplete. Micropyle endostomic, constricted or expanded. Embryosac roughly 2/3 length of ovule. Antipodals unclear, but apparently not yet proliferative (too young?). Synergids not clearly haustorial (too young?) (perhaps weakly haustorial), but do possess fine-grained starch. Polar nuclei medium sized.

(5 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, not significantly thickened, and lacking a clear stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Nucellar epidermis incomplete. Embryosac about 2/3 length of ovule. Antipodals not clearly proliferative. Synergids apparently haustorial (although they do not appear to protrude beyond the micropyle), with fine grained starch.

(2 ovules examined)

Pentaschistis eriostoma

DIC. Ovule hemianatropous, fairly large. Outer integument partial, not significantly thickened, and one with a stylar wedge. Inner integument incomplete. Nucellar cap incomplete. Micropyle endostomic, expanded. Some callose in micropylar area. Embryosac about 2/3-7/8 length of ovule, rather indiscrete. Antipodals proliferative, with large vacuoles, and in a distinct cluster. Synergids strongly haustorial, protrude from the micropyle, with fine grained starch. Some ovules appear to possess extra embryosacs, these being apomictic. One ovule 'invaded' by a number of large spherical cyst-like structures.

Pentaschistis holciformis

DIC. Some of the material examined rather young. Ovule hemianatropous. Outer integument collar-like to partial, unthickened, and lacking a distinct stylar wedge. Inner integument incomplete, rather thick abaxially in micropylar area (3-4 cells thick). Nucellar epidermis incomplete (complete nucellar epidermis in young ovules). Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule, rather indiscrete, cellular features unclear. Antipodals appear to be proliferative. Synergids only weakly haustorial (in some cases, not clearly haustorial at all) and do not protrude beyond the micropyle, with fine starch grain. Polar nuclei conspicuous. Streamer from polar nuclei to antipodal complex.

(12 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, perhaps slightly thickened near micropyle. Inner integument incomplete, thickened near micropyle (up to 3 cells thick here). Nucellar cap complete in some ovules (young?), incomplete in others. Micropyle endostomic, expanded. Embryosac about 3/4 length of ovule, feature unclear. Antipodals proliferative. Synergids with fine grain, only possibly slightly haustorial.

(1 ovule examined)

Pentaschistis pallescens

Plate 2c.

DIC. Ovule hemianatropous. Outer integument partial, not significantly thickened, and lacking a stylar wedge. Inner integument complete, or just barely incomplete.

Nucellar cap mostly complete, 4-6 cells thick, cells flattened tangentially. Micropyle endostomic, expanded to almost constricted. Embryosac approximately 1/2-2/3 length of ovule. Antipodals unclear, but apparently proliferative. Polar nuclei close together, medium. Synergids generally non-haustorial and lacking starch, although in one ovule, a haustorial synergid-like structure was observed breaking through the nucellar cap. Some ovules appear to possess apomictic embryosacs.

(12 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, thickened slightly in region of micropyle (3 cells thick), and possessing a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete (complete in younger ovules). Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule. Antipodals apparently proliferative, small. Synergids haustorial (although not protruding beyond micropyle), with fine starch grains.

Pentaschistis patula

DIC. Ovule hemianatropous. Outer integument collar-like, slightly thickened in micropylar area, and possessing a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule, quite discrete. Antipodals proliferative, aggregated in a discrete cluster. Synergids haustorial (do not protrude far beyond the micropyle), appear to lack starch or starch is fine grained. Synergids appear to have villous extensions apically. Polar nuclei quite large, in a crescent-shaped cell. Egg cell oval, nested at base of synergids. Streamer from polars to antipodals.

(8 ovules examined)

Pentaschistis pungens

DIC. Ovule hemianatropous. Outer integument collar-like, slightly thickened about micropyle, and with a slight stylar wedge. Inner integument incomplete to nearly complete, rather thick near micropyle. Nucellar cap complete, 1-2 cells thick, cells cuboid to columnar. Micropylar area unclear because callose present. Micropyle endostomic, expanded, rather oblique. Embryosac approximately 2/3 length of ovule, rather diffuse, features unclear. Synergids non-haustorial.

(12 ovules examined)

Pentaschistis tomentella

Plate 2d.

DIC. Ovule hemianatropous to almost pendulous. Outer integument collar-like, not significantly thickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap complete, 1 cell thick, rather insignificant in one ovule. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule, features rather unclear. Synergids apparently not haustorial (young?), but possess fine grained starch.

(8 ovules examined)

Section. Inner integument incomplete. Nucellar cap complete, 1 cell thick. Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule. Antipodals proliferative (6 in one ovule), tightly clustered. Synergids apparently non-haustorial (too young?), but having fine-grained starch. Polar nuclei conspicuous.

(2 ovules examined)

Pentaschistis velutina

Plate 2e,f.

DIC. Ovule hemianatropous. Outer integument collar-like, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac approximately 3/4 length of ovule, rather indiscrete, features unclear. Antipodals probably proliferative. Synergids very strongly haustorial, with fine grained starch, protrude from the micropyle, and of considerable length, usually reflexing back, externally, along the adaxial side of the ovule. Polar nuclei fairly conspicuous. Egg cell oval.

(11 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, unthikened, and lacking a clear stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule. Synergids strongly haustorial, with small to medium starch grains, protruding from the micropyle. Synergid haustoria are long, reflexing back externally.

(4 ovules examined)

PENTAMERIS

Pentameris macrocalycina

Plate 3a-c.

DIC. Ovule hemianatropous, possibly with slight adaxial indentation near micropyle. Outer integument collar-like, thickened at micropyle (up to 4 cells thick here), and lacking a stylar wedge. Inner integument apparently complete. Nucellar cap in some cases appears to be complete, but in other cases this is precluded by the existence of synergid haustorium-like structures. Nucellar cap 2 cells thick, cells cuboid to columnar. Micropyle endostomic, constricted. Embryosac about 3/4 length of ovule, poorly defined and difficult to interpret because of presence of callose. Synergids apparenly haustorial although they do not appear to pass through micropyle, finely grained (probably starch). Polar nuclei large. Egg cell elongated.

(11 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, slightly thickened at micropyle, and lacking a distinct stylar wedge. Inner integument complete, with proliferative thickening about the micropyle (several cells thick). Nucellar epidermis complete in most cases (1-2 cells thick, cells cuboid to columnar), but in at least one case incomplete. MIcropyle endostomic, constricted, slightly oblique. Embryosac about 3/4-7/8 length of ovule. Antipodals proliferative, large, and with large vacuoles. Synergids haustorial in at least one ovule, passing through the nucellar epidermis but not protruding through the micropyle. Synergids apparently granular, probably containing starch. Most ovules lack synergid haustoria. Polars conspicuous.

Pentameris thuarii

Plate 3d,e.

DIC. Ovule hemianatropous. Outer integument incomplete, with adaxial thickening near the micropyle, and without a stylar wedge. Inner integument complete. Nucellar epidermis apparently incomplete, or reduced. Micropyle endostomic, constricted, slightly oblique. Embryosac about 1/2 length of ovule. Antipodals obscure, but apparently proliferative. Synergids non-haustorial, lacking starch. Polar nuclei large, conspicuous, in crescent-shaped cell. Egg cell oval in shape, contains some starch (granular).

Section. Ovule hemianatropous. Outer integument partial to incomplete, with slight adaxial thickening at the micropyle, and lacking a stylar wedge. Inner integument complete. Nucellar epidermis probably incomplete, although in certain ovules, there appears to be a nucellar cap 2-3 cells thick (cells cuboid to slightly flattened). Micropyle endostomic, constricted, slightly oblique. Embryosac about 1/2-2/3 length of ovule. Antipodals proliferative, up to 10 nuclei per ovule. Synergids non-haustorial. Polar nuclei conspicuous.

(4 ovules examined)

PSEUDOPENTAMERIS

Pseudopentameris macrantha

Plate 3f.

DIC. Ovule hemianatropous, large, somewhat flattened abaxially. Outer integument collar-like, thickened at the micropyle (3-4 cells thick here), and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule, fairly discrete. Antipodals proliferative (up to 7 cells seen in one ovule), in a tight cluster. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei medium to large.

(9 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, thickened at micropyle. Inner integument incomplete. Nucellar epidermis incomplete, 2-3 cells

thick near micropyle, cells flattened. Micropyle endostomic, expanded. Embryosac approximately 2/3 length of ovule, rather discrete. Antipodals proliferative, with large vacuoles, and grouped into a tight cluster. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei conspicuous. Egg cell wedged between bases of synergids. Streamer from polars to antipodal complex.
(3 ovules examined)

KARROOCHLOA

Karroochloa purpurea

Plate 4a-f.

DIC. Ovule hemianatropous, small, and adaxially indented at micropylar end. Outer integument collar-like to partial, insignificantly thickened near micropyle (2 cells thick), one ovule with a small stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule. Antipodals proliferative, up to 10 per ovule. Synergids strongly haustorial, with large starch grains, protrude from the micropyle, may have tails proximally. Polar nuclei large. Paired streamers from polar cell to antipodals.
(10 ovules examined)

Section. Ovule hemianatropous, with adaxial indentation near micropyle. Outer integument collar-like, without significant thickening, and lacking a stylar wedge. Inner integument incomplete. Nucellar cap incomplete. Micropyle endostomic, expanded. Embryosac approximately 1/2-2/3 length of ovule. Polar nuclei large, close together. Synergids strongly haustorial, with large starch grains, protrude from the micropyle.
(3 ovules examined)

Karroochloa schismoides

Plate 5a,b.

DIC. Ovule hemianatropous, small, and slightly indented adaxially near the micropyle. Outer integument collar-like, not significantly thickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete.

Micropyle endostomic, expanded. Embryosac approximately 2/3 length of ovule, limits poorly defined. Egg cell oval, situated at base of synergids. Antipodals proliferative, up to 8 nuclei per ovule, large, and having large vacuoles in one ovule. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei medium sized. Streamer from polar cell to antipodals.

(4 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, unthickened, and lacking a significant stylar wedge. Inner integument incomplete. Nucellar cap incomplete. Micropyle endostomic, expanded. Embryosac roughly 3/4 length of ovule. Antipodals proliferative, large, baggy. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Streamer from polar region to antipodal complex.

Karroochloa tenella

Section. Ovule hemianatropous, small. Outer integument collar-like, unthickened, and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 2/3 length of ovule, fairly discrete. Antipodals proliferative, large, baggy (8 nuclei in one of the ovules examined). Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei medium sized.

(2 ovules examined)

MERXMUELLERA

Merxmuellera arundinacea

Plate 5c-f.

DIC. Ovule hemianatropous, almost pendulous, large, pointed at micropylar end. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, with proliferative thickening about the micropyle; also, large, orange, globular crystals in this region. Nucellar cap complete. Micropyle endostomic, constricted, oblique. Embryosac approximately 1/3-1/2 length of ovule, features unclear. Synergids apparently non-haustorial. Some ovules appear to contain starch (grainy) in area of synergids. Polar nuclei medium sized. Some ovules with more than one embryosac, some of these apomictic.

(11 ovules examined)

Section. Ovule hemianatropous, pointed at micropylar end. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, with proliferative thickening in the micropylar region. The micropylar part of the inner integument contains some crystalline material (globular, orange crystals). Nucellar cap possibly complete, 3-4 cells thick usually, cells cuboid to highly columnar. In some cases there appear to be slightly granular structures growing through the nucellar epidermis, into the micropyle: possibly, these are synergid haustoria. Micropyle endostomic, constricted, oblique. Embryosac roughly 1/3 length of ovule, features unclear. Antipodals proliferative (several per ovule). Synergids possibly haustorial, although this is not certain. Some ovules with more than one embryosac, some of these apomictic.

(3 ovules examined)

Merxmuellera disticha

Plate 6a.

DIC. Ovule hemianatropous, perhaps slightly adaxially indented near micropyle. Outer integument collar-like to partial, thickened near micropyle (up to 4 cells thick), and having a distinct stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 1/2 length of ovule. Antipodals proliferative (at least 9 nuclei seen in one ovule), large, rather baggy. Synergids strongly haustorial, with large starch grains, protrude from the micropyle. Polar nuclei conspicuous. Egg cell oval, situated at base of synergids.

(9 ovules examined)

Section. Ovule hemianatropous. Outer integument incomplete, and having a distinct stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 1/2 length of ovule. Antipodals probably proliferative, large and with large vacuoles. Synergids strongly haustorial, with large starch grains, protrude from the micropyle.

Merxmuellera dura

Plate 6b,c.

DIC. Ovule hemianatropous, slight adaxial indentation at micropylar end. Outer integument collar-like to partial, thickened near micropyle, and with a slight stylar wedge. Inner integument and nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac approximately 1/2-3/4 length of ovule. Antipodals proliferative, up to 20 nuclei counted per ovule, large, baggy, and with large vacuoles. Synergids strongly haustorial, with large or small starch grains, protrude from the micropyle. Polar nuclei conspicuous. One egg cell seen, oval. One ovule apparently with apomictic embryosacs.

(16 ovules examined)

Merxmuellera lanata

DIC. Ovule hemianatropous, large, pointed at micropylar end. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, with proliferative thickening in the region of the micropyle. Nucellar cap appears to be complete, although the presence of starch-filled structures (haustorial synergids?) in the micropylar area may preclude this. Micropyle endostomic, constricted, oblique. Embryosac poorly defined, probably about 1/2-2/3 length of ovule, cellular features unclear. Synergids possibly haustorial: in some ovules there appear to be finely grained (starch-filled?) structures growing into the micropyle, but not completely out of the ovule, and these could be synergids. This is, however, not clear.

(11 ovules examined)

Merxmuellera rufa

Plate 6d.

