HETEROSPORY: THE MOST ITERATIVE KEY INNOVATION IN THE EVOLUTIONARY HISTORY OF THE PLANT KINGDOM

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I. INTRODUCTION: THE NATURE OF HETEROSPORY

'Heterospory' *sensu lato* has long been one of the most popular review topics in organismal botany. However, with a few exceptions (e.g. Lyon, 1904; Pincher, 1935; Manton, 1950; Sussex, 1966; Andrews, Gensel & Forbes, 1974; Bell, 1979, 1989; Duckett & Pang, 1984; Turnau & Karczewska, 1987), reviewers have tended to view heterospory primarily as a precursor to the seed habit rather than a profound innovation in itself (e.g. Coulter, 1898; Thomson, 1927, 1934; Walton, 1953; Andrews, 1963; Meeuse, 1963; Smith, 1964; Long, 1966; Pettitt, 1970; Jonker, 1977; Chaloner & Sheerin, 1981; Steeves, 1983; Crane, 1985 a, b; Doyle & Donoghue, 1986; Chaloner & Pettitt, 1987; Stein & Beck, 1987; Beck & Wight, 1988; Rothwell & Scheckler, 1988;

Table 1. *Contrasting definitions of heterospory*

"...bearing spores of distinctly different types". (Jones, 1987: 411)

"...the condition of producing microspores and megaspores". (Weier *et al.*, 1982: 682)

"...having two types of spores: megaspores and microspores". (Taylor & Taylor, 1992: 840)

"...the condition in embryophytic plants in which spores are of two types: microspores and megaspores".
    (Traverse, 1988: 503)

"...the spores are of different sizes..." (Sporne, 1975: 11)

"...two sizes of spore are formed..." (Thomas & Spicer, 1987: 95)

"...the production of spores of two sizes (megaspores and microspores)". (Bell, 1992: 290)

"...plants which produce spores of two sizes and with two different developmental patterns". (Sussex, 1966:
    140)

"...the sporophytes...produce spores of two sizes...[and] also of different sexes". (Pettitt, 1970: 402)

"...plants producing both large and small spores (megaspores and microspores) which give rise to distinct
    female and male gametophytes respectively". (Beckett, ed., 1977: 119)

"...production of microspores that grow into male gametophytes and megaspores that develop into female
    gametophytes; the two kinds of spore may or may not differ in size". (Bold *et al.*, 1987: 833)

"...a condition where the sporangia are of two sorts, megasporangia containing a few large megaspores and
    microsporangia containing many small microspores". (Ingrouille, 1992: 305)

"...plants...producing two kinds of spores in different sporangia on the same plant". (Duckett & Pang, 1984:
    14)

"...microspores are produced in microsporangia and develop into male gametophytes...larger megaspores are
    produced in megasporangia and develop into female gametophytes". (Gifford & Foster, 1989: 55)

"...the production of sexually differentiated spores is associated, during female sporogenesis, with regular
    abortion or degeneration of some of the spore mother cells or their meiotic products". (Bell, 1979: 68)

DiMichele, Davis & Olmstead, 1989; Galtier & Rowe, 1989; Haig & Westoby, 1989; Chaloner & Hemsley, 1991; Hemsley, 1993). Hence, less emphasis has been placed on the homospory–heterospory transition than on the heterospory–seed habit transition.

Moreover, surprisingly few authors have attempted to formally define heterospory (or its presumed ancestral condition, homospory). When such attempts *have* been made the definitions show striking contrasts in content and/or emphasis (Table 1). The definition provided by Jones (1987) is too ambiguous to be of value, while those of Weier *et al.* (1982), Traverse (1988) and Taylor & Taylor (1992) merely transfer the need for definition to the subsidiary terms 'microspore' and 'megaspore'. Sporne's (1975) vague invocation of spore size differences was recast more explicitly as bimodality by Thomas & Spicer (1987); this bimodality was in turn used to define small microspores and large megaspores by Bell (1992a). Sussex (1966) correlated spore size bimodality with 'different developmental patterns', an ambiguous phrase that was translated into bimodality of gender in the resulting gametophytes by Pettitt (1970). Combining these concepts, Beckett (1977) defined microspores and megaspores on size differences and assumed a reliable correlation with male and female gametophytes respectively. Bold, Alexopoulos & Delevoryas (1987) evidently realized that gametophyte gender did not always correlate with spore size, and chose to give the former priority over the latter. In contrast, Duckett & Pang (1984), Gifford & Foster (1989) and Ingrouille (1992) added a third criterion to the definition, namely segregation of the two spore morphs in different sporangia; only Gifford & Foster tied size bimodality, gender bimodality and sporangial segregation of gender together in defining heterospory. In contrast, Bell (1979) referred all of the above phenomena to an unusually broad concept of anisospory, a term generally confined to spore size

bimodality within a single sporangium. Bell required instead a more stringent physiological criterion to define heterospory *sensu stricto*: the degeneration of spore mother cells and/or members of post-meiotic spore tetrads. Bell's decision was criticized by Duckett & Pang (1984), who argued that anisospory should be confined to morphologically bimodal spore populations occupying single sporangia (e.g. Vitt, 1968) and that size segregation in different sporangia was sufficient to define heterospory.

Thus, discussions presented under the banner of 'heterospory' have in practice encompassed much of the reproductive history of the plant kingdom that followed the acquisition of sporophyte dominance over the gametophyte in the 'pteridophytes' (Kenrick, 1994; Sheffield, 1994). Not surprisingly, the alternation of generations has become a terminological morass; often, one term represents several concepts or one concept is represented by several terms.

In this paper we have been obliged to redefine several key terms that reflect increasing differentiation and specialization of gametophytes, in order to accommodate our specific usage. We focus on several more discrete, narrowly defined aspects of that differentiation process: these are listed and defined in Table 2. Most importantly, we have divorced the concepts of spore size bimodality (*heterospory sensu stricto*, reflected in large megaspores and smaller microspores) and gametophyte gender dimorphy (*dioicy* = heterothally, reflected in obligately male androspores and potentially female gynospores: Doyle, 1953; Crum & Anderson, 1980).

This distinction is followed by four terms that encompass phenomena found in several lineages of heterosporous pteridophytes. They describe the apportionment of spore dimorphs among different sporangia (heterosporangy), the retention of the gametophyte within the spore wall (endospory), the retention of the megaspore(s) within the megasporangium (endomegasporangy), and the reduction of the contents of the megasporangium to a single viable megaspore (monomegaspory). This last phenomenon is the end-point of a trend of megasporocyte abortion to leave only one per sporangium, followed by abortion of three of the four meiotic products of the last remaining megasporocyte (e.g. Pettitt, 1970; Bell, 1979; Hemsley, 1993).

The remaining terms listed in Table 2 are most commonly (though not exclusively) applied to the pteridospermaleans. These earliest representatives of the seed-plant clade are widely (if simplistically) recognized as the great success story of increasingly sophisticated heterosporous reproduction. Extrasporangial tissue termed the integument became increasingly prominent (integumentation). The megasporangium, now termed the nucellus, becomes elaborated for pollen capture (lagenostomy), a function eventually co-opted by the integument (Arnold, 1938; Walton, 1953; Andrews, 1963; Meeuse, 1963; Smith, 1964; Long, 1966, 1977*b*; Pettitt, 1970; Steeves, 1983; Stewart & Rothwell, 1993). By this stage the megasporangium spends an increasing proportion of its existence attached to the sporophyte, allowing *in situ* pollination and/or *in situ* fertilization. Pollen tubes, initially formed as haustoria for microgametophyte nutrition, were subsequently co-opted to deliver spermatozoids (antherozoids) to the megagametophyte (siphonogamy: Chaloner, 1970; Haig & Westoby, 1989; Friedman, 1993), thus reaching a level of reproductive sophistication seen in, for example, extant *Pinus* (e.g. Chaloner & Pettitt, 1987; Pennell, 1988).

Together, these heterosporic phenomena have engendered an unusually large number of biological controversies (cf. Bell, 1979; Duckett & Pang, 1984; DiMichele

Table 2. *Authors preferred terminology for heterosporic phenomena*

heterospory:	viable spores dimorphic
cf. homospory:	viable spores monomorphic
microspore:	smaller viable spore morph
megaspore:	larger viable spore morph
cf. isospore:	monomorphic spore
dioicy[1]:	antheridia and archegonia borne on separate conspecific gametophytes
cf. monoicy[2]:	antheridia and archegonia borne on the same conspecific gametophyte
cf. dioecy:	male and female reproductive organs borne on separate conspecific sporophytes
cf. monoecy:	male and female reproductive organs borne on the same conspecific sporophyte
androspore:	obligately male viable spore morph
gynospore:	obligately or facultatively female viable spore morph
heterosporangy:	spore dimorphs apportioned among different sporangia
endospory:	mature gametophyte largely enclosed by spore wall
endomicrospory:	mature male gametophyte largely enclosed by spore wall
endomegaspory:	mature female gametophyte largely enclosed by spore wall
monomegaspory:	single viable megaspore per megasporangium
endomegasporangy:	megaspore(s) routinely dispersed within megasporangium
integumentation:	near-complete enclosure of megasporangium by sterile tissue
lagenostomy:	development of perforated distal chamber on megasporangium
in situ pollination:	retention of megasporangium on sporophyte until pollinated
in situ fertilization:	retention of megasporangium on sporophyte until fertilized
siphonogamy:	delivery of male gametes to megasporangium via haustorial tube

[1] Syn. heterothally *p.p.*, haploid dioecy: gametophytes are sexually dimorphic and usually allogamous (cf. Crum & Anderson, 1980).

[2] Syn. homothally *p.p.*, haploid monoecy: gametophytes are sexually monomorphic and usually assumed to be autogamous.

et al., 1989; Haig & Westoby, 1989; Chaloner & Hemsley, 1991) that reflect their pivotal importance in generating modern, seed-plant dominated communities (e.g. Knoll, 1986; Niklas, 1986; Bateman, 1991a; Behrensmeyer *et al.*, 1992). The remainder of this paper focuses on determining (1) the best criteria for recognizing the acquisition of heterosporic characters (especially in fossils), (2) their frequency of occurrence among different evolutionary lineages, (3) their relative order of appearance within lineages, (4) their underlying physiological controls, and (5) potential factors driving their evolution through the last 385 million years. The following account reveals serious gaps in current knowledge of heterospory that emphasize the need for phylogenies to elucidate patterns of character acquisition.

In order to discuss what *is* known (or suspected) about heterospory, we have introduced a long cast of botanical characters, both extant and extinct. We have therefore asterisked both extant species and genera that include extant species.