DIC. Ovule hemianatropous, nearly pendulous, large, pointed at micropylar end. Outer integument partial, unthickened, and lacking a stylar wedge. Inner integument complete, with proliferative thickening at the micropylar end. Nucellar cap complete, 1-4 cells thick, with the cells rather columnar in shape. Micropyle endostomic, constricted, oblique. Embryosac approximately 2/3 length of ovule, features rather unclear. Synergids possibly, although not clearly, haustorial (in a small number of ovules the situation is similar to that in *M. lanata*). Some fine granular material, probably starch, in the region of the egg apparatus. Some ovules appear to possess apomictic embryosacs.

(16 ovules examined)

Section. Ovule hemianatropous, large, pointed at micropylar end. Outer integument appears to be partial, perhaps slightly thickened near the micropyle (but not significantly), and lacking a stylar wedge. Inner integument complete, with proliferative thickening about the micropyle. Nucellar cap complete, 2-3 cells thick, cells cuboid. Micropyle endostomic, constricted, oblique. Embryosac roughly 2/3 length of ovule, fairly discrete, but features unclear. Synergids apparently non-haustorial. Possibly some apomictic embryosacs.

(3 ovules examined)

Merxmuellera stricta

Plate 6e,f, 7a.

DIC. Ovule hemianatropous, slight adaxial indentation near micropyle. Outer integument partial, adaxially thickened near micropyle (3 cells thick here), and lacking a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac approximately 1/2-2/3 length of ovule, fairly discrete. Antipodals proliferative, up to 12 nuclei per ovule. Synergids strongly haustorial, with fine or large starch grains (grain size a function of age?), protrude from the micropyle; one ovule of this species possessed the largest and most elaborate synergid haustoria encountered in this study. Polar nuclei quite large. Some ovules with extra, apomictic embryosacs.

(13 ovules examined)

Section. Ovule hemianatropous. Outer integument partial, not visibly thickened, and lacking a clear stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac about 1/2-2/3 length of ovule. Antipodals clearly proliferative, large, and with large vacuoles. Synergids haustorial, with large or small starch grains. Polar nuclei conspicuous. One ovule appears with streamer from polar nuclei to antipodals.

(4 ovules examined)

SCHISMUS

Schismus barbatus

Plate 7b-d.

DIC. Ovule hemianatropous, small, slender, adaxially slightly indented at micropylar end. Outer integument (partially damaged) probably collar-like, slightly thickened near micropyle. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac fairly discrete, about 2/3 length of ovule. Antipodals proliferative (up to 6 cells seen), tightly clustered, large and baggy, and with large vacuoles. Synergids strongly haustorial, with large starch grains, protrude from the micropyle, and possessing tails proximally. Polar nuclei large. Egg cell ovoid, lying at base of synergids, finely granular (starch?). Paired streamers from polar cell to antipodal complex.

(2 ovules examined)

Section. Ovule hemianatropous, perhaps slightly indented adaxially at micropylar end. Outer integument, collar-like, not clearly thickened, but possessing a distinct stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac fairly distinct, rougly 1/2-2/3 length of ovule. Antipodals proliferative (up to 9 seen). Synergids strongly haustorial, protrude from the micropyle . Polar nuclei distinct, very close. Several fine streamers from polar cell to antipodals.

(2 ovules examined)

DREGEOCHLOA

Dregeochloa pumila

Plate 7e.

DIC. Material studied immature. Ovule hemianatropous. Outer integument collar-like to partial, unthickened to slightly thickened (may be 2-3 cells thick), and lacking a distinct stylar wedge. Inner integument complete, may be slightly thickened near micropyle (up to 3 cells thick). Nucellar epidermis incomplete at micropyle (complete in young ovules), but may be very reduced. Micropyle endostomic, constricted. Embryosac about 1/2 length of ovule, cellular features unclear. One embryosac with megaspore nucleus only, another in the binucleate stage. Some ovules with a fairly mature embryosac. Antipodals proliferative (up to 9 nuclei counted in one ovule, often 2 per cell), large, baggy. Synergids apparently non-haustorial, but some starch present in the region of the polar nuclei and egg apparatus, in one instance extending almost throughout the entire embryosac (haustorial when mature?). Polar nuclei large.

(30 ovules examined)

Section. Material studied rather immature. Ovule hemianatropous. Outer integument incomplete, unthickened. Inner integument complete, thickened in region of micropyle. Nucellar epidermis probably complete. Micropyle endostomic, constricted, possibly slightly oblique. Embryosac incompletely developed (one in 2 nucleate stage, and one in 4 nucleate stage).

(2 ovules examined)

CENTROPODIA

Centropodia glauca

Plate 7f, 8a-c.

DIC. Ovule hemianatropous. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, with some thickening in the region of the micropyle (up to 3 cells thick). Nucellar cap complete, one cell thick. Micropyle endostomic, constricted, slightly oblique. Embryosac about 2/3 length of ovule, cellular arrangement rather unclear. Some starch-like material present in the region of the polar nuclei and egg apparatus, this extending even to the antipodal zone. Synergids non-haustorial.

(6 ovules examined)

Section. Ovule hemianatropous. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, with some proliferative thickening in the region of the micropyle. Nucellar cap complete, 1-2 cells thick, cells cuboid to columnar. Micropyle endostomic, constricted, somewhat oblique.

Embryosac approximately 1/2 length of ovule, fairly discrete. Antipodals proliferative, rather small. Synergids non-haustorial, apparently, in one ovule, possessing filiform apparati (pale, pink-staining regions at distal tips of synergids).
(6 ovules examined)

CORTADERIA

Cortaderia selloana

DIC. Ovule hemianatropous, somewhat flattened abaxially. Outer integument partial, thickened in region of micropyle (3-4 cells thick), and possessing a stylar wedge. Inner integument incomplete. Nucellar epidermis incomplete. Micropyle endostomic, expanded. Embryosac roughly 2/3 length of ovule, cellular features rather unclear. Antipodals probably proliferative. Polar nuclei medium sized. Synergids strongly haustorial, with large starch grains, protrude from the micropyle.
(10 ovules examined)

ARUNDO

Arundo donax

Plate 8d.

DIC. Material studied immature. Ovule hemianatropous, small. Outer integument partial, perhaps slightly thickened about micropyle. Inner integument complete. Nucellar cap complete, 1-2 cells thick, cells cuboid to columnar. Micropyle endostomic, constricted. Embryosac undeveloped.
(9 ovules examined)

SCHMIDTIA

Schmidtia pappophoroides

Section. Ovule hemianatropous, indented adaxially at micropylar end. Outer integument possibly collar-like to partial but this uncertain, slightly thickened near micropyle, and lacking a clear stylar wedge. Inner integument complete. Nucellar cap complete, one cell thick, cells cuboid. Micropyle endostomic, constricted. Embryosac approximately 2/3 length of embryosac, cellular features unclear. Synergids non-haustorial. Some granular material (starch?) in embryosac, especially near micropyle.

(2 ovules)

FINGERHUTHIA

Fingerhuthia africana

DIC. Ovule hemianatropous. Outer integument incomplete, unthickened, and lacking a stylar wedge. Inner integument complete, slightly thickened at micropyle. Nucellar cap very reduced/absent. Micropyle endostomic, constricted, tending to be very slightly oblique. Embryosac relatively large, about 7/8 length of ovule, cellular features rather indistinct. Two conspicuous nuclei near micropyle (identity unknown), surrounded by large granules (starch?). One ovule with 4 large nuclei. Synergids non-haustorial.

(6 ovules examined)

PANICUM

Panicum maximum

DIC. Ovule hemianatropous, with slight adaxial indentation near micropyle. Outer integument probably collar-like, unthickened (although possibly slightly thickened near micropyle). Inner integument barely incomplete to complete. Nucellar cap complete, up to 4 cells thick, cells cuboid. The outermost nucellar cap cells are

peculiar in being considerably enlarged, almost protruding from the micropyle. These enlarged cells have large vacuoles and conspicuous nuclei. Micropyle endostomic, constricted or nearly so. Embryosac about 1/2 length of ovule, poorly defined, arrangement unclear. Several embryosac nuclei, identities difficult to establish. Synergids non-haustorial.
(4 ovules examined)

UROCHLOA

Urochloa oligotricha

Plate 8e,f.

DIC. Ovule hemianatropous. Outer integument collar-like, slightly thickened near the micropyle (3 cells thick here), and possibly possessing a slight stylar wedge. Inner integument incomplete. Nucellar cap complete, about 3-4 cells thick, with cells generally cuboid but outermost cells being peculiar in that they are considerably enlarged, and have conspicuous nuclei. Micropyle endostomic, expanded. Embryosac about 1/2-2/3 length of ovule, quite globose, cellular arrangement rather unclear. Several nuclei present, identity of these uncertain. Synergids non-haustorial.
(10 ovules examined)

Section. Ovule hemianatropous. Outer integument collar-like, slightly thickened near micropyle, and lacking a clear stigmatic wedge. Inner integument incomplete. Nucellar cap complete, thick, cells generally cuboid but outermost cells peculiar in being greatly enlarged, and having a dark-staining content. Micropyle endostomic, expanded. Embryosac about 3/4 length of ovule, cellular features unclear. Synergids non-haustorial. Possibly more than one embryosac per ovule (apomixis?).
(3 ovules examined)

The Plates

Abbreviations used to label the plates are as follows:

a = antipodal
e = embryosac
eg = egg nucleus
h = haustorial synergid, or haustorial synergid-like structure
i = inner integument
m = micropyle
n = nucellar tissue, usually epidermis
o = outer integument
s = synergid
w = ovary wall

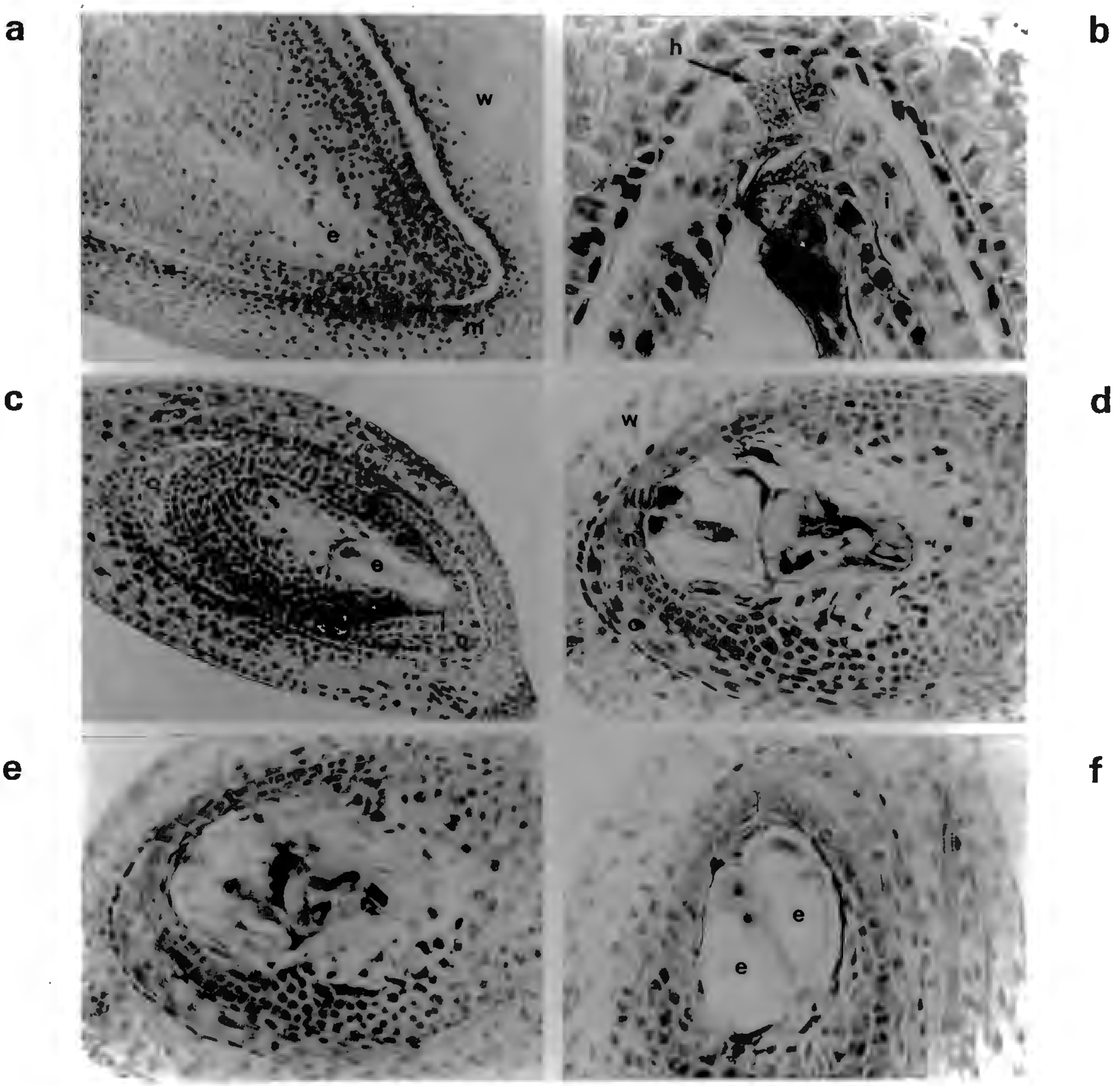

PLATE 1. a. *Arundinaria sp.*, long. section through ovary, showing apical half of ovule with complete inner and incomplete outer integument (200X). **b.** *Chaetobromus dregeanus*, long. section through micropylar region of ovule, with pair of grainy (starch) haustorial synergids protruding from micropyle (1000X). **c.** *C. dregeanus*, long. section through ovary, showing collar like outer integument with thickening near micropyle, haustorial synergids not visible (200X). **d,e.** *Pentaschistis argentea*, two sequential long. sections, through ovary. Embryosac (apomictic?) nuclei and complete nucellar cap visible (400X). **f.** *P. argentea*, oblique section through ovary, showing ovule with two distinct embryosacs (one apomictic) (400X).