II. GENERALIZED LIFE HISTORY OF A HOMOSPOROUS POLYSPORANGIOPHYTE: THE BASIS FOR EVOLUTIONARY EXCURSIONS INTO HETEROSPORY

Most authors select a generalized fern as representative of an equally generalized 'textbook' homosporous life history (Fig. 1a). In fact, the basic life history (albeit with minor variations: Haig & Westoby, 1988b) characterizes an enormous range of species that together constitute a putatively paraphyletic group (e.g. Jermy, Crabbe & Thomas, 1973; Lloyd, 1974; Dyer & Page, 1985). Its origin coincides with the evolution of the polysporangiophyte land-plants (*sensu* Kenrick & Crane, 1991: sporophytes producing
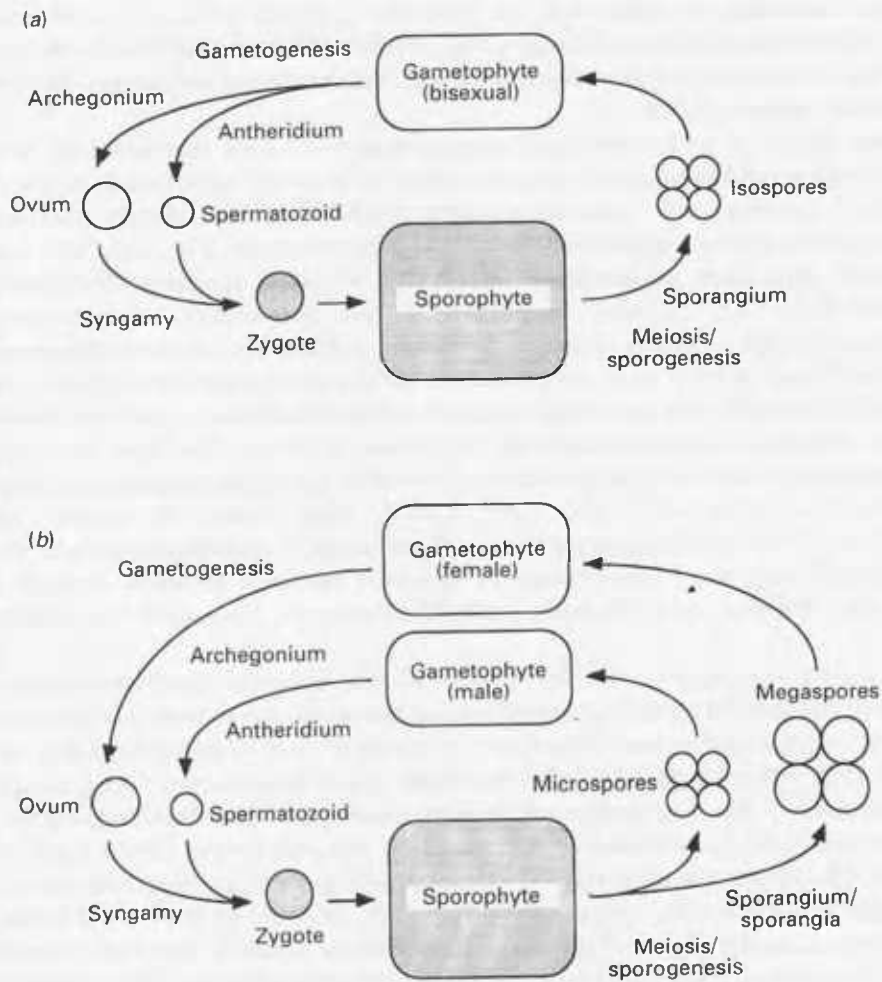
Fig. 1. (*a*) Textbook life-history of a homosporous pteridophyte. (*b*) Textbook life-history of a heterosporous pteridophyte. The diploid phase is stippled. The assumption that the transitions from homospory to heterospory and bisexual to unisexual gametophytes are coincident is questionable (see text). (Modified after Sporne, 1975, figs 1, 2.)

more than one sporangium) from a presumed bryophytic ancestor (e.g. Bremer, 1985; Mishler & Churchill, 1985; Knoll, Grant & Tsao, 1986; Haig & Westoby, 1988*b*; Hemsley, 1994), whereas the basic life history was modified in several lineages by the appearance of one more of the aforementioned heterosporic phenomena. Thus, the homosporous, biphasic life history of the polysporangiophytes is universally accepted as the basis for repeated evolutionary forays into varying degrees of heterospory (Fig. 1*b*). At least some primitive polysporangiophytes apparently possessed economically independent (biphasic) sporophyte (asexual diplophase) and gametophyte (sexual haplophase) generations of approximately equal size and longevity (isomorphic biphasy: cf. Stebbins & Hill, 1980; Keddy, 1981; Crane, 1990; Kenrick & Crane, 1991; Remy & Hass, 1991; Remy, Gensel & Hass, 1993; Kenrick, 1994).

Nonetheless, heterosporic phenomena are generally assumed to have evolved only in the more derived pteridophyte lineages that exhibit anisomorphic (heteromorphic) biphasy: the sporophytes are considered to be significantly larger and longer-lived than the conspecific gametophytes.

The gametophyte is an economically autonomous prothallus that develops from a haploid meiospore and is generally (though often incorrectly) regarded as monoicous (homothallic), bearing both male gametangia (antheridia) and female gametangia (archegonia) that generate spermatozoids and ova respectively (Fig. 1 a). The motile spermatozoids pass from antheridia to archegonia to effect syngamy (fertilization), restoring the diploid chromosome compliment in the zygote and the ensuing embryo. This eventually yields a mature sporophyte, which produces sporangia enclosing spore mother cells. These in turn undergo meiosis to yield a new generation of meiospores. Until recently, monoicy was generally assumed to favour autogamy (self-fertilization) rather than allogamy (cross-fertilization), with most ova being fertilized by spermatozoids originating from the same prothallus or another prothallus originating from the same sporophyte (Klekowski, 1969, 1979; Lloyd, 1974; Hickok & Kiriluk, 1984; Sheffield, 1994). This would engender the many profound (if contentious) consequences that accompany decreased interchange of genomic material between lineages (cf. Kimura, 1983; Willson, 1983; Hedrick, 1987; Charlesworth, Morgan & Charlesworth, 1993).

The simplicity and adaptive common-sense of this monoicy–facultative autogamy scenario have guaranteed its lasting appeal among botanists, but in reality it has become increasingly undermined as hard data have accumulated (e.g. Klekowski, 1969, 1979; Sheffield & Bell, 1987; Raghavan, 1989; Sheffield, 1990; Korpelainen, 1993, 1994). In practice, homospory has been diagnosed in most species, living or fossil, merely on the evidence of unimodal size distributions of small ($<$ 200 μm) spores produced by each sporophyte. The spores are then termed isospores and the species is usually said to be homosporous (e.g. Chaloner, 1967a, 1970). However, as noted by Stewart & Rothwell (1993), morphologically identical isospores can generate sexually dimorphic prothalli (monoicy). For example, several extant species of *Equisetum* subgenus *Hippochaete** are morphologically isosporous but routinely produce gametophytes of two physiological types: some yield only antheridial prothalli (dioicy), whereas others yield larger prothalli that initially are archegonial but later undergo a transition to an antheridial condition (sequential monoicy: cf. Duckett, 1970a, b, 1972, 1973, 1977, 1979a, b; Duckett & Duckett, 1980; Duckett & Pang, 1984). Sporne (1964, 1975) argued that individual prothalli experienced a brief period of bisexuality and thus facultative autogamy in culture, but such temporally restricted gametophytic bisexuality appears to be rare in nature (Duckett & Duckett, 1980). Higher ratios of dioicous to sequentially monoicous prothalli were induced experimentally in *E. telmateia** by altering environmental parameters; specifically, by decreasing incident light intensity and/or prothallial density on the artificial substrate (Duckett, 1972, 1977, 1979b). No correlation with spore size was observed. Similar strategies of mixed male dioicy and sequential monoicy have been recorded in a large proportion of the few pteropsids that have been studied in sufficient detail (cf. Sussex, 1966; Klekowski, 1969, 1979; Lloyd, 1974; Duckett & Duckett, 1980; Sheffield, 1994).

The filicalean pteropsid *Ceratopteris thalictroides** is a hydrophile, albeit less morphologically specialized than the strongly heterosporous Marsileales and Salviniales

(see below). Like *Equisetum**, this has unimodal spore size distributions with no obvious size segregation among sporangia (i.e. the plant is homosporous) and produces a mixture of antheridial and transitional archegonial–antheridial prothalli. Unlike *Equisetum**, there is a strong positive correlation between spore size and gametophyte gender. Smaller spores tend to produce strictly antheridial prothalli, implying gender control via metabolic microenvironments (Schedlbauer, 1976; Duckett & Pang, 1984; Hickok & Kiriluk, 1984).

Similar gametophyte dimorphism is evident in the filicalean pteropsid *Platyzoma microphylla**, but here this is reflected in subtle spore dimorphism and size bimodality that is expressed among rather than within sporangia. Some sporangia contain *ca.* 32 spores that consistently generate exclusively antheridial gametophytes, other contains *ca.* 16 larger spores that consistently generate sequentially monoicous gametophytes (Fig. 6*b*; Tryon, 1964; Tryon & Vida, 1967; Duckett & Pang, 1984). The difference in spore number reflects one less mitotic division of the archesporial cells rather than abortion of meiotic products (Haig & Westoby, 1988*a*).

In the case of *Platyzoma**, dioicy is detectable by heterospory (albeit subtly expressed). Nonetheless, dioicy can undoubtedly occur in homosporous pteridophytes. The frequency of such species is difficult to assess, even among extant pteridophytes, as so few have been studied in sufficient detail (Sheffield, 1990, 1994).

Another important and generally accepted cornerstone of the traditional view of pteridophytes, whether homosporous or heterosporous, monoicous or dioicous, is the 'dominance' of the asexual sporophyte over the sexual gametophyte. Evidence cited in support of this assertion includes the greater size, longevity, and morphological (especially organogenic) complexity of the sporophyte, reflected in the possession of abundant megaphyllous leaves, vascular tissues, epidermal cuticle, and stomata. These features are also said to confer on the sporophyte ecological dominance; specifically, wider ecological tolerances than those of the gametophyte. Thus, the gametophyte is widely perceived as the weakest link in any pteridophytic life history, especially in species characterized by prothalli that are thin, laminar, acuticular, and photosynthetic, and thus are restricted to the soil surface (e.g. Sporne, 1975: 11; Thomas & Spicer, 1987: 95; Raghavan, 1989).

However, some pteridophytes have been shown to possess gametophytes with geographic ranges considerably greater than those of conspecific sporophytes, able to persist and ramify for many years without recourse to sporophyte initiation (Rumsey & Sheffield, 1993; Sheffield, 1994). Moreover, several extant species of pteridophyte are capable of apospory: the production of gametophytes that are diploid rather than haploid, as a result of developing from sporophytes without the usual intervening phase of sporogenesis (Sporne, 1975; Sheffield & Bell, 1987; Bell, 1992*a*, *b*). The converse phenomenon, apogamy, has been even more widely demonstrated (Steil, 1939, 1951; Manton, 1950; Whittier & Steeves, 1960; Sporne, 1975; Sheffield & Bell, 1987; Bell, 1992*a*, *b*). Here, an atypically haploid (and thus sterile) sporophyte develops directly from a gametophyte without intervening gametogenesis. As in anisospory, environmental factors appear to be important in controlling both apospory and apogamy (Steil, 1939, 1951; DeMaggio & Wetmore, 1961; Sporne, 1975; Bell, 1992*a*, *b*). Another phenomenon that commonly complicates the genetics of gender in pteridophytes is polyploidy (e.g. Stace, 1993).

We will return to these topics later. For now, it is sufficient to demonstrate that there

is no simple transition from homospory to heterospory and that these two textbook life histories (Fig. 1) are not truly distinct. Gametophytic gender and reproductive strategy cannot be predicted with confidence simply by studying the morphology of spore populations. Rather, gametophytic gender, and indeed the willingness to alternate generations at all, are strongly influenced by intrinsic metabolic factors and extrinsic environmental factors. In short, the evolution and regulation of heterosporic phenomena appear decidedly 'fuzzy'.

III. DETECTION OF HETEROSPORY IN FOSSILS

(1) *The need to extrapolate from sporophyte to gametophyte*

In our opinion, the first critical step in the suite of evolutionary innovations traditionally termed heterospory is dioicy (heterothally); the transition from predictably bisexual to potentially unisexual gametophytes. Sadly, preservation of recognizable fossil gametophytes (and the all-important gametangia) is rare, as it requires exceptional anatomical preservation. Further problems are caused among free-sporing species by the difficulty of demonstrating conspecificity for physically unconnected gametophytes and sporophytes, well illustrated by remarkable research on the classic early land-plant assemblages from Rhynie, Scotland (reviewed by Remy & Hass, 1991; Remy *et al.*, 1993; Kenrick, 1994). Interestingly, most other examples of fossil gametophytes represent the most derived (and most strongly heterosporous) portions of the two main clades of euvascular land-plants: the rhizomorphic lycopsids (reviewed by Phillips, 1979; Bateman, 1992*a*) and the gymnospermopsids (reviewed by Taylor, 1982). Another problem is posed by the ability of some extant pteridophyte gametophytes to change gender during ontogeny. Fossils cannot provide the frequent observations of an individual gametophyte throughout its ontogeny that are necessary to detect such diachronous bisexuality; the only incontrovertible observation possible is synchronous bisexuality (monoicy) of a single fossil gametophyte.

In practice, we usually attempt to infer gametophyte gender by extrapolation from observations of the sporophyte (specifically, from spore assemblages), not only for fossil species (where the main constraint on determining gender is the rarity of identifiable gametophytes) but also for extant pteridophytes (where ontogenetic studies remain disappointingly few). As with heterosporic phenomena, spore assemblage analysis has engendered a complex terminology that has to be assimilated to enable meaningful discussion (Fig. 2) (Chaloner, 1967, 1970; Traverse, 1988).

Given that all spores *sensu lato* are the sporopollenin-coated products of meiosis, they can be termed meiospores. Dispersed meiospores are then divided into large megaspores (including those contained within ovules) and small miospores (note spelling and potential confusion with 'meiospore'), using an arbitrary size threshold (200 μm is most commonly selected; Zerndt, 1934; Guennel, 1952; Chaloner, 1967*a*; Turnau & Karczewska, 1987).

The term megaspore carries with it an implicit assumption of heterospory, and this in turn is assumed to indicate dioicy; in particular, the megaspore is perceived as the precursor of a female gametophyte. These covert biological assumptions do not extend to miospores, which include both the isospores of homosporous species (isospores are putative precursors of bisexual, monoicous prothalli) and the microspores of heterosporous species (microspores are putative precursors of male prothalli, and

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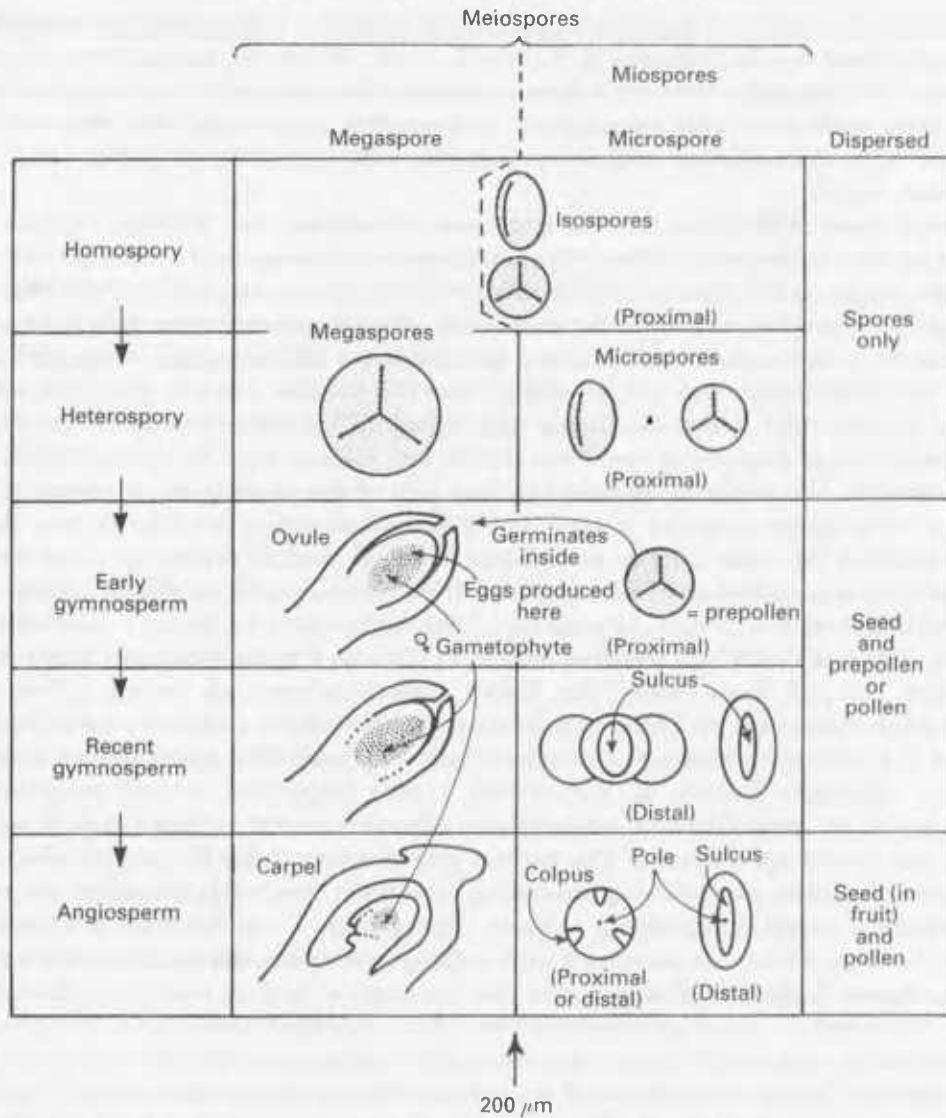
Fig. 2. Evolution of spores, from homospory to the derived seed habit of angiospermaleans. Light stippling indicates the proximal hemisphere of a spore, dense stippling indicates megaspores that were retained in the megasporangium for pollination. (Modified from Chaloner, 1970, fig. 1 and Traverse, 1988, fig. 8.9.)

include the prepollen and pollen of seed-plants). The pollen grains of derived seed-plants (including angiospermaleans) can usually be distinguished by their apomorphic morphology and wall ultrastructure. However, confident discrimination of isospores from similarly proximally-germinating prepollen and microspores is in practice achieved only through knowledge of the presence of conspecific megaspores in heterosporous species and knowledge of their absence in homosporous species. This leads to an awkward paradox, for isospory must be regarded as the null hypothesis until the conspecificity of a particular megaspore and microspore has been conclusively demonstrated, yet the conclusive demonstration of the *absence* of megaspores from a

species (and thus the unambiguous recognition of its spores as isospores) is impossible in disarticulated fossils (Bateman & Rothwell, 1990). Moreover, among microspores *sensu lato*, the distinction between microspores *sensu stricto* and more derived prepollen again rests with correlated megaspores; non-ovulate megaspores are assumed to correlate with microspores, ovulate megaspores with prepollen or pollen (Fig. 2) (Chaloner, 1970).

Beyond these difficulties lie two questions concerning the arbitrary threshold separating the size-delimited categories of megaspore and miospore: (1) How predictive are these categories for separating the precursors of female gametophytes (physiological megaspores = gynospores) from the precursors of male gametophytes (physiological microspores = androspores) and bisexual gametophytes (physiological isospores)? (2) If the size-delimitation method is fallible, does the popular 200-μm threshold offer optimal predictivity? Before discussing these issues it is necessary to define the most appropriate single measure of spore size (sadly, few authors describe their methods of measurement). We prefer to measure the long axis of the spore body, irrespective of whether it is radial or (more commonly) longitudinal–polar; we also believe that elaborations of the exine such as sacci, equatorial and laesural expansions, and other emergent ornamentation should be excluded from measurement, as should additional external layers such as perine. In a survey of the microspores *s.l.* of 2251 *extant* plant species, Traverse (1988: 59) reported only 75 (3 %) with a mean maximum dimension exceeding 100 μm (presumably, far fewer exceed 200 μm). A review of extant pteridophytic isospores by Erdtman & Sorsa (1971) revealed a maximum mean size of 164 μm in *Ceratopteris cornuta**. Correspondingly few *fossil* microspore species exceed 100 μm. Although Turnau & Karczewska (1987) implicated several progymnospermopsids, the most frequent demonstrable offenders are the earliest group of seed-plants, the pteridospermaleans. The earliest pteridospermaleans (Lyginopteridaceae) produced triradiate, proximally-germinating pre-pollen that rarely exceeded 100 μm. One marginal exception averaging 110 μm, 'Sporangium C' of Bateman & Rothwell (1990), has been tentatively correlated with *Solpingostoma dasu*, the largest known Early Carboniferous lyginopteridacean ovule (the megaspore is 8–12 mm long: Gordon, 1941). However, in the Late Carboniferous the Lyginopteridaceae gave rise to the Medullosaceae, a group of wetland specialists that yielded exceptionally large spores of both genders. Ovulate megaspores of several species exceeded 30 mm in length and at least one species reached 48 mm (Hoskins & Cross, 1946; Taylor, 1965, fig. 8; Chaloner & Hemsley, 1991; Stewart & Rothwell, 1993). Their monocolpate pollen reached 600 μm in maximum dimension (Millay, Eggert & Dennis, 1978), exceeding in size the *mega*spores of many other contemporaneous species.

Such occurrences would not be problematic if physiological megaspores always greatly exceeded the 200 μm size threshold. In relatively derived groups such as the rhizomorphic lycopsids and gymnospermopsids this is normally the case – their megaspores tend to be measured in millimetres rather than micrometres. However, there are many exceptions among the more primitive extinct heterosporous pteridophytes, and a few exceptions among the living (e.g. *Platyzoma**: Tryon, 1964; Duckett & Pang, 1984; *Regnellidium**: Erdtman & Sorsa, 1971; Haig & Westoby, 1988*a*). Small megaspores were especially prevalent during the Late Devonian and Carboniferous, when heterospory evolved in several phylogenetically disparate pteridophytic lineages.

Among dispersed spore assemblages of that age, many form-species cannot be attributed to classes or orders, let alone to whole-plant species. It is therefore particularly interesting that miospores found *in situ* in fossil reproductive structures rarely exceed 100 μm in diameter. From the mid-Early Devonian to the mid-Late Carboniferous the largest spore-species recorded in dispersed assemblages approximated 200 μm (Chaloner & Sheerin, 1981: 95), but the number of spore-species with size-range distributions straddling that threshold peaked in the Givetian stage of the Middle Devonian (Chaloner, 1967 a: 88) (see Fig. 11 for time-scale). Chaloner argued that most of these medium-sized spore-species were physiological megaspores (gynospores) produced by heterosporous plants, though this assertion was challenged by Turnau & Karczewska's (1987) study of dispersed Middle Devonian spores. We conclude that the optimal size boundary for distinguishing megaspores and microspores in dispersed assemblages should be determined primarily using *in situ* spore populations (living and fossil), where a much wider range of evidence is available to distinguish megaspores, microspores, and isospores (see below). Even the optimal threshold (which probably lies a little below 200 μm) will undoubtedly conceal a significant number of exceptions: size-delimited megaspores that are physiological miospores (androspores or isospores), and size-delimited miospores that are physiological megaspores (gynospores). The latter are probably most common among relatively primitive heterosporous species, when other types of evidence of spore gender differentiation (ornamentation, wall ultrastructure, sporangium–sporophyll differentiation and segregation) are also least evident. In other words, heterospory is most difficult to detect in those primitive species most likely to provide crucial information on the origins of the early stages of gametophyte gender differentiation.

Although they are rarely explicitly stated, several criteria are in practice used to infer the occurrence (and degree) of heterospory in fossils. Comparison of putative conspecific megaspores and microspores focuses on differences in intrinsic properties such as spore size and shape; aperture morphology and position; exine ornamentation, thickness, density, and ultrastructure; and (in the case of some megaspores) attached abortive tetrad members. Satisfactory comparison of even these intrinsic properties primarily requires study of *in situ* rather than dispersed spore populations. Admittedly, there is a risk that spores occurring within pre-dehiscent sporangia could be immature and thus misleading in size and morphology, but this can often be tested by comparing *in situ* spores with similar, presumably mature morphs in dispersed assemblages extracted from the inorganic matrix surrounding the spore-containing fossil(s).

Previous studies tended to characterize the spore size of each species via a single aggregate arithmetic histogram; many specified neither the precise methods of spore measurement nor the precise source of the spores. Most commonly, spores were macerated *in situ* from several sporangia that were closely spaced on a single fossil. One such example, from the progymnospermopsid *Protopitys* (Smith, 1962 a), is reproduced in Figure 3 a. This bimodal distribution can be interpreted as two broad, overlapping unimodal populations representing microspores and megaspores respectively. However, many of the larger measurements are extrapolations from damaged spores. Moreover, photographs of intrasporangial populations (Fig. 6 g) suggest low intrasporangial variation but high intersporangial variation (Walton, 1957; Smith, 1962 a). The possibility of polymodality has led to the heterosporous status of *Protopitys* being

Fig. 3. (a) Spore size spectrum for the Lower Carboniferous progymnospermopsid *Protopitys scotica*. (b) Spore size spectrum for the Upper Carboniferous equisetalean *Calamostachys americana*. In both cases, spores were pooled from several juxtaposed sporangia. Note that there is slight overlap of the two putative unimodal distributions in (a), whereas in (b) there is a slight discontinuity and the two distributions were plotted separately and on different scales. ((a) modified from Smith, 1962a, fig. 2, (b) from Good, 1975, figs 1, 2.)