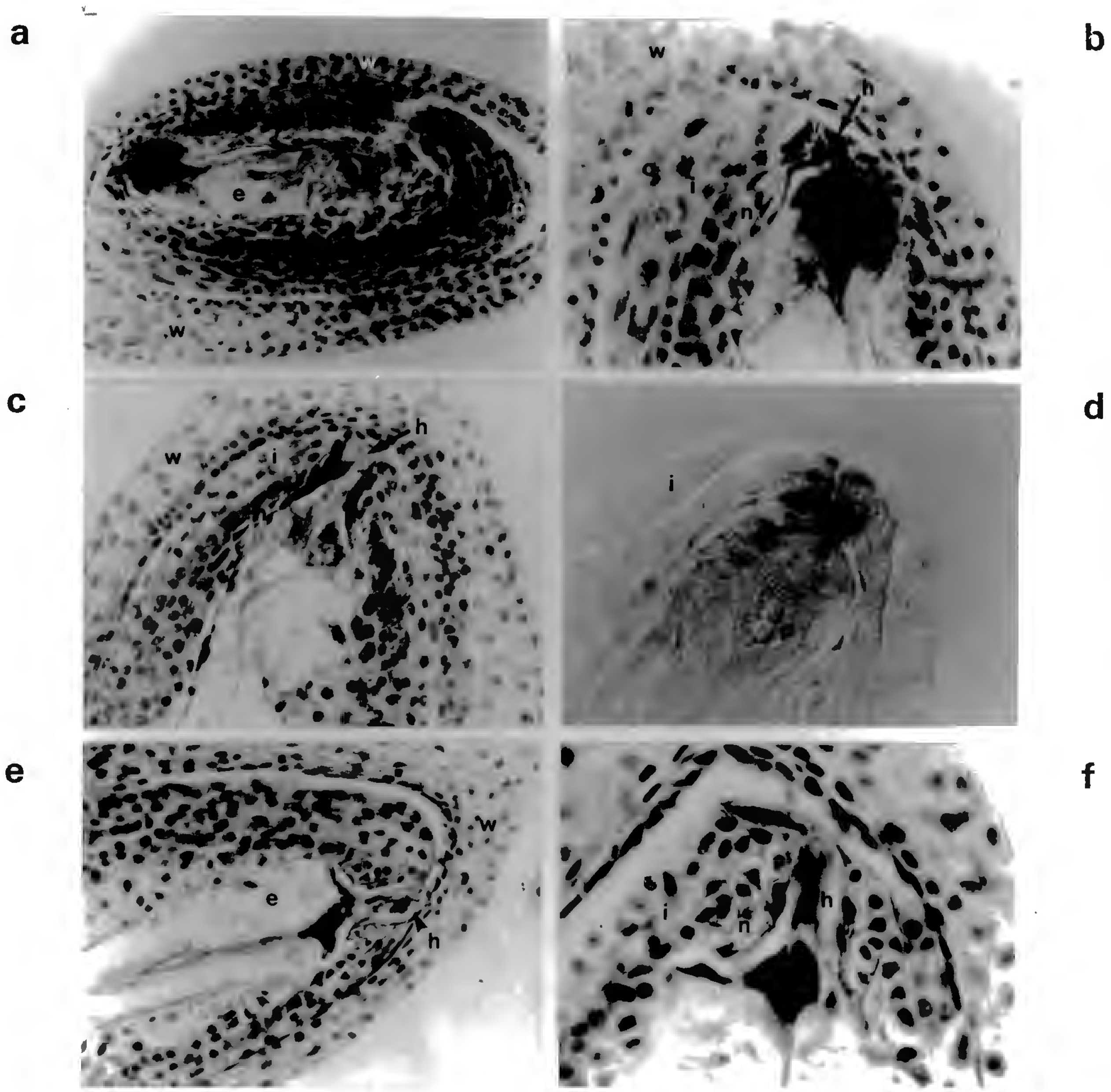

PLATE 2. a. *Pentaschistis chippendalliae*, long. section through ovule, showing collar-like outer integument, and non-protruding synergid haustorium (400X). **b.** *P. chippendalliae*, detail of micropylar region (from a.), showing non-protruding synergid haustorium, and incomplete inner integument and nucellar epidermis (1000X). **c.** *P. pallescens*, long. section of ovary, showing apical portion of ovule, with non-protruding haustorial synergid(s), and incomplete inner integument and nucellar epidermis (400X). **d.** *P. tomentella*, DIC, apical section of ovule, with polar nuclei clearly visible, nucellar epidermis complete, inner integument incomplete (1000X). **e.** *P. velutina*, long. section through ovary, showing apical half of ovule (400X). **f.** *P. velutina*, long section of apical portion of ovule, with protruding haustorial synergids visible, and incomplete nucellar epidermis and inner integument (1000X).

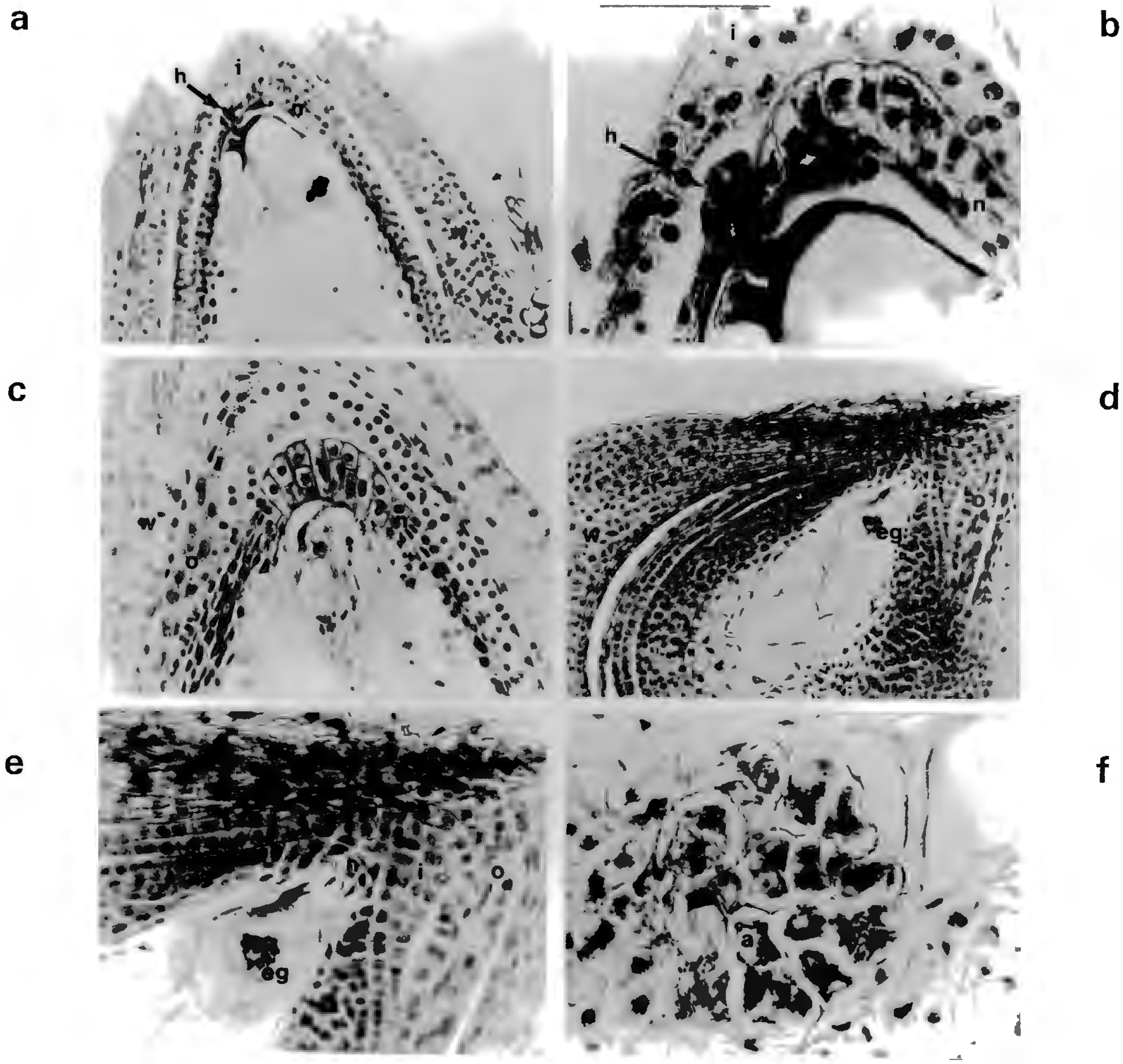

PLATE 3. a. *Pentameris macrocalycina*, long. section through apical half of ovule and part of ovary wall: inner integument complete, despite presence of haustorial synergid-like structure (200X). **b.** *P. macrocalycina*, detail of haustorial synergid-like structure (from **a.**) (1000X). **c.** *P. macrocalycina*, long. section of ovary, showing the condition more usual for this species, with the nucellar cap complete, and no synergid haustoria (400X). **d.** *P. thuarii*, long section, ovary, with micropyle at top right: egg nucleus clearly visible. (200X) **e.** *P. thuarii*, detail of micropylar region (from **d.**). Nucellar cap and inner integument complete (400X). **f.** *Pseudopentameris macrantha*, longitudinal section through complex of multiplied antipodals (1000X).

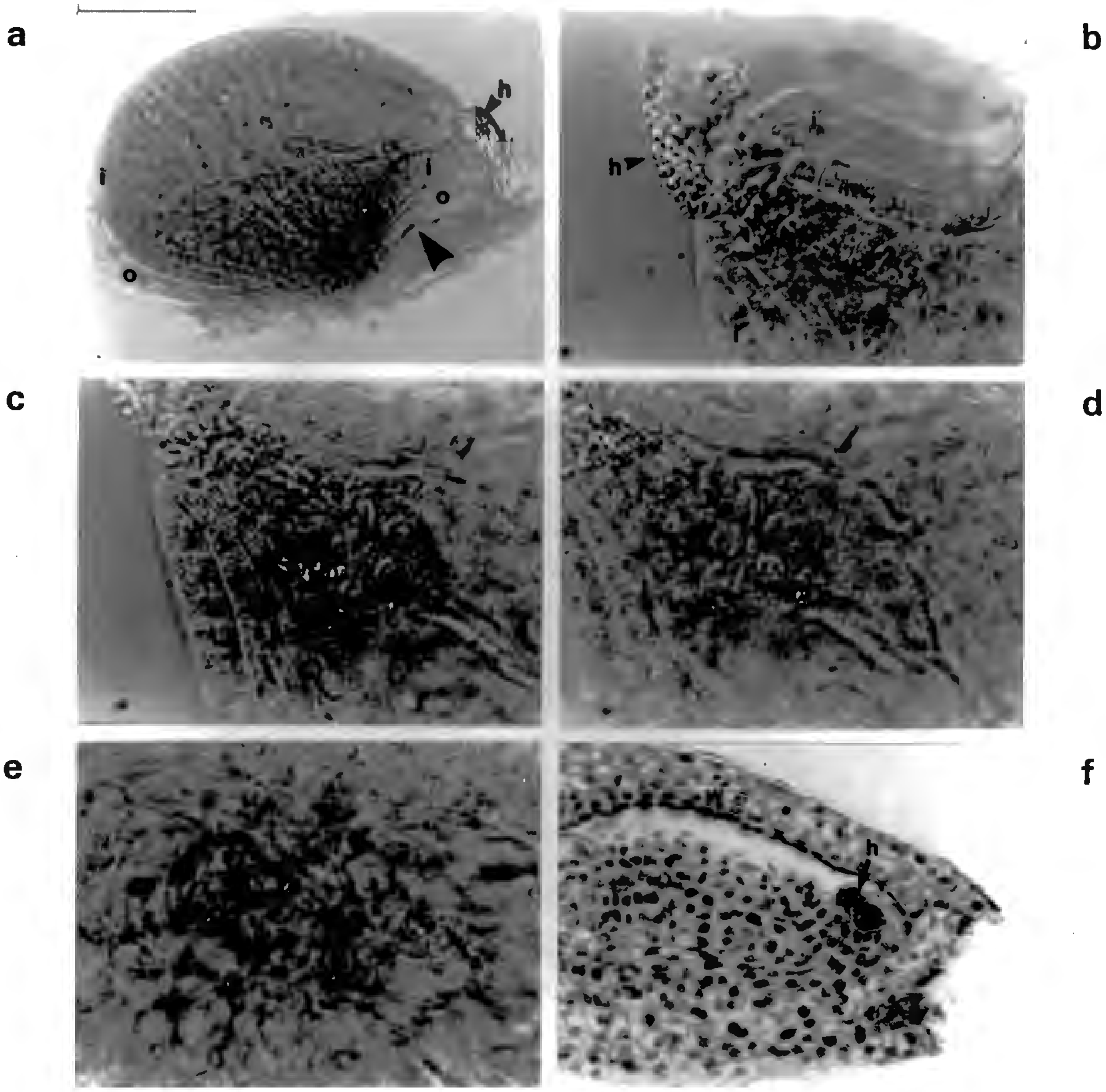

PLATE 4. a. *Karroochloa purpurea*, DIC, entire ovule, showing collar-like outer integument, haustorial synergid, and adaxial indentation near micropyle (large arrow) (200X). **b-e.** *K. purpurea*, DIC, detail of haustorial synergids, polar nuclei, and antipodals (1000X). **f.** *K. purpurea*, long. section, showing haustorial synergids protruding into ovular locule (400X).