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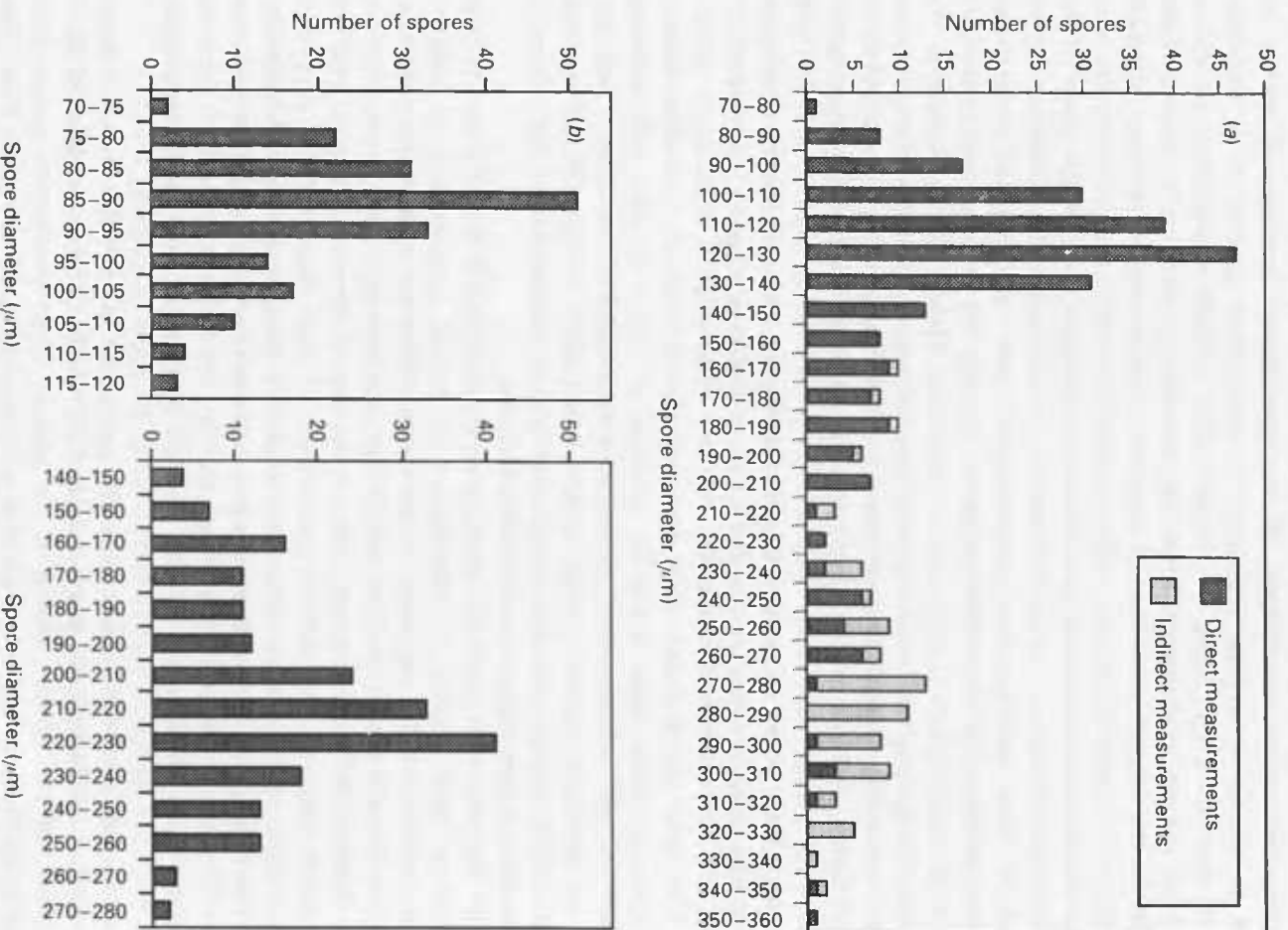
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Fig. 3. (a) Spore size spectrum for the Lower Carboniferous progymnospermopsid *Protopitys scotica*. (b) Spore size spectrum for the Upper Carboniferous equisetalean *Calamostachys americana*. In both cases, spores were pooled from several juxtaposed sporangia. Note that there is slight overlap of the two putative unimodal distributions in (a), whereas in (b) there is a slight discontinuity and the two distributions were plotted separately and on different scales. ((a) modified from Smith, 1962a, fig. 2, (b) from Good, 1975, figs 1, 2.)

Fig. 4. Mean diameters and sample standard deviation bars for intrasporangial spore populations from the Lower Carboniferous equisetaleans *Protocalamostachys farringtonii* (heterosporous: Oxroad Bay) and *P. arranensis* (homosporous: Loch Humphrey Burn). Microspore populations represented by circles occurred on sporangiophores that also bore megasporangia. (Reproduced from Bateman, 1991 *a*, fig. 12.)

questioned (e.g. Stubblefield & Rothwell, 1989). Alternatively, it is not difficult to envisage a pteridophytic plant capable of developing small spores that produce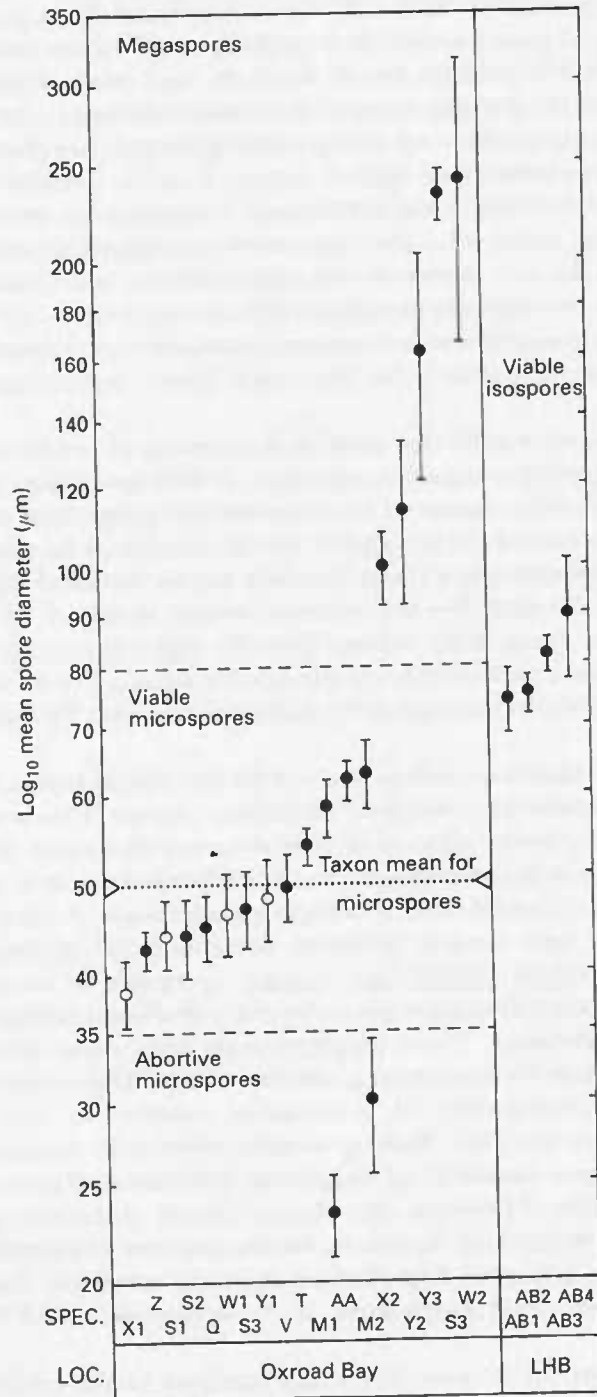 male prothalli, large spores that produce female prothalli, and medium-sized spores that produce bisexual prothalli. A wider range of life-history strategies may have occurred in the past than have yet been observed among extant pteridophytes (further discoveries seem likely in this under-subscribed field of study). A similar problem surrounds the study of spore size in the calamitacean sphenopsid *Calamostachys americana* (Fig. 3*b*; see also Fig. 7*b*) (Good, 1975). This also represents an amalgam of several sporangial populations, but here the two modes do not quite overlap; consequently, they were originally presented as two separate histograms (Good, 1975, figs 1, 2). Without being able to relate these two histograms to intrasporangial populations, interpretation is little improved over similar histograms for dispersed spore assemblages (Turnau & Karczewska, 1987).

Bateman (1991*a*, 1992*a*) argued that analysis is necessary at two hierarchical levels: within sporangia, and among conspecific sporangia. Within sporangia containing more than one spore, size should be measured for a representative statistical population, and the number of spores counted. If the spores are too numerous to count, as in most isosporangia and microsporangia, a rough estimate can be obtained using the simple formula $N = (0.74M)/S$, where N = the estimate number of spores, M = sporangium volume, and S = mean spore body volume (usually assessable using $4/3\pi r^3$). This assumes that the spores are perfect isodiametric spheres arranged in the closest possible spatial packing (rhombohedral, giving 26% porosity) (see also Phillips, Andrews & Gensel, 1972: 65).

Figure 4 presents the results of such an analysis for the earliest known heterosporous sphenopsid, *Protocalamostachys farringtonii* (Bateman, 1991*a*). This was preserved as disarticulated sporangiophores: clusters of four recurved sporangia (Fig. 7*c*). Most sporangiophores bore only microsporangia, but a few bore one or two megasporangia (altogether 10% of the 73 undehisced sporangia encountered). A clear discontinuity separates mean values and sample standard deviations for microsporangia and megasporangia, but variation within and among sporangia is much greater for megasporangia than for microsporangia (once the many abortive microspores have been omitted from the calculations). Three megasporangia have mean values below the artibrary 200 *µ*m threshold for megaspores, and two above. The overall impression is of poorly-controlled development of megaspores relative to the microspores. Interestingly, microsporangia that share sporangiophores with megasporangia have unusually small mean spore sizes (Fig. 4), suggesting polarization of spore development across the sporangiophore. Moreover, the closely related, putatively isosporous *P. arranensis* has spores intermediate in size to the megaspores and microspores of *P. farringtonii*, offering an attractive hypothetical ancestral condition from which the smaller microspores and larger megaspores of *P. farringtonii* could have diverged developmentally.