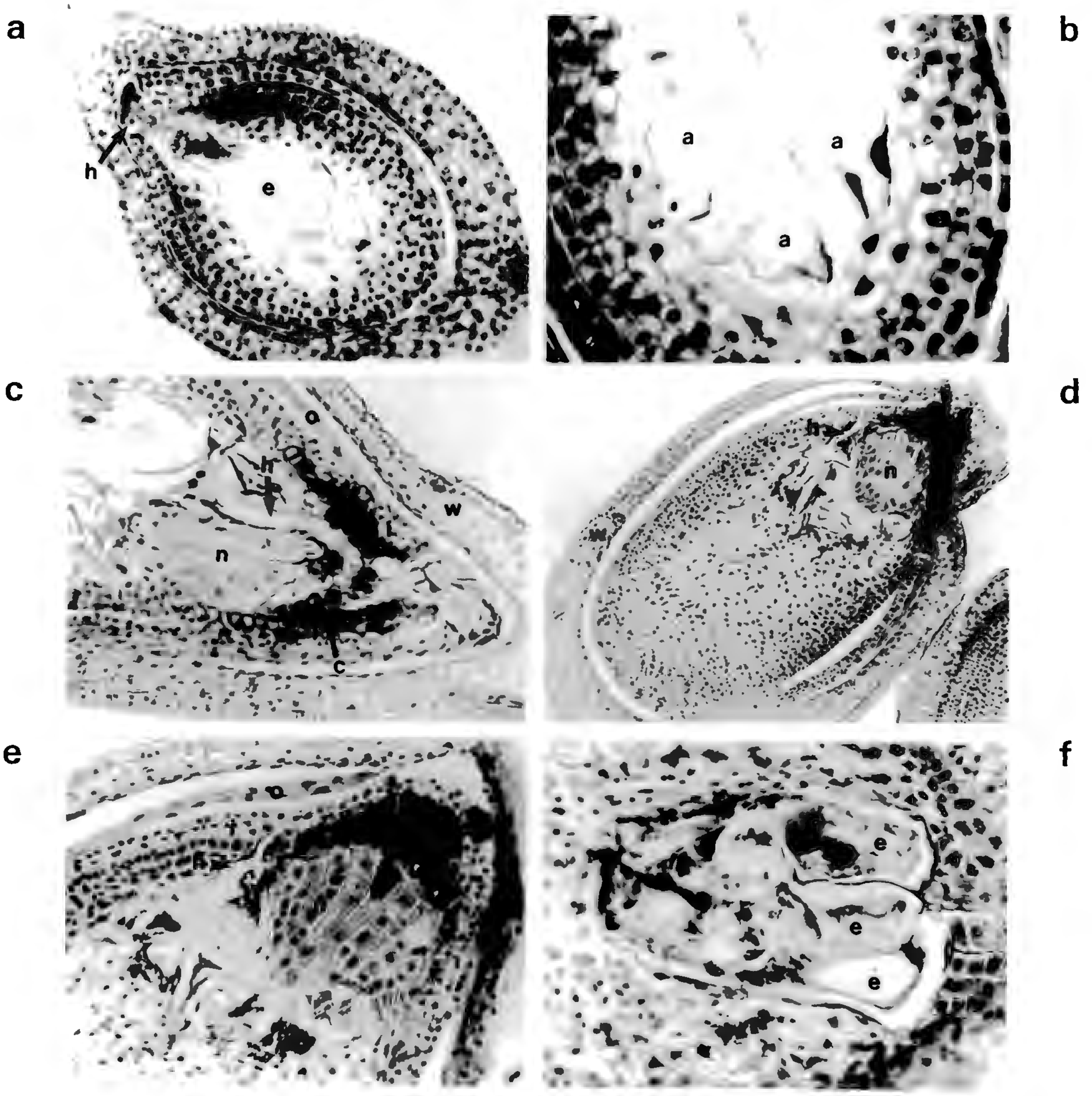

PLATE 5. a. *Karroochloa schismoides*, long. section through ovary, showing ovule with haustorial synergids (400X). **b.** *K. schismoides*, long. section through antipodal complex (1000X). **c.** *Merxmuellera arundinacea*, long. section through ovary, showing apical portion of ovule, with haustorial synergid-like structure growing through highly thickened nucellar epidermis, into micropyle. At the micropyle, the inner integument is thickened, and contains dark crystalline granules (c) (200X). **d.** *M. arundinacea*, long. section through entire ovary, showing haustorial synergid-like structure, thickened nucellus, and crystalline material at micropyle (200X). **e.** *M. arundinacea*, long. section, showing detail of micropylar area (400X). **f.** *M. arundinacea*, long. section through ovule with micropyle on right, showing presence of at least three embryosacs, two apomictic (400X).

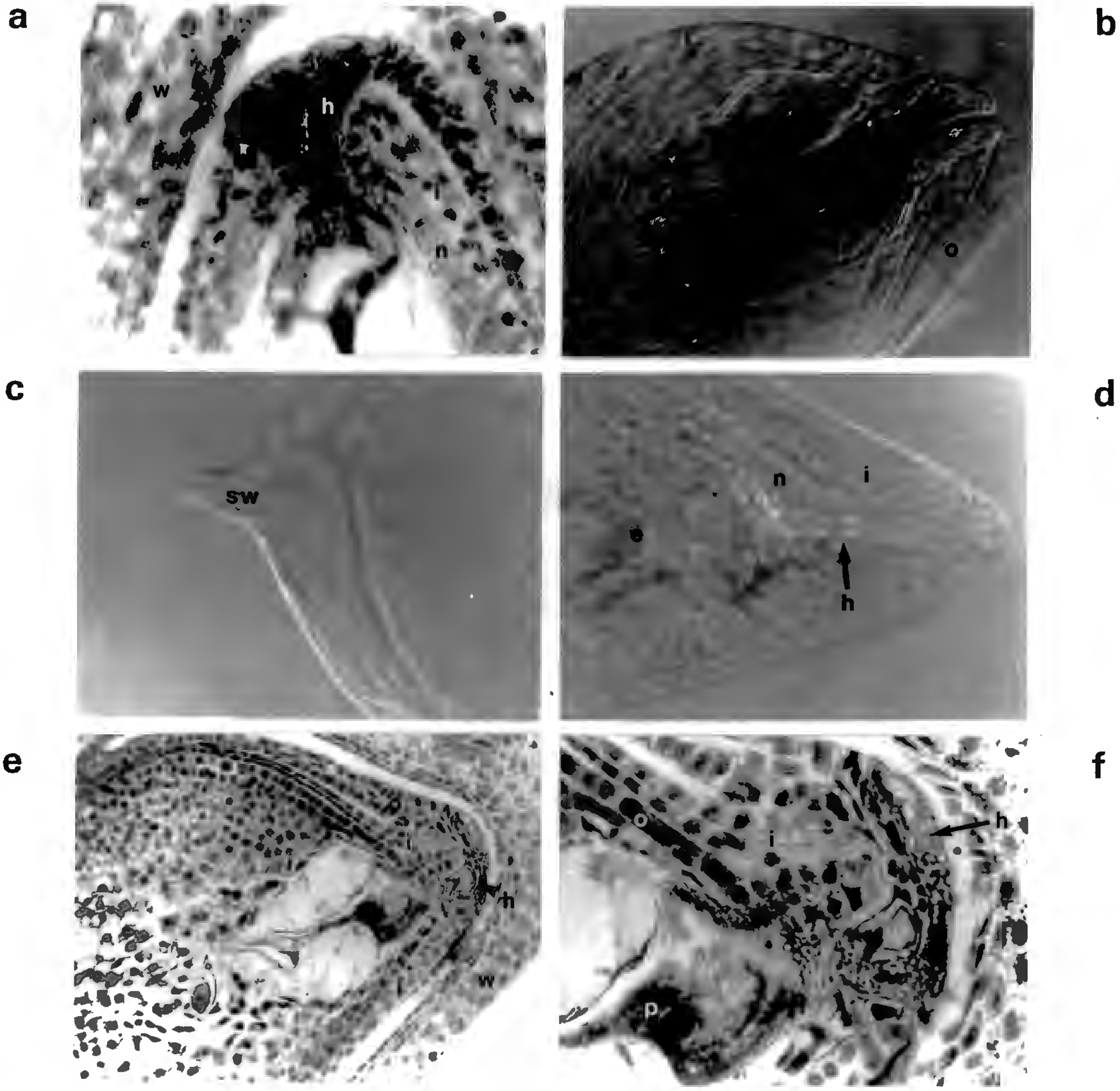

PLATE 6. a. *Merxmuellera disticha*, long. section through apical portion of ovule, showing well developed, granular (starch) haustorial synergids protruding strongly from the micropyle. **b.** *M. dura*, DIC, portion of ovule, showing presence of haustorial synergids, two embryosacs (two polars visible in one), and a reduced outer integument (400X). **c.** *M. dura*, DIC, basal (stylar) portion of ovule, showing thickening of outer integument to form a distinctive wedge of tissue (stylar wedge) (400X). **d.** *M. rufa*, DIC, apical region of ovule, showing presence of haustorial synergid-like structure in micropyle, and thickening of inner integument at micropyle (200X). **e.** *M. stricta*, long. section through ovary, showing well developed synergid haustorium, and integuments (400X). **f.** *M. stricta*, detail of synergid haustorium (from e.), with starch grains (1000X).

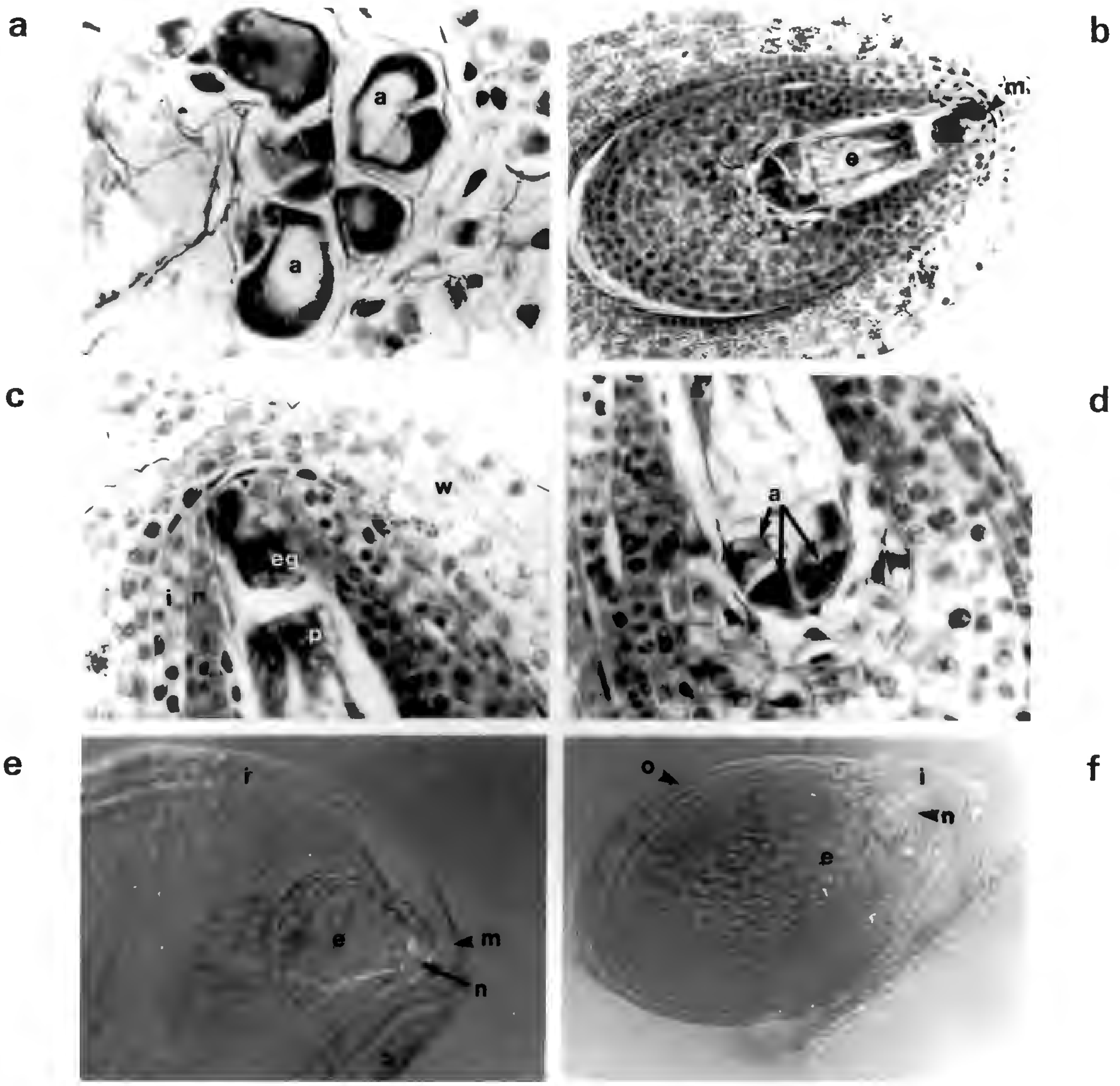

PLATE 7. a. *Merxmuellera stricta*, long. section through complex of multiplied antipodals (1000X). **b.** *Schismus barbatus*, long. section through ovule (400X), showing embryosac. **c.** *S. barbatus*, detail of apical portion of ovule (from **b.**), showing an the egg nucleus and one of the polar nuclei. The haustorial nature of the synergids is not clearly visible (1000X). **d.** *S. barbatus*, detail of antipodal complex (from **c.**) (1000X). **e.** *Dregeochloa pumila*, DIC, portion of ovule, showing complete nucellar cap and inner integument. Synergids non-haustorial (400X). **f.** *Centropodia glauca*, DIC, entire ovule, showing the complete nucellar cap and inner integument, and the incomplete outer integument. Synergids non-haustorial (200X).