Figure 5 presents data for a spore size study confined to the megaspores of the progymnospermopsid *Archaeopteris latifola*. Chaloner & Pettitt (1987, fig. 5) originally presented these data as a bivariate scattergram of the number of viable megaspores per megasporangium versus the mean spore size in that megasporangium. They demonstrated that spore number clustered around multiples of four (i.e. meiotic
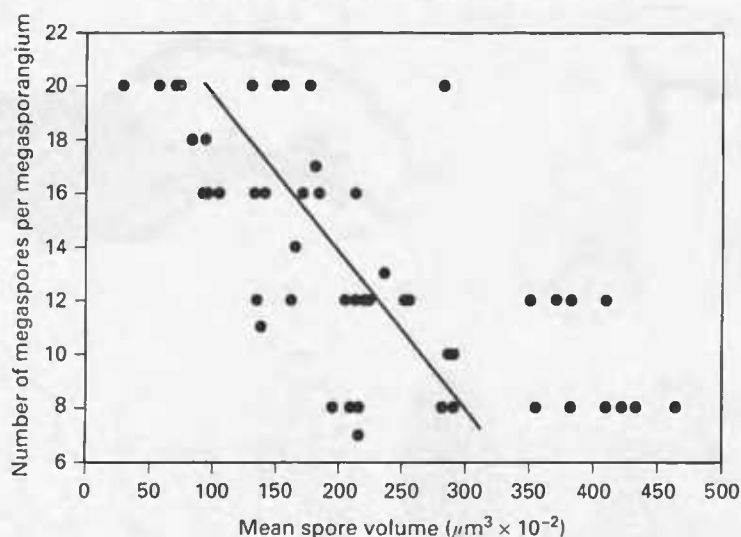
Fig. 5. An analysis of intrasporangial megaspore populations of the Upper Devonian progymnospermopsid of *Archaeopteris latifolia*, plotting spore number per sporangium against mean spore volume. A crude ($r^2 = 0.50$) negative correlation is evident, implying limited resources within individual sporangia. Note that spore numbers tend to increase in multiples of four, each reflecting the development of a tetrad from a single megasporocyte. (Modified from Chaloner & Pettitt, 1987, fig. 5.)

tetrads), with occasional deviations that presumably reflected abortion of individual tetrad members. Overall spore numbers varied between 7 and 20 (i.e. 2–5 tetrads; Fig. 6d), and showed a negative correlation with mean spore diameter that Chaloner & Pettitt regarded as indicating differential abortion of spore mother cells and consequent differential appointment of nutrients to the resulting tetrads. If so, volume is a more appropriate measure of the potential nutrient content of a spore than its diameter. The data have been transformed accordingly in Fig. 5. Although statistically significant, the correlation between mean spore volume and viable megaspore number per megasporangium is relatively poor ($r^2 = 0.50$); the aggregate volume of megaspore populations varies among megasporangia by an order of magnitude. There is clearly strong competition for nutrients among megasporangia as well as within them, suggesting that heterospory in *A. latifolia* shows little advance over that in *P. farringtonii*.

In conclusion, the analyses of Chaloner & Pettitt (1987) and Bateman (1991a) illustrate the much greater interpretative power of studies that compare morphometrically the spore content of many sporangia per sporophyte. Not only is heterospory more readily and convincingly identified, but also the degrees of heterospory and of the spatial segregation of the spore morphs can be ascertained. This in turn is more likely to elucidate underlying control mechanisms.

(2) *Spatial criteria and the physiological control of heterospory*

Even if the occurrence of heterospory has been demonstrated conclusively in a particular species, it remains important to determine the spatial scale of microspore and megaspore segregation relative to the bauplan of the sporophyte:
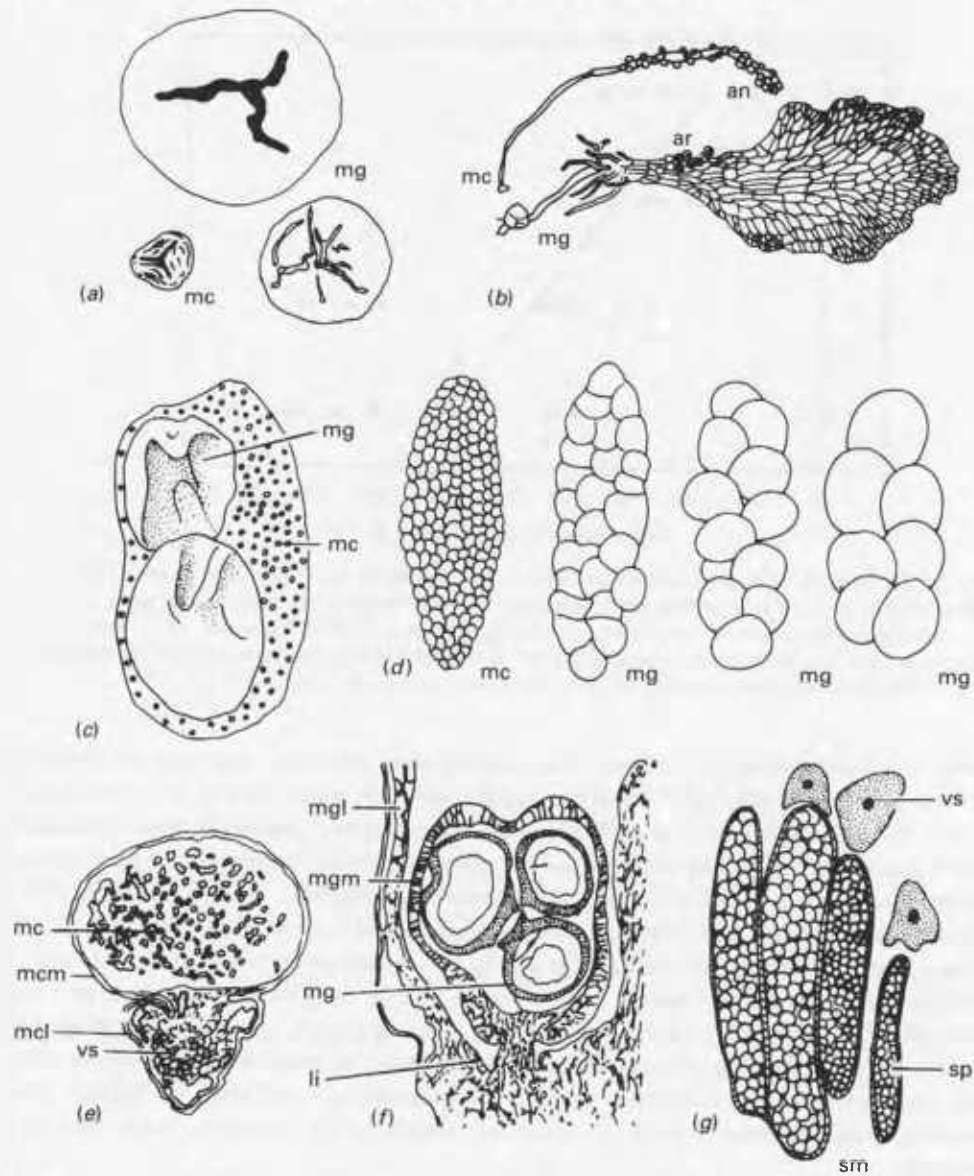
Fig. 6. Examples of heterosporous species, 1. (a) Spore size range in *Chaleuria cirrosa* (Progymno-spermopsida, ×215). (b) Antheridial and sequentially bisexual gametophytes of *Platyzoma microphylla**
(Pteropsida, ×19). (c) Anisospory in intrasporangial contents of *Barinophyton citrulliforme* (Zostero-phyllopsida, ×225). (d) Comparison of contents of microsporangium (left) and three megasporangia of
Archaeopteris latifolia (Progymnospermopsida, ×24). (e–f) TS microsporangium and LS mega-sporangium respectively of *Selaginella selaginoides** (Lycopsida, ca. ×35). (g) Variable intersporangial
spore size in LS sporangial cluster of *Protopitys scotica* (Progymnospermopsida, ×15). (Modified from
(a) Andrews *et al.*, 1974, pl. 56; (b) Bierhorst, 1971, fig. 16.18*f–g*; (c) Taylor & Taylor, 1992, fig. 13.3;
(d) Chaloner & Hemsley, 1991, fig. 8.1; (e–f) Bierhorst, 1971, figs 3.5*b*, *d*; (g) Walton, 1957, fig. 14.)

   Labels to Figs 6–8: sp, spore; sm, sporangium; mc, microspore; mcm, microsporangium; mcma,
aborted microsporangium; ma, microsporangial massula; mcl, microsporophyll; mg, megaspore; mga,
aborted megaspore; fl, megaspore floats; mgm, megasporangium; mgl, megasporophyll; an, antheridium;
ar, archegonium; ov, ovum; nu, nucellus; nub, nucellar break; la, lagenostome; pc, pollen chamber; cc,

(1) Within the sporangium ('anisospory' as defined by most authors).

(2) Among the sporangia but on the same sporophyte (this category is subdivisible according to the degree of spatial separation of mega- and microsporangia across the bauplan of the individual sporophyte).

(3) Among sporophytes (i.e. sporophytically controlled unisexuality: dioecy, as opposed to the obligate monoecy of categories (1) and (2)).

Many examples of category (1) and (2) fossils are illustrated in Figures 6–8.

Given the inevitable fragmentation of all but the smallest fossil sporophytes, category (1) heterospory is most readily observed, because spore morph differentiation is on the smallest scale (Figs 6a–c). However, the fact that the two spore morphs occupy the same sporangium means that it becomes especially important to demonstrate that the putative megaspores and microspores are not merely viable and non-viable spores respectively of a single gender. This second hypothesis can be confirmed without detailed scrutiny of the spores if subsequent intersporangial comparisons reveal spores of the opposite gender (i.e. a third morph) located in sporangia borne elsewhere on the sporophyte (category 2 above: Fig. 4) or on other conspecific sporophytes (category 3). Unless a third spore morph is detected, the presence of abortive spores can only be inferred. Small spores of similar morphology to their larger sporangial cohabitants but possessing walls of equal or greater thickness are traditionally suspected of being abortive, having acquired a full quota of sporopollenin but failed to undergo subsequent expansion of the exine associated with protoplasmic proliferation (e.g. Thoday, 1906; Smith, 1962a; Hemsley, 1990; Bateman, 1991a). Such arguments are more convincing when three abortive spores remain associated with a single fertile spore in a tetrad, as occurs in the sporangia of several rhizomorphic lycopsids (Phillips, 1979; Hemsley & Bartram, 1991; Hemsley, 1993), the extant pteropsid *Marsilea** (Pettitt, 1970), and the earliest pteridospermalean seed-plants (Pettitt & Beck, 1968; Pettitt, 1969, 1970; Galtier & Rowe, 1989).

Thus, putative examples of intrasporangial heterospory (anisospory) present difficulties of (1) demonstrating that two spore morphs co-occur (i.e. that the perceived bimodality is statistically significant), (2) demonstrating that both of the morphs are viable, and (3) explaining how such intrasporangial differentiation could arise. These questions are important, as anisospory characterizes the earliest reported examples of heterospory, such as the putative aneurophytalean progymnospermopsid *Chaleuria cirrosa* (Eifelian/Givetian: Andrews *et al.*, 1974; Gensel & Andrews, 1984; fig. 6a) and the barinophytalean zosterophyllopsids *Barinophyton richardsonii* (Famennian: Pettitt, 1965), *B. citrulliforme* (Famennian: Arnold, 1939; Pettitt, 1970; Brauer, 1980; Taylor & Brauer, 1983; Cichan, Taylor & Brauer, 1984; fig. 6c), and *Protobarinophyton pennsylvanicum* (?Famennian: Brauer, 1981; Cichan *et al.*, 1984). Sporangial cohabitation of megaspores and microspores has also been reported in two Indian species of the sole surviving rhizomorphic lycopsid genus, *Isoetes** (Goswami & Arya, 1968; Thomas & Spicer, 1987); these require detailed ontogenetic observation.