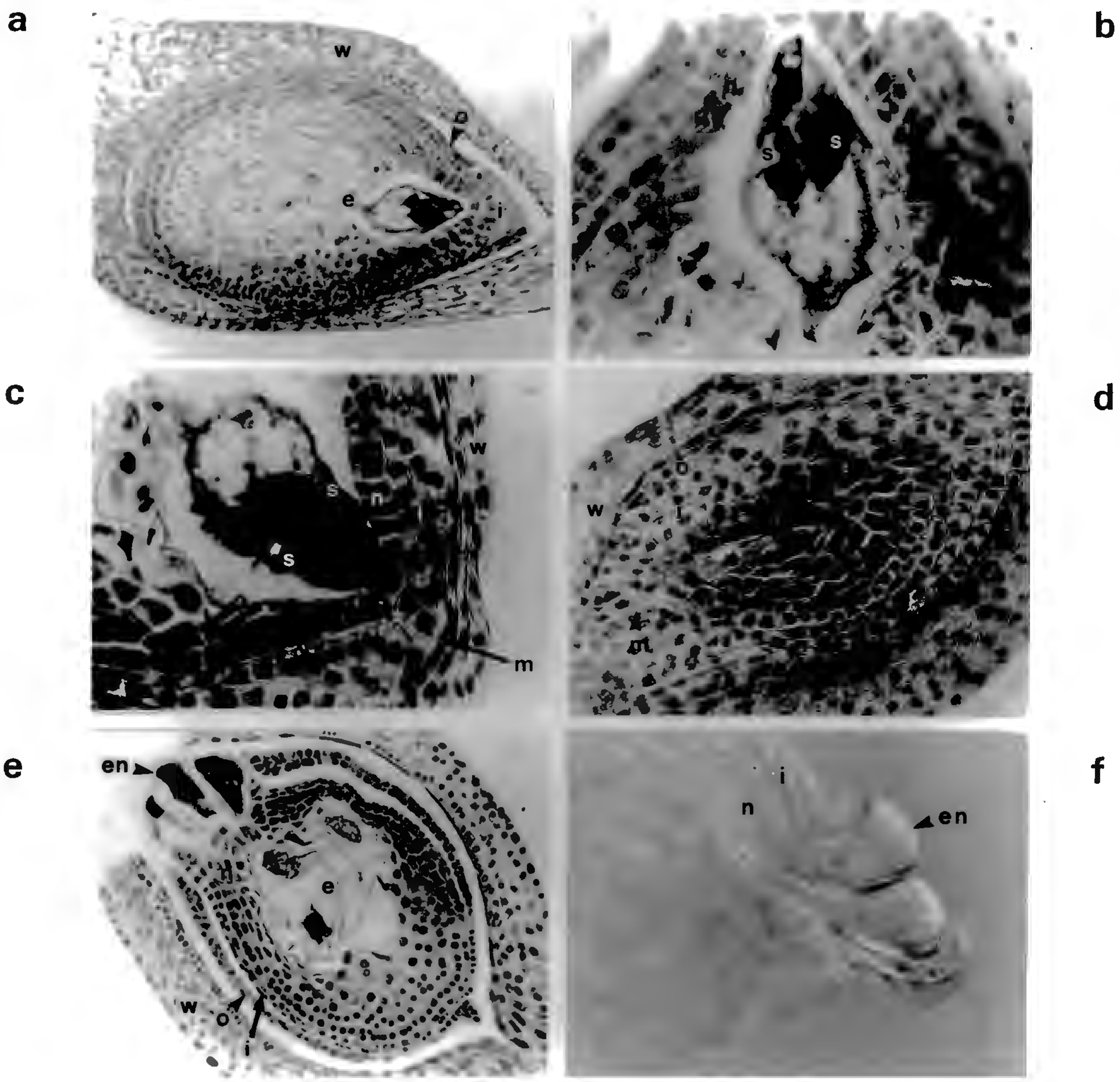

PLATE 8. a. *Centropodia glauca*, long section through ovary, showing ovule with inner integument and nucellus complete, and outer integument incomplete (200X). **b.** *C. glauca*, detail of egg complex (from **a.**), showing clearly the non haustorial nature of the synergids (1000X). **c.** *C. glauca*, long section through apical region of ovule showing egg complex with non-haustorial synergids. Synergids apparently with filiform apparatus (pale areas near micropyle). Nucellus and inner integument complete (1000X). **d.** *Arundo donax*, long. section through very young ovary, showing immature ovule with megaspore (ms) (400X). **e.** *Urochloa oligotricha*, long. section through ovary, showing ovule with incomplete inner integument, and highly expanded nucellar cap cells (en) (200X). **f.** *U. oligotricha*; DIC, apical portion of ovule, with incomplete inner integument and expanded nucellar cells (en) (400X).

DISCUSSION

The selection of ovule characters for investigation was done on the basis of their reliability, ease of quantification and intraspecific constancy. Despite this, the assessment of character states was not always straight-forward, and to minimise subjective biases, character ambiguities have been pointed out, as far as possible, wherever they occur. The characters selected show considerable overlap with those recommended by Kapil and Bhatnagar (1991) for use in taxonomic study.

Although the set of characters studied (Table 3) was too small for a complete cladistic analysis to be performed, the results of this study do show some interesting patterns, and these are most easily examined when the data are arranged in the form of a character matrix such as that presented in Table 4. The ordering of taxa in this summary table is such that those taxa that share characters lie close together (parsimony). Only certain characters, those judged most reliable and consistent, have been used in this ordering procedure. Further, those taxa for which the

TABLE 3. A list of the characters investigated, with codes used in Table 4.

1. Haustorial synergids. 0=absent, 1= weakly developed, 2= strongly developed.
2. Synergid starch. 0= no starch, 1= starch fine-grained, 2= starch large-grained, 1*a*·starch present but does not appear to be restricted to synergids.
3. Inner integument. 0= incomplete, 1= complete.
4. Thickening of inner integument near micropyle. 0= absent, 1= present, but slight, 2= present, and prominent.
5. Outer integument. 0= collar-like, 1= partial, 2= incomplete, 3= complete.
6. Nucellar epidermis at micropyle. 0= incomplete, 1= complete.
7. Micropyle. 0= constricted, 1= expanded.
8. Adaxial indentation of ovule near micropyle. 0= absent, 1= present but weakly developed, 2= present, and prominent.
9. Thickening of outer integument near micropyle. 0= absent, 1= present but slight, 2= present and fairly prominent.
10. Proliferation of antipodals. 0= absent, 1= present.
11. Micropyle. 0= not oblique, 1= slightly oblique, 2= strongly oblique.
12. Stylar wedge. 0= absent, 1= present.
13. Synergids. 0= not tailed, 1= tailed.
14. Streamer from polar nuclei to antipodals. 0= absent, 1= present.
15. Apomictic embryosacs. 0= absent, 1= present.
16. Approximate length of embryosac relative to length of ovule.

TABLE 4. Matrix of ovule characters for the 42 species investigated. Character codes are provided in Table 3. Characters 1-8 were used to order the taxa. ***= Study material very immature (data ignored), *= Material possibly slightly immature (data used). ?= missing or ambiguous data.

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chaetobromus dregeanus	2	2	0	0	0	0	1	0	2	1	0	1	1	0	0	0.71
Chaetobromus involucratus	2	2	0	0	0	0	1	0	2	1	0	0	0	0	0	0.56
Urochlaena pusilla	2	2	0	0	1	0	1	0	0	1	0	0	0	0	0	0.63
Cortaderia selloana	2	2	0	0	1	0	1	0	2	1	0	1	0	0	0	0.67
Pseudopentameris macrantha	2	2	0	0	0	0	1	0	2	1	0	0	0	1	0	0.59
Schismus barbatus	2	2	0	0	0	0	1	1	1	1	0	?	1	1	0	0.59
Tribolium obliterum	2	2	0	0	01	0	1	2	1	0	0	?	0	1	0	0.75
Karroochloa purpurea	2	2	0	0	01	0	1	2	0	1	0	1	1	1	0	0.59
Karroochloa schismoides	2	2	0	0	0	0	1	2	0	1	0	0	0	1	0	0.71
Karroochloa tenella	2	2	0	0	0	0	1	0	0	1	0	0	0	0	0	0.67
Merxmuellera disticha	2	2	0	0	01	0	1	1	2	1	0	1	0	0	0	0.50
Merxmuellera dura	2	2	0	0	01	0	1	1	2	1	0	1	0	0	1	0.59
Merxmuellera stricta	2	2	0	0	1	0	1	1	2	1	0	0	0	1	1	?
Pentaschistis velutina	2	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0.75
**Pentaschistis holciformis*	1	1	0	2	01	0	1	0	0	1	0	0	0	1	0	0.71
Pentaschistis eriostoma	2	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0.77
Pentaschistis patula	1	1	0	0	0	0	1	0	1	1	0	1	0	1	0	0.50
**Pentaschistis chippendalliae*	1	1	0	0	0	0	1	0	1	?	0	0	0	0	0	?
Pentaschistis pallescens	1	01	0	0	01	0	1	0	0	1	0	1	0	0	1	0.59
Pentaschistis ampla	1	1	0	0	01	0	1	1	0	1	0	0	0	0	0	0.67
Pentameris macrocalycina	1?	1	1	0	0	01	1	1	2	?	0	0	0	0	0	0.75
Pentaschistis tomentella	0	1	0	0	0	01	1	0	0	?	0	0	0	0	0	0.50
Pentaschistis argentea	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	0.50
Pentaschistis aristidoides	0	1	0	0	01	1	1	0	0	1	0	0	0	0	0	0.63
Pentaschistis aristifolia	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0.50
Pentaschistis pungens	0	?	0	1	0	1	1	0	1	?	1?	1	0	0	0	0.67

TABLE 4. Continued

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Merxmuellera arundinacea	1?	1	1	2	2	01	0	0	0	1	2	0	0	0	1	0.42
Merxmuellera rufa	1?	1	1	2	1	01	0	0	0	?	2	0	0	0	1	0.67
Merxmuellera lanata	1?	1	1	2	2	01	0	0	0	?	2	0	0	0	0	0.59
Pentameris thuarii	0	0	1	0	2	0	0	0	2	1	1	0	0	0	0	0.59
**Dregeochloa pumila*	0	1*a*	1	1	01	01	0	0	1	1	1	0	0	0	0	0.50
Centropodia glauca	0	1*a*	1	1	2	1	0	0	0	1	1	0	0	0	0	0.34
Fingerhuthia africana	0	1*a*	1	1	2	0	0	0	0	?	1	0	0	0	0	0.88
Schmidtia pappophoroides	0	1*a*	1	0	1	1	0	1	1	?	?	0	0	0	0	0.67
Arundinaria sp.	0	1*a*	1	1	2	1	0	0	0	?	1	1	0	0	0	0.33
Ehrharta pusilla	0	?	1	1	1	1	0	?	0	1	?	1	0	0	0	0.63
Urochloa oligotricha	0	0	1	0	0	1	1	0	1	?	0	1	0	0	0	0.59
Panicum maximum	0	0	01	0	0	1	01	1	?	?	0	0	0	0	0	0.50
****Tribolium hispidum*	?	?	0	0	1	1	?	0	0	?	?	0	0	0	0	?
****Prionanthium ecklonii*	?	?	0	0	0	1	?	0	1	?	?	0	0	0	0	?
****Prionanthium dentatum*	0	1	0	0	1	01	1	0	0	1	0	1	0	1	0	0.63
****Arundo donax*	?	?	1	0	1	1	0	0	?	?	?	?	0	0	0	?

material examined was too immature for reasonable comparison (semaphoront rule) have not been ordered, but are listed at the bottom of Table 4 (and marked with three asterisks), and are essentially ignored in this discussion.

The characters considered in this study may be allocated to a small number of distinct organ systems: specifically, the integuments, the nucellus, and the embryosac(s). Although each of these systems is discussed independently, there is, naturally, considerable interplay between them.

The nucellus and integument systems examined in this study showed considerable variation, even within the Arundineae (*sensu* Clayton and Renvoize 1986), and so provide taxonomic characters that are useful at and below the sub-familial level. Further, these characters appear to be fairly reliable and consistent. However, the most reliable and unambiguous characters seem to be those that relate to the nature of the synergids, in particular whether these are haustorial or not, and whether or not they contain starch. The few remaining embryosac characters investigated, however, seem weak, and rather inconsistent. The assessment of detailed cellular characters of the embryosac presents various problems, and, to be reliable, would require a more detailed survey than this one, one in which ontogenetic changes in the embryosac over time are also considered (see, for example, the embryological studies on *Stipa elmeri*, *Agrostis interrupta* and *Festuca microstachys* by Maze and Bohm [1972, 1973, 1977]).

Variation in synergid structure

Philipson (1977) and Philipson and Connor (1984) reported the occurrence of haustorial synergids in a range of arundinoid genera including *Chionochloa*, *Cortaderia*, *Danthonia*, *Erythanthera*, *Lamprothyrsus*, *Pyrrhanthera*, *Rytidosperma*, *and Sieglingia*. They considered this feature to be apomorphic, and hypothesised that the character should be found in African danthonioids with a West Gondwanaland history, such as *Merxmuellera* and *Karroochloa*. The results of the present investigation appear to support this hypothesis, with synergid haustoria being identified in at least 19 species of southern African arundinoids, and possibly in four others. This constitutes 72 percent of the African arundinoids for which mature material was examined, and comprises a range of core danthonioid genera including species of *Chaetobromus*, *Karroochloa*, *Merxmuellera*, *Pentaschistis*, *Pentameris*, *Pseudopentameris*, *Schismus*, *Tribolium* and *Urochlaena*. In all cases, haustorial synergids appear to be granular and contain starch. The ovules of four species, *Merxmuellera arundinacea*, *M. lanata*, *M. rufa* and *Pentameris macrocalycina*, possess grainy structures that may well be haustorial synergids, although this is not certain.