Category (2) heterospory can be subdivided according to the relative distance

central column; tp, tent-pole; in, integument; inl, integumentary lobe; mp, micropyle; sg, sporangiophore; sc, sporocarp; sr, sporophore; so, sorus; ps, perispore; li, ligule; br, bract; ca, cone axis; vs, vascular strand.
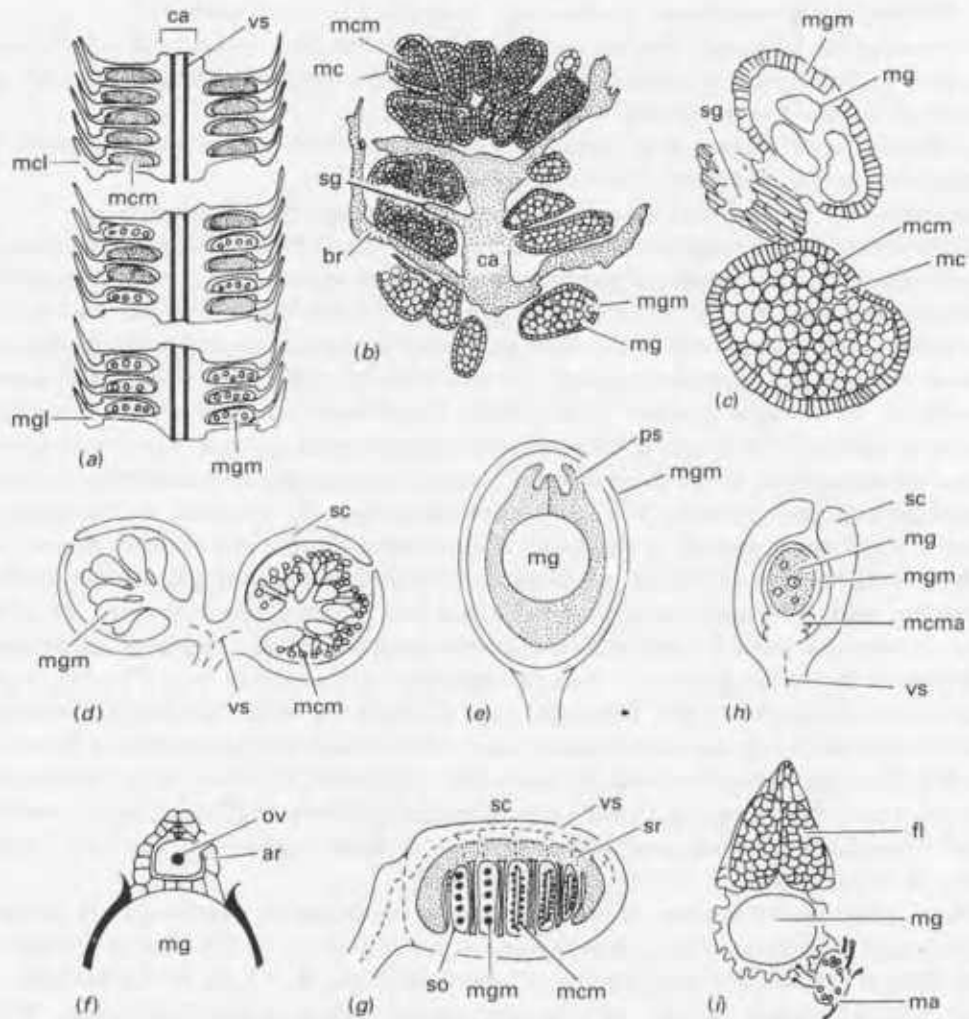
Fig. 7. Examples of heterosporous species, 2. (a) LS bisexual cone of *Flemingites diversus* (Lycopsida, ca. ×3·7). (b) LS bisexual cone of *Calamostachys casheana* (Sphenopsida, ca. ×7·7). (c) Near-LS bisexual sporangiophore of *Paracalamostachys farringtonii* (Sphenopsida, ×42). (d) LS megasporangial and microsporangial sporocarps of *Salvinia natans** (Pteropsida, ×7·7). (e) LS megasporangium of *Salvinia natans** (Pteropsida, ×185). (f) LS megaspore proximal pole of *Marsilea vestita** (Pteropsida, ×98). (g) LS bisexual sporocarp of *Marsilea vestita** (Pteropsida, ×10·5). (h) LS immature megasporangial sporocarp of *Azolla filiculoides** (Pteropsida, ×98). (i) Dispersed megaspore and microsporangial aggregate of *Azolla filiculoides** (Pteropsida, ca. ×63). (Modified from (a–b) Andrews, 1961, figs 8.12, 9.10; (c) Bateman, 1991a, fig. 51; (d–h) Sporne, 1975, figs 37c, d, 35g, c, 36b; (i) Stewart & Rothwell, 1993, fig. 20.10a.) For labels see Figure 6.

separating megasporangia and microsporangia on the sporophyte bauplan. In the least differentiated species (category 2a), megasporangia and microsporangia coexist on the same polysporangiate sporophyll or sporangiophore. Fossil examples include equisetaleans such as *Protocalamostachys farringtonii* (Fig. 7c; Bateman, 1991a) and non-aneurophytalean progymnospermopsids such as *Archaeopteris latifolia* (Fig. 6d;

Arnold, 1939; Chaloner & Pettitt, 1987; Chaloner & Hemsley, 1991), *Protopitys scotica* (Fig. 6g; Walton, 1957; Smith, 1962), and *Cecropsis luculentum* (Fig. 8d; Stubblefield & Rothwell, 1989). The classic extant examples in category (2a) are the specialized water-ferns of the Salviniales (Figs 7d–e, h–i; Hossain, 1971; Dunham & Fowler, 1987; Collinson, 1980, 1991, 1992) and the Marsileales (Figs 7f–g; Shattuck, 1910; Collinson, 1991).

The next possible level of gender differentiation is among sporophylls or sporangiophores (category 2b), which are usually aggregated along portions of axes into terminal cones or, less frequently, non-terminal fertile zones (e.g. DiMichele, Mahaffy & Phillips, 1979; Pigg & Rothwell, 1983; Stubblefield & Rothwell, 1989). This level of spatial differentiation characterizes most of the selaginellalean and less derived members of the rhizomorphalean lycopsids (Figs 6e–f, 7a; Felix, 1954; Phillips, 1979; Bateman *et al.*, 1992; Phillips & DiMichele, 1992), as well as most of the heterosporous equisetalean and sphenophyllalean sphenopsids (Fig. 7b; Boureau, 1964; Good, 1975; Thomas & Spicer, 1987) and the noeggerathialean progymnospermopsids (Halle, 1954; Němeje, 1963; Bourcau, 1964; Beck, 1981). In most cones microsporangia are concentrated towards the axial apical meristem, though there are exceptions (for example, among the selaginellaleans: Duerden, 1929; Horner & Arnott, 1963; Sota & Morbelli, 1981). Often, spatial separation of sporangia according to gender is perfect (category 2bii), but in other cases there is an intermediate zone of one or more sporophyll whorls that bear commingled mega- and microsporangia (category 2bi; Fig. 7a). Perfectly and imperfectly differentiated cones can characterize closely related species (e.g. the bisporangiate cones of the fossil rhizomorphalean lycopsid *Oxroadia gracilis* are typically category 2bii but the only known cone of *O. conferta* is category 2bi; Bateman, 1992a), and both cone forms can even occur within some species of *Selaginella**. Obviously, sporangium segregation according to gender means that substantial portions of cones are needed to detect the megasporangium–microsporangium transition and thereby demonstrate that they are bisporangiate. Extending this logic, only a complete cone can be regarded with certainty as monosporangiate. Moreover, the sporophyte could be capable of producing both bisporangiate and monosporangiate reproductive organs, either as a normal aspect of an unusually complex life history (e.g. the extant angiospermalean *Primula vulgaris**: Webster & Grant, 1990; Barrett, 1992) or as a product of developmental teratology. Examples of terata have even been recognized in fossils, most notably an anomalously bisexual ovulate cupule of the early pteridospermalean *Pullaritheca longii* (Fig. 9) (Long, 1977a; see also Bateman & Rothwell, 1990; Rothwell & Wight, 1991). *Stachygynandrum (Selaginella) kraussianum** exhibits unusually strong developmental canalization; each bisexual cone contains only one basal megasporangium (Bierhorst, 1971).

With rare exceptions among small hydrophilic species (e.g. *Azolla schopfii*; Sweet & Chandrasekharam, 1973; see also Collinson, 1980, 1982), the fossil record does not preserve intact sporophytes with all organs still fully articulated. Thus, it is impossible to determine whether a sporophyte that produced monosporangiate reproductive organs is monoecious (bisexual: category 2) or dioecious (unisexual: category 3), let alone any of the more complex strategies observed in extant plants (such as sequential monoecy, when gender changes during ontogeny: Bawa, 1980; Givnish, 1980, 1982;
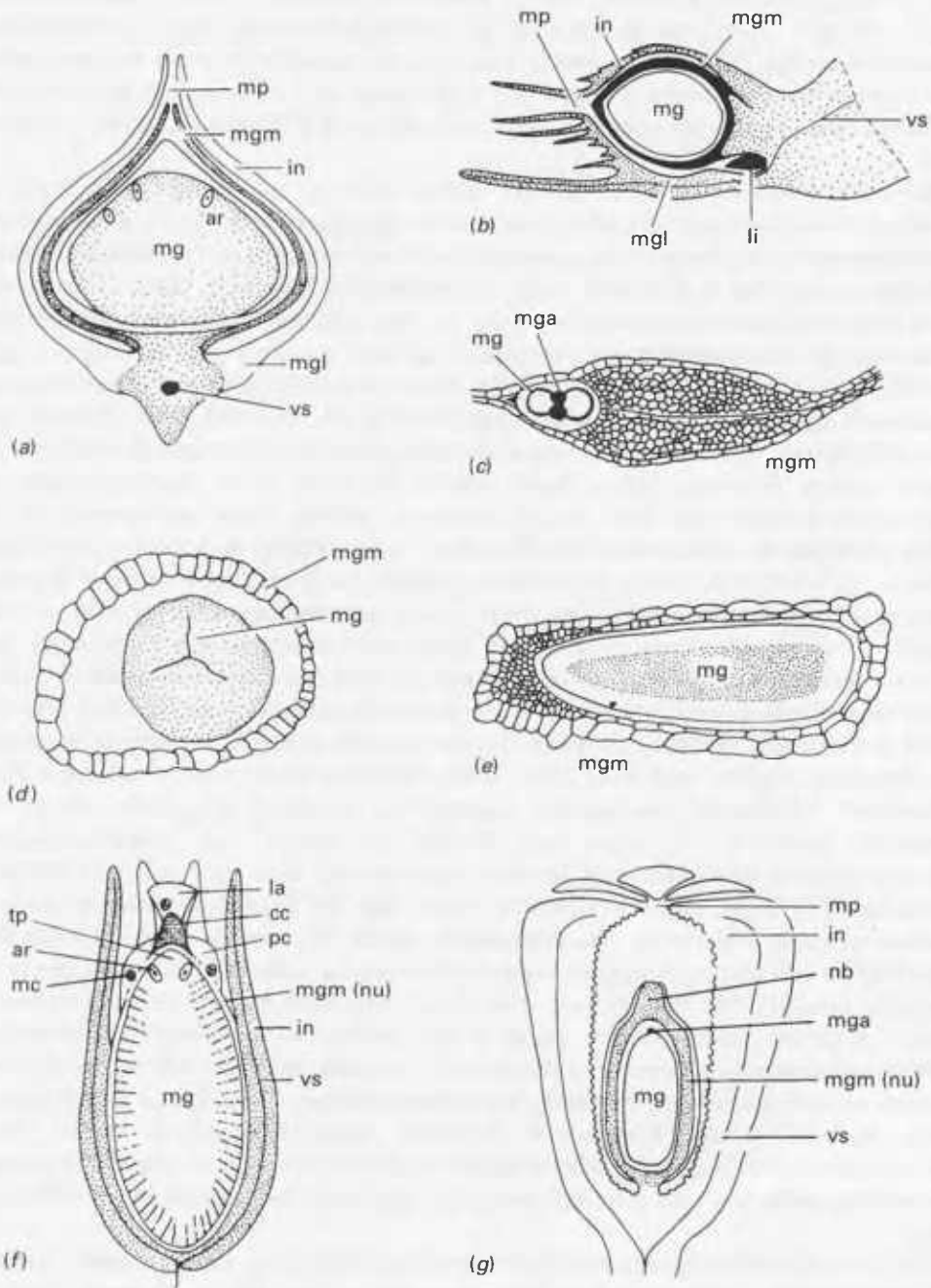
Fig. 8. Examples of heterosporous species, 3. Seeds and seed-like structures. (a) TS megasporophyll–megasporangium complex of *Lepidocarpon lomaxi* (Lycopsida, × 4·9). (b) LS megasporophyll–megasporangium complex of *Miadesmia membranacea* (Lycopsida, × 14). (c) LS megasporangium of *Stauropteris burntislandica* (Pteropsida, ca. × 38). (d) TS megasporangium of *Cecropsis luculentum* (Progymnospermopsida, × 45). (e) LS megasporangium of *Calamocarpon insignis* (Sphenopsida, ca. × 17). (f) LS fertilized ovule of cf. *Hydrasperma tenuis* (Gymnospermopsida, ca. × 15). (g) LS ovule of
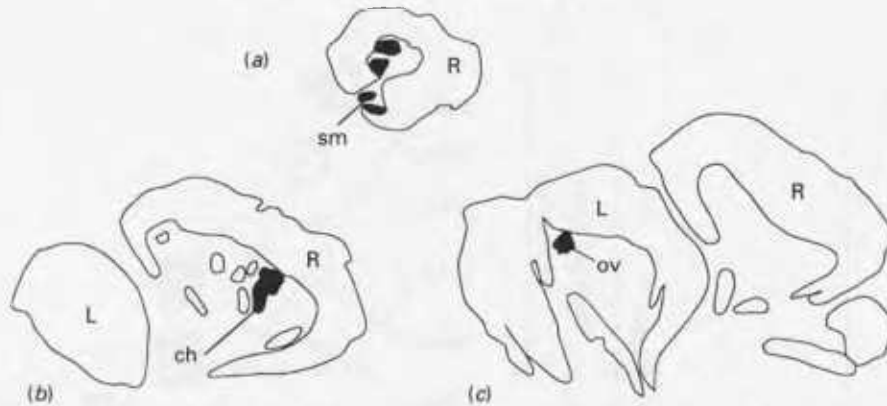
Fig. 9. A developmentally anomalous fossil. LS margin of an exceptional specimen the early pteridospermalean cupule *Pullaritheca longii*, showing a transition from (*c*) regulated expression of ovules to (*a*) atavistic expression of microsporangia via (*b*) non-functional structures of indeterminate gender (Gymnospermopsida, × 5·4). ((*a-c*) modified from Long, 1977*a*, figs 1*c*, *e*, *i*.) L, left hemisphere; R, right hemisphere; ov, ovule; mcm, microsporangium; ch, chimeric structure possessing features of both ovule and microsporangium.