The non-arundinoid taxa examined lacked synergid haustoria, supporting earlier suggestions that the feature is very unusual not only in grasses, but in angiosperms as a whole, and particularly in the monocotyledons (Davis 1966; Philipson 1977; Philipson and Connor 1984; De Triquell 1986). Philipson and Connor (1984) argued that the extreme rarity of haustorial synergids indicates that the condition is derived, and the fact that synergid haustoria have not been found in other Poaceae, particularly, or in allied families (Hamann 1975; Campbell and Kellogg 1986; Kircher 1986; Rudall and Linder 1988) provides strong support for this argument.

The absence of synergid haustoria in five species of *Pentaschistis*, arguably, may reflect different taxonomic affinities of these taxa. However, this extreme conclusion seems unjustified, since various workers have shown that there is considerable overlap in morphological and anatomical features of these taxa, and other African arundinoids in which haustorial synergids do occur (De Wet 1954, 1960; Linder and Ellis 1990; Ellis and Linder 1992). It is more likely that the condition in these species represent secondary losses of haustorial synergids, this notion being supported by the fact that the synergids of these species, although non-haustorial, do possess some fine starch, and that the synergids of some species of *Pentaschistis*, namely *P. ampla*, *P. holciformis*, *P. pallescens* and *P. patula*, are only weakly haustorial, and do not protrude completely from the micropyle. A third possible explanation for the absence of synergid haustoria in these taxa is that the material examined was not quite mature, and the synergid haustoria not yet developed. However, this seems unlikely since for at least one of these species (*Pentaschistis aristidoides*), a large number of ovules of variable age were examined, and many of these had otherwise fully mature embryosacs.

Three other African arundinoids, *Centropodia glauca* and *Dregeochloa pumila* and *Pentameris thuarii* also lack haustorial synergids. The first two of these, unlike the

It is interesting that *Cortaderia selloana* lies at the heart of this core of danthonioid taxa characterised by strongly developed synergid haustoria, as this brings into question the removal of this genus from the tribe Danthonieae by Zotov (1963) and, more recently, Conert (1986) to a new tribe Cortaderieae.

Of the remaining species studied here, some of the arundinoids do possess weakly haustorial synergids, but the starch contained by these is finer-grained, suggesting that the degree of haustorial synergid development is somehow related to the nature of the starch they contain.

The synergids of some species have other peculiar features. In *Schismus barbatus* and *Karroochloa purpurea*, and possibly *Pseudopentameris macrantha*, for example, synergids possess tapering, tail-like extensions proximally. Although there is some evidence to suggest that the first two of these taxa are closely related (De Wet 1956; Conert 1971; Tomlinson 1985), the significance of this character is uncertain because its apparent absence in other *Karroochloa* species suggests that it may be easily overlooked. Another synergid peculiarity is to be found in the ovules of *Pentaschistis patula*, whose synergids have minute hair-like villi on their apical surfaces. Howvever, this feature appears to be autapomorphic, and is probably of little taxonomic value.

Other features of the embryosac

The embryosacs of some species that lack haustorial synergids, were found to possess starch, although this was not necessarily restricted to the synergids. This is the case in the non-arundinoid *Arundinaria sp.* and *Fingerhuthia africana*, and possibly *Schmidtia pappophoroides*, all of which have complex embryosacs with a very different cellular arrangement to that found in the arundinoids. In these species the starch appears to be concentrated in a zone just below the micropyle, usually around a large nucleus, presumably the egg. A similar situation is found in *Centropodia glauca* and *Dregeochloa pumila* in which the distribution of starch in the embryosac may be quite extensive, stretching from the micropyle, almost to the antipodal zone (this was observed infrequently in the latter species, but possibly because some of the material examined was immature).

species discussed thus far, are not clearly married into the danthonioid grasses by their anatomical and morphological features, but, in contrast, have a rather unstable taxonomy and have been considered by various authors to occupy a very isolated position in the Danthonieae (De Wet 1954, 1956, 1960; Conert 1971; Tomlinson 1985). Integument characters place these taxa outside the main danthonioid group, suggesting that their lack of haustorial synergids is primary, rather than secondary. The situation in *Pentameris thuarii* is difficult to assess since it has received little study. On the basis of ovular characters alone, however, it is probably best grouped with *C. glauca* and *D. pumila.*

The condition of the synergids in *Merxmuellera arudinacea*, *M. lanata*, *M. rufa* and *Pentameris macrocalycina* remains uncertain. In some ovules of these *Merxmuellera* species there appear to be finely grained structures that pass through the nucellar epidermis and grow partially into the micropyle, but because the inner integument here is highly thickened, they do not protrude from the micropyle, which is rather constricted. Although these structures may well be synergid haustoria, they differ in appearance from haustorial synergids in other species, and this may be a result of their rather atypical circumstances (in most 'haustorial' species, the inner integument is typically thin and the micropyle expanded so that protrusion of the haustorial synergids is easily achieved). The situation in *Pentameris macrocalycina* is rather similar: again the inner integument is considerably thickened, and the haustorial synergids only grow through the nucellar epidermis.

The results of this study suggest that there is a core of danthonioid species (including the first 14 species listed in Table 4) whose synergids are particularly strongly haustorial, such that they pass completely through the micropyle and into the ovary cavity, and with one exception (*Pentaschistis velutina*), the synergids of these species possess massive globular, starch grains. Philipson and Connor's (1984) illustrations of synergid haustoria in *Rytidosperma setifolium* and *Danthonia spicata* suggest that these taxa, at least, would also be included in this group. Unfortunately, a lack of embryological data for many of the smaller tropical African and Australasian arundinoid genera (Table 1) makes it impossible to assess the taxonomic position of these taxa in relation to this group, and so to determine its total inclusiveness. This is something that desreves more study.

In the embryosacs of some species, the polar cell appears to be 'connected' to the antipodal complex by a long, streamer-like structure. This structure was particularly prominent in the ovules of *Karroochloa purpurea*, *K. schismoides*, *Tribolium obliterum* and *Pseudopentameris macrantha*, although it was seen in some other species as well. I suspect that the distribution of this feature has been underestimated, and that it may be more widely distributed, particularly among those species in which haustorial synergids also occur. Nevertheless, its prominence in the taxa named here may suggest that these are related.

The observed length of the embryosac relative to the total length of the ovule is variable, but much of this variability is probably of little taxonomic significance (character dependent on ontogenetic state, orientation of material when viewed, method of preparation of material etc.), and indeed may be considerable even within individual plants. The length of the embryosac relative to that of the ovule may, however, be more useful for revealing taxonomic patterns at higher levels of universality. In the arundinoids examined this measure was found to have an approximate mean (± std) of about 0.6 ± 0.1, which contrasts sharply with that in *Arundinaria sp.* in which it is about 0.3.

Although attempts were made to note the relative size of the polar nuclei, this character is difficult to quantify, and no clear patterns were found across the range of taxa investigated. However, polar nuclei are generally large and highly conspicuous in the danthonioids, and this makes them easy to identify. The polars are also easily identified in these taxa, because the cellular arrangement of the danthonioid embryosac seems more basic than that in the other, non-arundinoid grasses examined. This is, possibly, a further indication of the primitiveness of the Danthonieae (Stebbins 1956; Clayton 1981; Clayton and Renvoize 1986).

Earlier workers have noted that antipodal proliferation is characteristic of members of the grass family (Maheshwari 1950; Davis 1966), to the extent that Anton and Cocucci (1984) formally recognised the 'Poaceae variant' of the normal Polygonum type embryosac as one which has more than three antipodals at maturity. In the present investigation antipodal multiplication was positively observed in the majority of species examined (particularly in the arudinoid taxa), and where it was not, this may have been due to immaturity of study material, or failure of observation.

Davis (1966) suggested that apomixis is of unlikely value as a taxonomic character, and noted that it is of common occurrence in the Poaceae. Connor (1981) reported that within the Arundinoideae, apomixis had been reported from only two genera, *Cortaderia* and *Lamprothyrsus*. In the present investigation, apomixis was noted in a further two arundinoid genera, being observed in four species of *Merxmuellera*, and in three of *Pentaschistis*.

Patterns in integumental development

In the majority of grasses the ovule is typically bitegmic, with the outer integument often reduced, so that the micropyle is endostomic (Davis 1966). The ovules of all species considered in the present study conform to this general pattern. However, there is considerable variation in the degree to which the ovule is covered by the two integuments, and this seems to be taxonomically related.

Inner integument

To some extent, the level of development of the inner integument may be determined by the presence of haustorial synergids: if the synergids grow out through the micropyle, then it follows that the micropyle will invariably be somewhat enlarged, and the inner integument therefore incomplete. However, the presence of an expanded micropyle does not appear to be dependent on the synergids being haustorial, and integumental features and the state of the synergids can therefore be treated as independent characters.

With the exception of *Pentameris macrocalycina*, *Merxmuellera arundinacea*, *M. lanata* and *M. rufa*, all the species examined that possess haustorial synergids also have an expanded micropyle and incomplete inner integument. This is also true for *Cortaderia jubata*, *Danthonia spicata* and *Rytidosperma setifolium* (Philipson 1977; Philipson and Connor 1984). In addition, this condition is also found in those species of *Pentaschistis* in which haustorial synergids do not occur, providing some support for the notion that their lack of synergids is secondary. Outside this danthonioid group, the only other species examined which have an expanded micropyle at maturity are *Urochloa oligotricha* and possibly *Panicum maximum*, in which the outermost nucellar cap cells are enlarged to such an extent that they can no longer be accomodated within the inner integument, and emerge through the micropyle which is expanded.

In both *Centropodia glauca* and *Dregeochloa pumila* the inner integument is complete at maturity and the micropyle constricted and slightly oblique, a condition that is probably also found in *Arundo donax* (see illustration in Philipson and Connor [1984]). The fact that the inner integument is complete in the other grasses examined (i.e. *Arundinaria sp.*, *Ehrharta pusilla*, *Fingerhuthia africana*, and *Schmidtia pappophoroides*) suggests that this condition is more general and primitive in the Poaceae, and the possession of an expanded micropyle (and haustorial synergids) derived. This notion is further supported by the complete nature of the inner integument in the probable sister taxa to the Poaceae (Hamann 1975; Campbell and Kellogg 1986; Rudall and Linder 1988), and in a range of other grasses (Maze and Bohm 1972 [*Stipa elmeri*], 1973 [*Agrostis interrupta*], 1977 [*Festuca microstachys*]; Mahalingappa 1977 [*Eleusine compressa*]; Aulbach-Smith and Herr 1984 [*Eustachys petraea* and *E. glauca*]).

The condition of the micropyle and inner integument in *C. glauca*, *D. pumila* and, possibly, *A. donax* contrasts sharply with that in most of the danthonioids examined and appears to provide support for the removal of these species from the Danthonieae, and brings into question the position of the subtribe inside the Arundineae. However a similar condition occurs in *Merxmuellera arundinacea*, *M. lanata*, *M. rufa*, possibly *Pentameris macrocalycina* and *P. thuarii*. The first four of these species do appear to possess synergid haustorium-like structures, suggesting that they do belong in the danthonioids. If this is correct then their atypical micropylar/ inner integument is either analogous to that in the other taxa in which it occurs, or they form a primitive cluster at the base of the Danthonieae. The situation in *P. thuarii*, however, remains difficult to assess in the absence of more data on this species, although anatomical and morphological data certainly place it close to the Danthonieae.

Another interesting feature of the inner integument is its tendency in some taxa to become considerably thickened or enlarged in the region of the micropyle. This condition is carried to the extreme in the *Merxmuellera arundinacea-lanata-rufa* group in which the cells of the inner integument proliferate to such an extent at the ovular apex, that the whole ovule gains a pointed appearance, and these taxa clearly appear to be very closely related. Slight thickening of the inner integument in the region of the micropyle is also found in two species of *Pentaschistis*, *P. holciformis* and *P. pungens*, (one of which possesses synergid haustoria) as well as *Pentameris thuarii*, *Centropodia glauca*, *Dregeochloa pumila*, *Arundinaria sp.* and *Fingerhuthia africana*, although it is not clear that this thickening is homologous in all of these cases. This fact and the scattered distribution of this character suggests that it is of limited taxonomic value. Nevertheless, it is apparent that micropylar thickening is relatively infrequent in the danthonioids, particularly in those that possess synergid haustoria.

Another character that relates to the inner integument is the orientation of the micropyle. From the data it is readily apparent that the distribution of this character is almost entirely restricted to those taxa whose micropyles are constricted. This pattern is probably largely artifactual, and arises because it is almost impossible to determine the orientation of an expanded micropyle. Thus, for the purposes of the present study, micropyle orientation is a poor character, although the marked obliqueness of the micropyle in species in the *Merxmuellera arundinacea-lanata-rufa* group does seem to further demonstrate the link between these taxa.

Outer integument

Typically, the outer integument of grasses in the Danthonieae are considerably reduced, being in most cases collar-like or partial. This condition is found in almost all the taxa investigated in this study in which haustorial synergids were also to be found, as well as in those species of *Pentaschistis* in which the synergids are either only weakly haustorial or lack synergids altogether. Significantly, Philipson and Connor (1984) found a similar condition in a number of other arundinoid genera that possess synergid haustoria. They indicated that in *Chionochloa* the outer integument is collar-like, while in *Erythanthera*, *Rytidosperma*, *Pyrrhanthera* and *Lamprothyrsus* it is partial, to nearly incomplete. A reduced outer integument is almost certainly apomorphic in the grasses. In those families that seem most likely sister taxa to the grasses, especially the Joinvilleaceae and Restionaceae (Campbell and Kellogg 1986; Linder 1987), the outer integument is generally complete, and encloses the ovule entirely. Further, in two of the non-arundinoid taxa investigated (e.g. *Arundinaria sp.* and *Fingerhuthia africana* the outer integument is incomplete but almost entirely covers the ovule, a condition that is repeated in a range of other non-arundinoids (Maze and Bohm 1972 [*Stipa elmeri*], 1973 [*Agrostis interrupta*], 1977 [*Festuca microstachys*]; Mahalingappa 1977 [*Eleusine compressa*]; Aulbach-Smith and Herr 1984 [*Eustachys petraea* and *E. glauca*]). This condition, probably primitive, could be expected to occur in those arundinoid taxa which, for various reasons, do not appear to belong to the group of core danthonioid taxa. These include *Arundo*, *Phragmites* (Clayton and Renvoize 1986; Conert 1986; Hilu and Esen 1990), and probably, *Centropodia* and *Dregeochloa* (this study; De Wet 1954, 1956, 1960; Tomlinson 1985; N.P. Barker pers. comm.). However, this trend seems weak as in both *Arundo* (Philipson and Connor 1984) and *Dregeochloa pumila* the outer integument is reduced, being partial (although tending to incompleteness), while an extended, incomplete inner integument occurs in three species that are probably danthonioid, *Merxmuellera arundinacea*, *M. lanata* and *Pentameris thuarii*, the former two possessing what are probably haustorial synergids.

Interestingly, the outer integuments of the two panicoids examined in this study, *Panicum maximum* and *Urochloa oligotricha* were also found to be highly reduced, being collar-like, and in fact, De Triquell (1986) has noted that this condition is usual in the panicoids. If, however, reduction of the outer integument is derived in the Poaceae then it seems doubtful that the panicoid condition is homologous with the situation found in the majority of the Danthonieae.

The outer integuments of several species considered in the present investigation are locally thickened, particularly in the region of the micropyle, and in the basal (stylar) region of the ovule, where thickening often produces a wedge of tissue that fits tightly into the ovary wall. Philipson and Connor (1984) reported similar features for some of the species investigated by them. The presence or absence of thickening, as recorded in the present study, does not, however, appear to be a reliable taxonomic character, as its recognition depends, among other things, on the orientation of the ovule when viewed. The distribution of the two types of thickening across the range of taxa examined seems inconsistent, and the patterns produced vague. At most, it appears that both micropylar thickening and the presence of a stylar wedge are more frequent among species that are typically danthonioid.

Features of the nucellar epidermis

In grass ovules the nucellus is tenuinucellate or pseudocrassinucellate (Davis 1966). In the species investigated, the nucellus is variable in thickness, as well as in whether it is complete at the micropyle. In ovules that show development of haustorial synergids the nucellar epidermis is apically ruptured where these structures pass through it. Thus in those danthonioids that possess these structures, the nucellus is typically incomplete. In species of *Pentaschistis* that do not possess haustorial synergids but in which the inner integument is typically incomplete, the nucellus tends to be complete (albeit very thin in some cases). Further, a complete nucellar cap is present in most of the non-danthonioid taxa examined, in which synergid haustoria are absent. This suggests that there is a strong relationship between the presence of haustorial synergids and the completeness of the nucellus. Two exceptions to the correlation are *Pentameris thuarii* and *Dregeochloa pumila*, ovules of which sometimes have an incomplete nucellus, but non-haustorial synergids. The implications of these observations, however, remain uncertain.

Where a nucellar cap is present, its thickness may vary considerably, because of variability both in the number of cells, and the size and shape of these cells. In some ovules of *Merxmuellera arundinacea*, in which synergid haustoria were not found (in some species, the occurrence of haustorial synergids is not unanimous, perhaps because the ovules vary in age, or even because they are genuinely variable for this character) the nucellar cap was particularly massive, being up to 4 cells thick, with these cells being elongated and rather columnar. However, as a taxonomic character, nucellar cap thickness does not appear to provide great insight into the problems at hand.

General characters of the ovule

Both Davis (1966) and De Triquell (1986) remarked on the variability in ovule type in grasses, noting that this may be anatropous, hemianatropous, campylotropous, or any of a host of intermediate forms. However, all ovules examined in the present study, appear to be hemianatropous, and the character appears to be of little taxonomic value at the level of this investigation.

Ovule size, too, appears to be of limited use, although it is perhaps noteworthy that the ovules of *Karroochloa, Schismus* and *Tribolium* are all rather small. Whether this reflects a relationship between these taxa is uncertain, although De Wet (1960), Conert (1971), and Tomlinson (1985) have suggested a close relationship between the first two of these genera. The ovules of members of the *Merxmuellera arundinacea-lanata-rufa* group are also, perhaps, linked by their size, the ovules of all of these species being quite large, and elongated.

A final feature that is found in some species, is the presence of an indentation on the adaxial side of the ovule, quite near the micropyle. While this feature is rather characteristic in some taxa, particularly *Karroochloa purpurea*, *K. schismoides* and *Tribolium obliterum*, in other taxa it is only weakly developed, and may be nearly absent, so that the character is somewhat subjective.

CONCLUSION

The picture that emerges from the foregoing discussion can be presented as a simple, albeit tentative, hypothesis. The hypothetical ancestor of the Danthonieae and, possibly, the remainder of the grasses is assumed to have the following characters: (1) synergids non-haustorial, (2) inner integument complete, and micropyle constricted, (3) nucellus complete (4) inner integument possibly thickened around near micropyle, and (5) outer integument incomplete, and almost covering entire ovule (Fig. 2: position X). This condition describes *Arundinaria sp.*, *Ehrharta pusilla*, *Fingerhuthia africana*, *Schmidtia pappophoroides* and a range of other non-arundinoid grasses (Maze and Bohm 1972, 1973, 1977; Mahalingappa 1977, Aulbach-Smith and Herr 1984). To some extent, the arundinoid taxa *Arundo donax*, *Centropodia glauca* and possibly *Dregeochloa pumila* also reflect these characters. Further, haustorial synergids have not been reported from the families that are possible sister taxa to the Poaceae (e.g. Joinvilleaceae, Restionaceae) and in

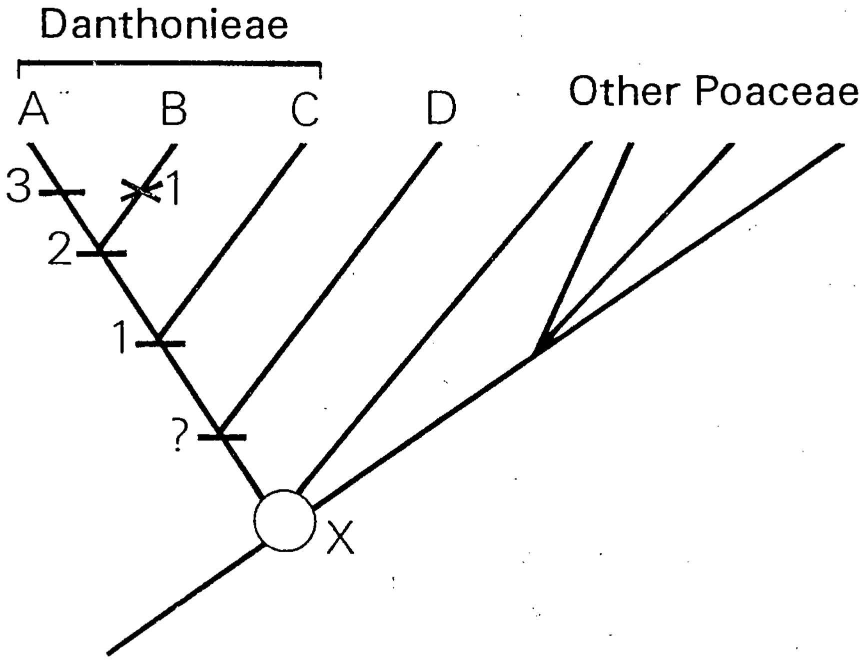

FIGURE 2. A cladistic hypothesis to explain the distribution of ovular characters across the range of arundinoid taxa that have been embryologically studied. Explanation in text. Bars represent character gains, crosses represent losses. Characters: (1) haustorial synergids, (2) expanded micropyle, (3) large starch grains in synergids.

these taxa, both integuments tend to be almost completely developed, or nearly so, with the micropyle being constricted (Campbell and Kellogg 1986; Rudall and Linder 1988).

The Danthonieae is defined as a monophyletic group (Fig. 2: terminals A-C) by the possession of haustorial synergids, a fairly strong synapomorphy, since this character is not found in other grass taxa, or in members of related families (Philipson and Connor 1984; De Triquell 1986; Rudall and Linder 1988). In most taxa, the presence of haustorial synergids has led to an expanded micropyle, and incompleteness of the inner integument. In some taxa (*Merxmuellera arundinacea*, *M. lanata*, *M. rufa* and *Pentameris macrocalycina*), though, the haustorial synergids do not grow completely through the micropyle, and the latter has remained constricted. These taxa may occupy terminal C in Fig. 2, assuming that this condition is primary, or alternatively lie nearer B if it is assumed to be secondary. Some species of *Pentaschistis*, a genus with typically danthonioid morphology and anatomy, lack haustorial synergids. However, these taxa do possess starch, and an expanded micropyle, and this, along with the fact that some congenerics possess rather weakly developed synergid haustoria, suggests that the absence of these structures may be secondary in these taxa (Fig. 2: terminal B).

Although the genera *Centropodia* and *Dregeochloa* are presently included in the Danthonieae/Arundineae (Renvoize 1981; Clayton and Renvoize 1986; Conert 1986), ovular features, suggest that these taxa probably belong outside the tribe, either near its base (Fig.2: terminal D), or nearer the remainder of the Poaceae. This suggestion is very much in accordance with the findings of De Wet (1954, 1956, 1960) who indicated that on the basis of leaf anatomy, gross morphology and basic chromosome number, these genera are quite different from other danthonioids, and even went so far as to imply a relationship between these taxa and the Paniciformes. More recently, Conert (1971) and Tomlinson (1985) pointed out new morphological and anatomical features which further separate these genera from the danthonioids.

The characters investigated in the present study provide limited insight into the relationships between taxa within the Danthonieae. However, it is possible to identify a core of species in which the synergids are particularly strongly haustorial such that they protrude from the micropyle and possess large, globular starch grains. This group constitutes the following species: *Chaetobromus dregeanus*, *C. involucratus*, *Cortaderia selloana*, *Karroochloa purpurea*, *K. schismoides*, *K. tenella*, *Merxmuellera dura*, *M. disticha*, *M. stricta*, *Pseudopentameris macrantha*, *Schismus barbatus*, *Tribolium obliterum*, and *Urochlaena pusilla*. Monophyly of this assemblage is may be inferred if the possession of large starch grains is treated as the definitive synapomorphy. This assumes that the finer starch found in the synergids of most *Pentaschistis* ovules is more primitive, an assumption for which, perhaps, evidence is lacking. In addition to the species forming this core, other species that may be included in the Danthonieae in terms of the hypothesis outlined earlier include all species of *Pentaschistis* examined (although *P. pungens* is problematic), as well as *Merxmuellera arundinacea*, *M. lanata*, *M. rufa* and *Pentameris macrocalycina*. In addition, the findings of Philipson and Connor (1984) suggest that the genera *Chionochloa*, *Cortaderia*, *Danthonia*, *Erythanthera*, *Lamprothyrsus*, *Pyrrhanthera*, *Rytidosperma* and *Sieglingia* also deserve inclusion. Although *Pentameris thuarii* resembles the main group of danthonioid taxa anatomically and morphologically, this is not reflected by its ovular features and this species deserves further study.

Unfortunately, on current knowledge it is not possible to determine the full extent of the Danthonieae as defined here. The embryology of a large number of danthonioid-arundinoid genera, chiefly small tropical African and Australasian taxa, has not yet been investigated (Table 1), and until this is done, the taxonomic position of these taxa in relation to the Danthonieae as defined here, in terms of ovule characters, will remain a mystery. This problem, therefore, certainly deserves more attention.