Donoghue, 1989). Once again we are faced with a frustrating paradox; the less common and typically more derived condition, dioecy, must be treated as the null hypothesis, and only when sporangia of both genders have been found on a single sporophyte can the fossil species be classed as unequivocally monoecious.

To summarize, our understanding of spore gender differentiation patterns in fossil plants is constrained primarily by the inevitable disarticulation of sporophytes into their constituent organs. The probability of correctly interpreting their reproductive biology is increased when (1) the megaspores and microspores occur close together on the sporophyte hauplan, (2) at least one fertile specimen of the sporophyte is relatively well articulated, and/or (3) much effort has been expended to reconstruct the conceptual whole-plant by various methods of organ correlation (Chaloner, 1986; Bateman & Rothwell, 1990; Bateman, 1992*c*). Criteria (2) and (3) also help to determine the taxonomic affinities of the species, so that it can be placed in its phylogenetic context. It is vital to establish the degree of heterospory, the relative frequency of megaspores and microspores, and their spatial distribution across the sporophyte bauplan, not only to confirm the occurrence of heterospory but also to infer potential physiological mechanisms controlling its expression in both sporophyte and gametophyte.

IV. ITERATIVE EVOLUTION OF HETEROSPORY

It has long been accepted that there were several independent origins of heterospory during the evolutionary history of the plant kingdom. The number and phylogenetic position of these origins would be most satisfactorily assessed by describing an appropriate range of taxa (preferably species), using as many discrete characters as

Coumiasperma remyi (Gymnospermopsida, *ca.* × 7). (Modified from (*a-c*) Stewart & Rothwell, 1993, figs 11.20*c*, 10.13, 17.8*c*; (*d*) Stubblefield & Rothwell, 1989, fig. 27; (*e-f*) Stewart & Rothwell, 1993, figs 16.8*c*, 22.11*a*; (*g*) Galtier & Rowe, 1991, fig. 6*b*.) For labels see Figure 6.

Zosterophyllopsids

Aste

Drep

Bara
Hupe*

Lyco*

Phyl*

Leci

Stac*

Sela*

Paur

Oxro

Para

Isoe*
Chal

Sigi

Diap

Sync

Hize

Lepn

Leps

Sporophyllata

Ligulata

Heterospora

Rhizomorpha
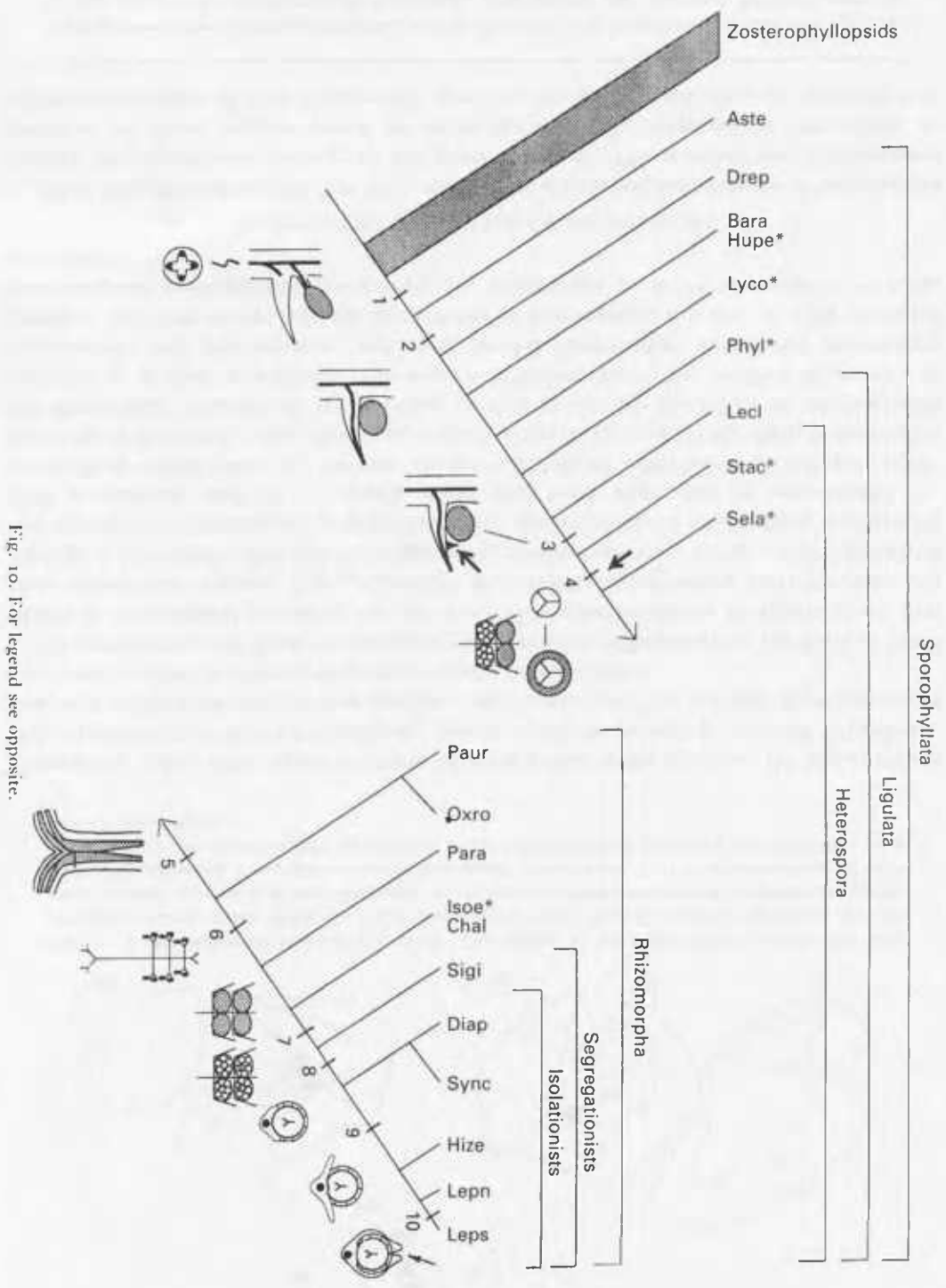
Segregationists

Isolationists

Fig. 10. For legend see opposite.

possible, and subjecting the resulting data to parsimony analysis in order to generate cladograms. Unfortunately, most cladograms published to date have been inappropriate for addressing this question, due to one or more of the following constraints:

(1) The operational taxonomic units (OTUs) were not species but higher taxa, leading to over-generalization of character states and the possibility of scoring as positively correlated two or more character states that did not in reality co-occur in any one species of that higher taxon.

(2) Extinct OTUs were excluded due to *a priori* prejudice against fossils (most cladistic studies: see Bateman, 1992b), so that several major heterosporous groups and some key homosporous taxa phylogenetically linking those groups were inevitably omitted from the analysis.

(3) The OTUs chosen were too closely related, so that all ingroup OTUs were either homosporous (Hill & Camus, 1986) or, more frequently, heterosporous (e.g. Crane, 1985a, b, 1988; Doyle & Donoghue, 1986, 1992; Donoghue, 1989; Donoghue & Doyle, 1989; Bateman, DiMichele & Willard, 1992).

(4) The OTUs chosen were too distantly related or too few in number, so that many heterosporous clades were either represented by only one OTU (thereby eliminating heterospory as a functional synapomorphy) or excluded entirely (e.g. Bateman, 1991a; Kenrick & Crane, 1991).

The three cladistic studies more appropriate for assessing heterospory provided useful information only on the lycophytes (lycopsids plus zosterophyllopsids: Crane, 1990; Bateman, 1992a; Gensel, 1992), the less analytically intimidating of the two main clades of euvascular plants (Fig. 11: see below). All three authors selected, from among several to many most-parsimonious trees, cladograms that showed only a single origin for heterospory within the monophyletic lycopsid (clubmoss) clade, as a synapomorphy of the Selaginellales plus the Rhizomorphales (lepidodendraleans plus isoetaleans: DiMichele & Bateman, 1994), together constituting the most derived portion of the clade (Fig. 10). Other workers (e.g. Chaloner, 1967b, personal communication, 1993) do not perceive the Selaginellales plus Rhizomorphales as monophyletic, and hence would argue for separate origins of heterospory in these two lycopsid orders. Although Crane (1990) and Gensel (1992) analyzed several zosterophyllopsid OTUs, neither

Fig. 10. Composite cladogram of the Lycopsida, showing the acquisition of key characters including single irreversible origins for heterospory, dioicy, type 2 heterosporangy and endospory (4, arrowed), endomegaspory and type 3 heterosporangy (7), monomegaspory (8) and integumentation (10). Full list of character acquisitions: (1) exarch xylem maturation, independent vascularization of microphyll and sporangium, (2) shared vascularization of sporophyll and adaxial sporangium, (3) ligule appears on microphylls and distal to the sporangium on sporophylls, (4) heterospory and heterosporangy, (5) the rhizomorphic syndrome of rhizomorphic rootstocks, determinate bipolar growth, and secondary thickening, (6) the tree habit (absent from some members of the derived clade), (7) segregation of megasporangia and microsporangia into separate cones, and retention of megaspores in megasporangium during dispersal, (8) reduction to a single viable megaspore per megasporangium, (9) lateral expansion of megasporophyll, (10) enclosure of megasporangium by laterally expanded megasporophyll, forming a linear micropyle (arrowed). Extant genera are asterisked; genera listed from left to right: zostero-phyllopsids, *Asteroxylon, Drepanophycus, Baragwanathia, Huperzia, Lycopodium, Phylloglossum, Leclercqia, Stachygynandrum* (heterophyllous *Selaginella*), *Selaginella s.s., Paurodendron, Oxroadia, Paralycopodites, Isoetes, Chaloneria, Sigillaria, Diaphorodendron, Synchysidendron, Hizemodendron, Lepidodendron s.s., Lepidophloios.* (Modified from Bateman, 1992a, figs 15, 16; see also Bateman *et al.,* 1992.)

included any of the heterosporous barinophytaleans. Nonetheless, both authors agreed that the Zosterophyllopsida is likely to be a paraphyletic group that gave rise to the Lycopsida, most probably beginning with the evolution of the paraphyletic group of homosporous lycopsids from a zosterophyllopsid ancester (Fig. 10) (Crane, 1990; Niklas & Banks, 1990; Gensel, 1992; but see Hueber, 1992). Thus, we can be confident that heterospory evolved independently in the barinophytaleans (the earliest acceptable evidence occurring in the Lower Frasnian stage of the Upper Devonian: Pettitt, 1965; Fig. 6c) and the selaginellalean–rhizomorphalean clade (the slightly later Famennian stage of the Upper Devonian: Fairon-Demaret, 1977); at least two origins must be postulated for heterospory in the zosterophyllopsid–lycopsid clade.