The hypothesis outlined here is at odds with earlier work that has attempted to integrate the Danthonieae and the Arundineae (e.g. Renvoize 1981; Clayton and Renvoize 1986). A phylogeny of the Arundineae, as proposed by Clayton and Renvoize (1986) is illustrated in Fig. 3. These authors separated a number of taxa which, on the basis of ovular characters analysed here, belong together, and grouped others together, which are separated here. Moreover, for their scheme to be correct, it requires that the absence of haustorial synergids or an ~~expanded~~ constricted

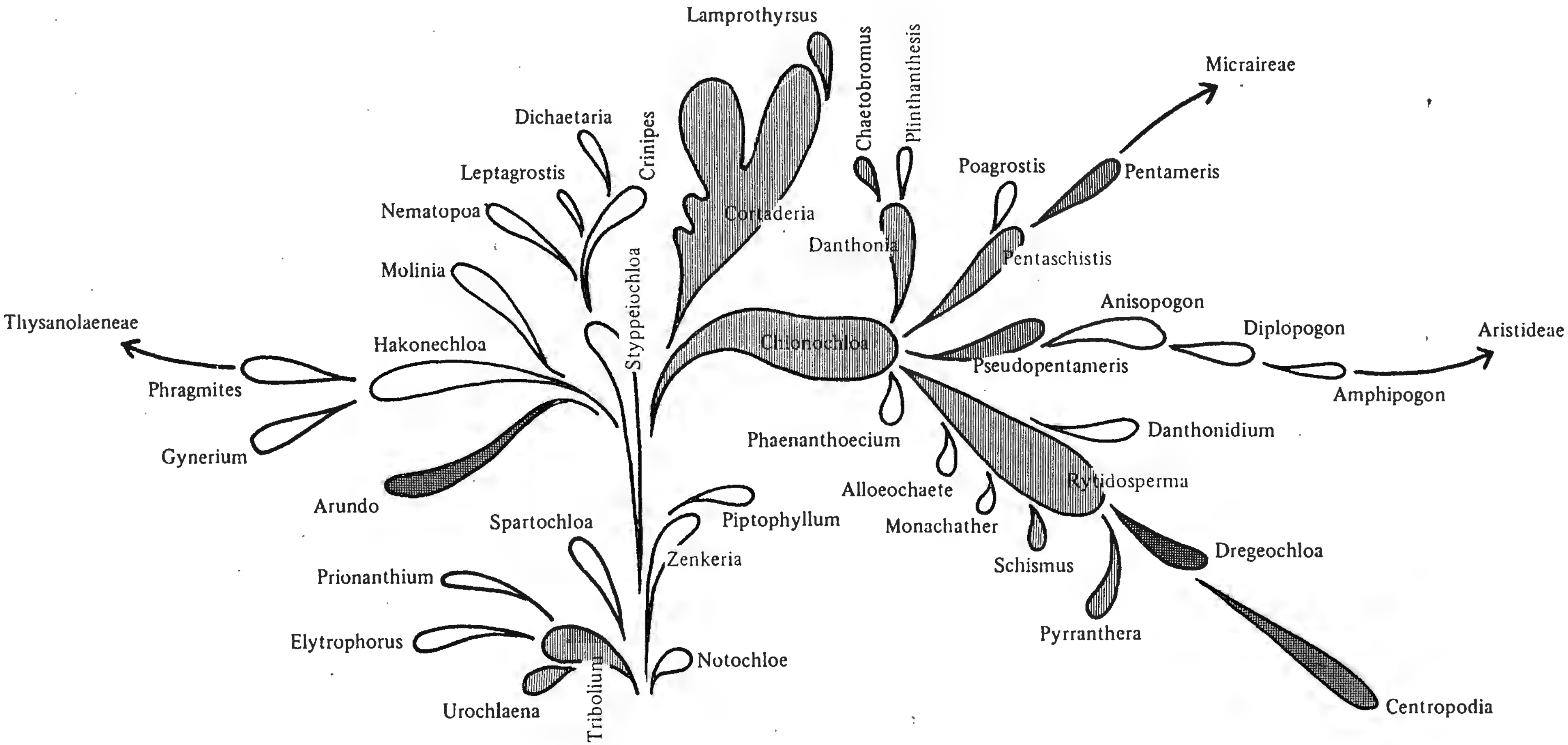

FIGURE 3. A phylogeny of the Arundineae, following Clayton and Renvoize (1986). Taxa that are included in the Danthonieae as defined in this study are hatched, while those that do not are cross-hatched. Taxa that have not been embryologically studied have been left blank.

micropyle in *Arundo*, *Phragmites*, *Centropodia*, and *Dregeochloa* be secondary, a notion that is not supported in the present study. It is further apparent that Zotov's (1963) and, subsequently, Conert's (1986) removal of *Cortaderia* from the Danthonieae to a new tribe Cortaderieae is probably erroneous, since this genus lies at the centre of the danthonioid core.

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LITERATURE CITED

ANTON, A.M. and COCUCCI, A.E. 1984. The Grass Megagametophyte and its Possible Phylogenetic Implications. **Pl. Syst. Evol. 146**: 117-124.

AULBACH-SMITH, C.A. and HERR, J.M. 1984. Development of the ovule and female gametophyte in *Eustachys petraea* and *E. glauca* (Poaceae). **Amer. J. Bot. 71**: 427-438.

BLAKE, S.T. 1982. *Plinthanthesis* and *Danthonia* and a review of the Australian species of *Leptochloa* (Gramineae). **Contrib. Qd. Herb. 14.**

CAMPBELL, C.S. 1985. The Subfamilies and Tribes of Gramineae (Poaceae) in the Southeastern United States. **Journal of the Arnold Arboretum 66**: 123-199.

CAMPBELL, C.S. and KELLOGG, E.A. 1986. Sister Group Relationships of the Poaceae. In: **Grass Systematics and Evolution** (eds. T.R.Soderstrom, K.W.Hilu, C.S.Campbell and M.E.Barkworth). International Grass Symposium. Smithsonian Institution Press, Washington D.C. pp 217-224.

CLAYTON, W.D. 1981. Evolution and Distribution of Grasses. **Ann. Missouri Bot. Gard. 68**: 5-14.

CLAYTON, W.D. and RENVOIZE, S.A. 1986. Genera Graminum: Grasses of the World. **Kew Bull. Additional Series XIII**. 389pp.

CONERT, H.J. 1961. **Der systematik und anatomie der Arundineae**. Verlag von J.Cramer, Weinheim.

CONERT, H.J. 1966. *Dregeochloa*, eine neue Gattung der Gramineen (Gramineae, Arundinoideae). **Senckenberg. Biol. 56**: 293-313.

CONERT, H.J. 1971. The Genus *Danthonia* in Africa. **Mitt. Bot. Staatssamml. Munchen 10**: 299-308.

CONERT, H.J. 1986. Current Concepts in the Systematics of the Arundinoideae. In: **Grass Systematics and Evolution** (eds. T.R.Soderstrom, K.W.Hilu, C.S.Campbell and M.E.Barkworth). International Grass Symposium. Smithsonian Institution Press, Washington D.C. pp 239-250.

CONERT, H.J. and TUERPE, A.M. 1969. *Karroochloa*, eine neue Gattung der Gramineen. **Senckenberg Biol. 50**: 289-318.

CONNOR, H.E. 1983. Names and types in *Cortaderia* Stapf (Gramineae) II. **Taxon 32**: 633-634..

CONNOR, H.E. 1981. Evolution of reproductive systems in the Gramineae. **Ann. Missouri Bot. Gard. 68**: 48-74.

CONNOR, H.E. and EDGAR, E. 1974. Names and types in *Cortaderia* Stapf (Gramineae). **Taxon 23**: 595-605.

CONNOR, H.E. and EDGAR, E. 1979. *Rytidosperma* Steudel (*Notodanthonia* Zotov) in New Zealand. **New Zealand J. Bot. 17**:311-337.

DAHLGREN, R.M.T., CLIFFORD, H.T. and YEO, P.F. 1985. The Families of the Monocotyledons. Springer-Verlag, Berlin.

DE TRIQUELL, A.A. 1986. Grass Gametophytes: Their Origin, Structure, and Relation with the Sporophyte. In: **Grass Systematics and Evolution** (eds. T.R.Soderstrom, K.W.Hilu, C.S.Campbell and M.E.Barkworth). International Grass Symposium. Smithsonian Institution Press, Washington D.C. pp 11-20.

DE WET, J.M.J. 1954. The Genus *Danthonia* in Grass Phylogeny. **Am. J. Bot. 41**: 204-211.

DE WET, J.M.J. 1956. Leaf Anatomy and Phylogeny in the Tribe Danthoniae. **Amer. J. Bot. 43**: 175-182.

DE WET, J.M.J. 1960. Leaf Anatomy and Morphology in South African Species of *Danthonia*. **Bothalia 7**: 303-310.

ELLIS, R.P. 1977-1988. (A series of papers describing features of the leaf anatomy of a number of African arundinoid taxa, including members of the genera *Dregeochloa*, *Merxmuellera*, *Pentameris*, *Pseudopentameris* and *Chaetobromus*.) **Bothalia 12**: 209-213, **13**: 185-190, 191-198, 487-491, 493-500, **14**: 89-93, 95-99, 197-203, **15**: 561-566, 567-571, 573-578, 579-585, **18**: 195-209.

ELLIS, R.P. and LINDER, H.P. 1992. Atlas of the Leaf Anatomy in *Pentaschistis* (Arundineae: Poaceae). **Mem. Bot. Survey of South Africa 60.**

GIBBS-RUSSELL, G.E., WATSON, L.,KOEKEMOER, M., SMOOK, L., BARKER, N.P., ANDERSON, H.M. and DALLWITZ, M.J. 1990. Grasses of southern Africa. **Mem. Bot. Survey S.A. 58.**

HAMANN, U. 1975. Neue Untersuchungen zur Embryologie und Sytematik der Centrolepidaceae. **Bot. Jahrb. Syst. 96**: 154-191.

HERR, J.M. 1971. A new clearing-squash technique for the study of ovule development in angiosperms. **Amer. J. Bot. 58**: 785-790.

HILU, K.W. and ESEN, A. 1990. Prolamins in systematics of Poaceae subfam. Arundinoideae. **Pl. Syst. Evol. 173**: 57-70.

HILU, K.W. and WRIGHT, K. 1982. Systematics of the Gramineae: a Cluster Analysis Study. **Taxon 3**: 9-36.

HUBBARD, C.E. 1934. Gramineae. In: **The Families of Flowering Plants. II. Monocotyledons** (ed. J.Hutchinson). Macmillan, London.

JACOBS, S.W.L. 1982. Comment on proposal 520: Conservation of *Notodanthonia* Zotov (Gramineae). **Taxon 31**: 737-743.

JOHANSEN, D.A. 1940. **Plant microtechnique**. McGraw Hill, New York.

KAPIL, R.N. and BHATNAGAR, A.K. 1991. Embryological evidence in angiosperm classification and phylogeny. **Bot. Jahrb. Syst. 113**: 309-338.

KELLOGG, E.A. 1990. Ontogenetic Studies of Florets in *Poa* (Gramineae): Allometry and Heterochrony. **Evolution 44**: 1978-1989.

KELLOGG, E.A. and CAMPBELL, C.S. 1986. Phylogenetic Analyses of the Gramineae. In: **Grass Systematics and Evolution** (eds. T.R.Soderstrom, K.W.Hilu, C.S.Campbell and M.E.Barkworth). International Grass Symposium. Smithsonian Institution Press, Washington D.C. pp 310-322.

KIRCHER, P. 1986. Untersuchungen zur Blueten- und Infloreszenzmorphologie der Restionaceen in Vergleich mit Gramineen und Verwandte Familien. **Dissertationes Botanicae 94**: 1-219.

KRUPKO, S. 1962. Embryological and cytological investigations in *Hypodiscus aristatus* Nees (Restionaceae). **J. S. Afr. Bot. 28**: 21-44.

LINDER, H.P. 1986. The evolutionary history of the Poales/ Restionales - a hypothesis. **Kew Bulletin 42**: 297-318.

LINDER, H.P. and ELLIS, R.P. 1991. A Revision of *Pentaschistis* (Arundineae: Poaceae). **Contrib. Bol. Herb. 12.** 124pp.

MAHALINGAPPA, M.S. 1977. Gametophytes of *Eleusine compressa.* **Phytomorphology 27**: 231-239.

MAHESHWARI, P. 1950. **An Introduction to the Embryology of Angiosperms.** McGraw-Hill, New York.

MAZE, J. and BOHM, L.R. 1973. Comparative embryology of *Stipa elmeri* (Gramineae). **Can. J. Bot. 51**: 235-247.

MAZE, J. and BOHM, L.R. 1974. Embryology of *Agrostis interrupta* (Gramineae). **Can. J. Bot. 52**: 365-379.

MAZE, J. and BOHM, L.R. 1977. Embryology of *Festuca microstachys* (Gramineae). **Can. J. Bot. 55**: 1768-1782.

NICORA, E.G. 1973. Novedades agrostológicas patagónicas. **Darwiniana 18**: 80-106.

PHILIPSON, M.N. 1977. Haustorial synergids in *Cortaderia* (Gramineae). **New Zealand J. Bot 15**: 777-778.

PHILIPSON, M.N. 1981. The haustorial synergids of *Cortaderia* (Gramineae) at maturity. **Acta Soc. Bot. Pol. 50**: 151-160.

PHILIPSON, M.N. and CONNOR, H.E. 1984. Haustorial Synergids in Danthonioid Grasses. **Bot. Gaz. 145**:78-82.

REEDER, J.R. 1957. The Embryo in Grass Systematics. **Amer. J. Bot. 44**: 756-768.

RENVOIZE, S.A. 1981. The sub-family Arundinoideae and its position in relation to a general classification of the Gramineae. **Kew Bull. 36**: 85-102.

RENVOIZE, S.A. 1986. A survey of leaf blade anatomy in grasses VIII: Arundinoideae. **Kew Bull. 41**: 323-342.

RUDALL, P.J. and LINDER, H.P. 1988. Megagametophyte and Nucellus in Restionaceae and Flagellariaceae. **Amer. J. Bot. 75**: 1777-1786.

STEBBINS, G.L. 1956. Cytogenetics and Evolution of the Grass Family. **Amer. J. Bot. 43**: 890-905.

TOMLINSON, K.L. 1985. Comparative Anatomical Studies in *Danthonia sensu lato* (Danthonieae: Poaceae). **ALISO 11**: 97-114.

VELDKAMP, J.F. 1980. Conservation of *Notodanthonia* Zotov (Gramineae). **Taxon 29**: 293-298.

WATSON, L. and CLIFFORD, H.T. 1976. The Major groups of Australian Grasses: a Guide to Sampling. **Aust. J. Bot. 24**: 489-507.

WATSON, L., CLIFFORD, H.T. and DALLWITZ, M.J. 1985. Classification of the Poaceae: Subfamilies and Supertribes. **Aust. J. Bot. 33**: 433-484.

ZOTOV, V.D. 1963. Synopsis of the Grass Subfamily Arundinoideae in New Zealand. **New Zealand J. Bot. 1**: 78-163.