To assess the frequency of occurrence of heterospory in the major taxa of the other, far more speciose eutracheophyte clade (Trimerophytopsida–Cladoxylopsida–Sphenopsida–Pteropsida–Progymnospermopsida–Gymnospermopsida), we must for the present turn to the less rigorous, non-numerical phylogeny presented in Figure 11.

The Sphenopsida as delimited here includes two main lineages, the Equisetales (horsetails) and the Sphenophyllales, that probably diverged early in the history of the group (?Frasnian stage of the Upper Devonian: Boureau, 1964; Gensel & Andrews, 1984; Stein, Wight & Beck, 1984). Character compatibility analyses by Stein *et al.* (1984) generated ambiguous results concerning the relationships of these groups to each other and to their putative progenitors, the uniformly homosporous Cladoxylales *sensu lato* (including the 'Hyeniales' and 'Iridopteridales') and Trimerophytopsida (see also Stewart & Rothwell, 1993). Heterospory appears to be restricted to relatively derived equisetalean species. Of the three families, the Archaeocalamitaceae contains at least one heterosporous species (Fig. 7c; Upper Tournaisian stage of the Lower Carboniferous: Bateman, 1991a; Hemsley, Galtier & Clayton, 1994), the Calamitaceae several (e.g. Figs 7b, 8c; Westphalian stage of the Upper Carboniferous: Good, 1975), but the extant Equisetaceae none (e.g. Bierhorst, 1971; Duckett & Duckett, 1980; Duckett & Pang, 1984). Bateman's (1991a, fig. 14) preliminary cladistic analysis of the Sphenopsida included only one relatively derived species of each family, thereby allowing the hypothetical origin of heterosporous calamitaceans from the heterosporous archaeocalamitacean, with a postulated return to homospory in the derived equisetaceans. This is an improbable scenario; it is more likely that heterosporous archaeocalamitaceans and heterosporous calamitaceans evolved independently, from a main lineage of homosporous equisetaleans that eventually gave rise to the uniformly homosporous extant Equisetaceae. Thus, we recognise a minimum of one origin for heterospory in the equisetaleans, but suspect that the true figure is higher, involving several origins that spanned the Carboniferous.

Evidence for low-grade heterospory in some sphenophyllalean species is highly equivocal (Taylor & Taylor, 1992). Although we suspect that heterospory occurred in the group (Thoday, 1906; Thomas & Spicer, 1987), we cannot justify including the Sphenophyllales in our absolute minimum estimate of heterosporic origins (see section V3).

The Pteropsida (ferns) is probably the eutracheophyte class most recalcitrant to morphologically based cladistics, due to lack of structure in character-state distributions and to possible polyphyly of the group (Wagner, 1973, 1987; Lugardon, 1990; Bateman, 1991b; Stewart & Rothwell, 1993). The earliest recorded experiment in
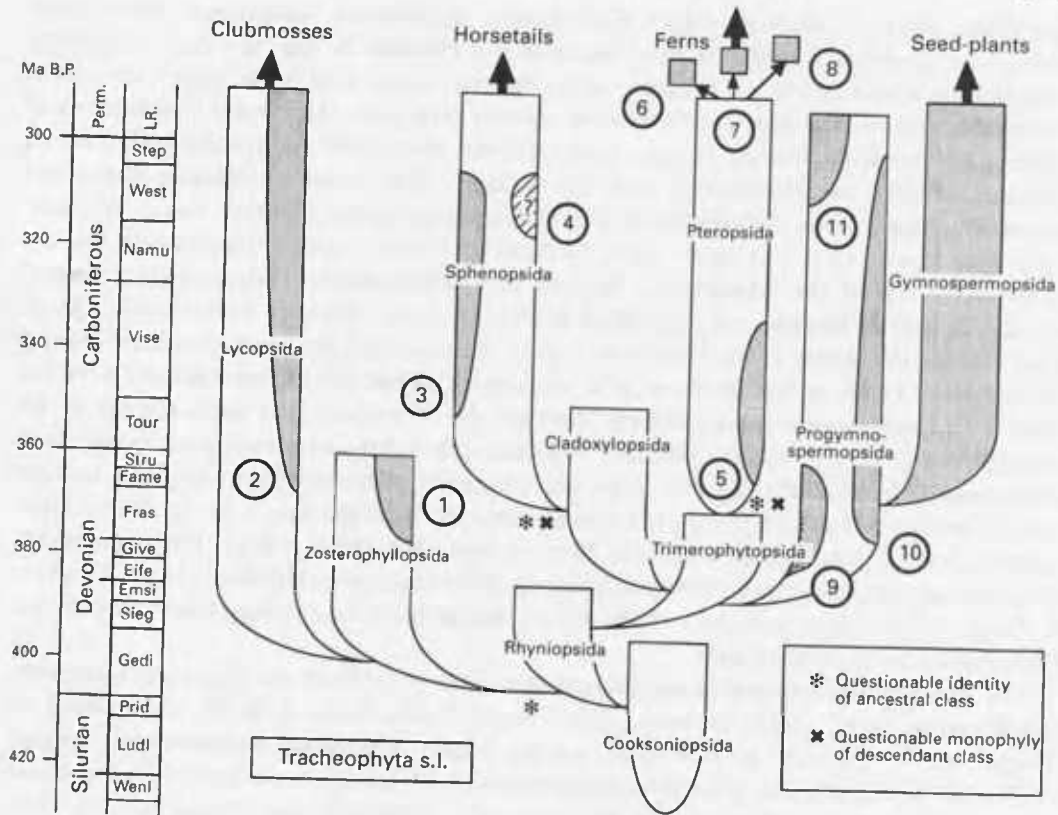
Fig. 11. Tentative non-numerical phylogeny of all tracheophyte classes, showing putative ancestor–descendant relationships and divergence dates; note that the entire class-level radiation occurred within the Devonian. Stippling indicates the minimum number of potentially independent origins of heterospory: (1) some Barinophytales, (2) all Selaginellales and Rhizomorphales, (3) some Equisetales, (4) some Sphenophyllales (doubtful), (5) some Stauropteridales, (6) all Salviniales, (7) all Marsileales, (8) some Filicales (e.g. *Platyzoma**), (9) some Aneurophytales, (10) some Archaeopteridales, ?all Protopityales, all Cecropsidales, (11) some Noeggerathiales. Note that the Gymnospermopsida inherit heterospory from their putative progymnospermopsid ancestor (see also Fig. 12).

heterospory among the pteropsids, *Gillespiea randolphensis*, occurs in the Upper Devonian (Erwin & Rothwell, 1989). *Gillespiea* is the oldest known member of the Stauropteridales, which probably evolved from an early member of the Zygopteridales (e.g. Stewart & Rothwell, 1993). Other heterosporous stauropteridaleans – *Stauropteris berwickensis* (Upper Tournaisian: Long, 1966) and *S. burntislandica* (Fig. 8c; Upper Visean: e.g. Chaloner, 1958; Chaloner & Pettitt, 1987) – evolved during the main pteropsid radiation in the Lower Carboniferous, which generated most of the widely recognized orders of ferns (e.g. Galtier & Scott, 1985; Rothwell, 1987b).

Another two groups of heterosporous ferns appeared during the radiation of the derived filicalean pteropsids in the Cretaceous and Palaeogene. The Salviniales originated in the Upper Cretaceous (Figs 7d–e, h–i; Collinson, 1992; see also Hall, 1969, 1974; Jain, 1971; Collinson, 1980, 1991). The fossil record of the Marsileales is more ambiguous, though it also may date from the Upper Cretaceous (Figs 7f–g;

Dorofeev, 1981; Collinson, 1991). Convergent hydrophilic adaptation rather than common evolutionary origin is now traditionally invoked to explain their numerous morphological similarities (Bierhorst, 1971; Sporne, 1975; Collinson, 1991), though in a brief description of a new heterosporous aquatic fern from the Upper Creataceous of Alberta Rothwell & Stockey (1993: 112) reported characters suggesting 'affinities to Filicales as well as Marsileales and Salviniales'. The most commonly suggested ancestral group of the Salviniales is the Hymenophyllaceae (Bower, 1935; Wagner, 1969; Bierhorst, 1971; Sporne, 1975; Gifford & Foster, 1989). Suggestions for the ancestral group of the Marsileales include the Schizaeaceae (Bower, 1935; Eames, 1936; Thomas & Spicer, 1987; Gifford & Foster, 1989; Stewart & Rothwell, 1993), Lygodiaceae (Wagner, 1969; Bierhorst, 1971), Anemiaceae, Stromatopteridaceae, and Pteridaceae. Thus, in the absence of a phylogeny, separate origins appear likely for these two heterosporous late-comers (though the Marsileales at least appear to be monophyletic: Pryer, 1993). The last example, the subtly heterosporous extant fern *Platyzoma microphylla** (Fig. 6b), lacks a fossil record. Although its sporophyte is more readily recognized as a fern than the aforementioned hydrophiles, it too is a taxonomic enigma, having similarities with the Matoniaceae (Bierhorst, 1971), Gleicheniaceae, Adiantaceae (Sporne, 1975), Polypodiaceae and Schizaeaceae (Holttum, 1956; Duckett & Pang, 1984). Thus, present evidence indicates at least four independent origins for heterospory in the Pteropsida.

The Progymnospermopsida are thought to have evolved from the Trimerophytopsida (Beck, 1970, 1976, 1981; Stewart, 1981; Stein, 1987; Stein & Beck, 1987; Beck & Wight, 1988; Stewart & Rothwell, 1993), which somewhat surprisingly appears uniformly homosporous. Five progymnospermopsid groups have been given ordinal status (Fig. 12): the Aneurophytales (Fig. 6a; Middle–Upper Devonian), Archaeopteridales (Fig. 6d; Upper Devonian), Protopityales (Fig. 6g; Lower Carboniferous), Noeggerathiales (Upper Carboniferous–Lower Permian), and Cecropsidales (Fig. 8d; Uppermost Carboniferous). The range of genera included in the aneurophytales is contentious, and the progymnospermous affinities of the last three orders are not universally accepted. Moreover, the phylogenetic relationships of the orders have not been satisfactorily resolved, though there is general agreement that the Aneurophytales is the most primitive (e.g. Doyle & Donoghue, 1986; Stein, 1987; Stein & Beck, 1987; Stewart & Rothwell, 1993). Life histories have been inferred in only one species each of the Protopityales (Walton, 1957; Smith, 1962a) and the Cecropsidales (Stubblefield & Rothwell, 1989); both were regarded as heterosporous. The other three orders are considered to contain both homosporous and heterosporous species, the earliest evidence of heterospory being the putative aneurophytalean *Chaleuria cirrosa* in the Eifelian stage of the Middle Devonian (Fig. 6a; Andrews *et al.*, 1974; Gensel & Andrews, 1984). (Meyen (1987) argued that *Chaleuria* was attributed to the Aneurophytales tautologically, simply *because* it possessed low-grade heterospory.) If we make the (admittedly contentious) assumptions that (1) all five orders are correctly attributed to the Progymnospermopsida, (2) none of the five orders is polyphyletic (i.e. has multiple evolutionary origins), (3) three of the five orders contain homosporous species, and (4) heterospory is both derived and irreversible, a minimum of three origins is required for heterospory within the Progymnospermopsida, irrespective of the phylogenetic relationships of the orders. However, if we argue that (1) current
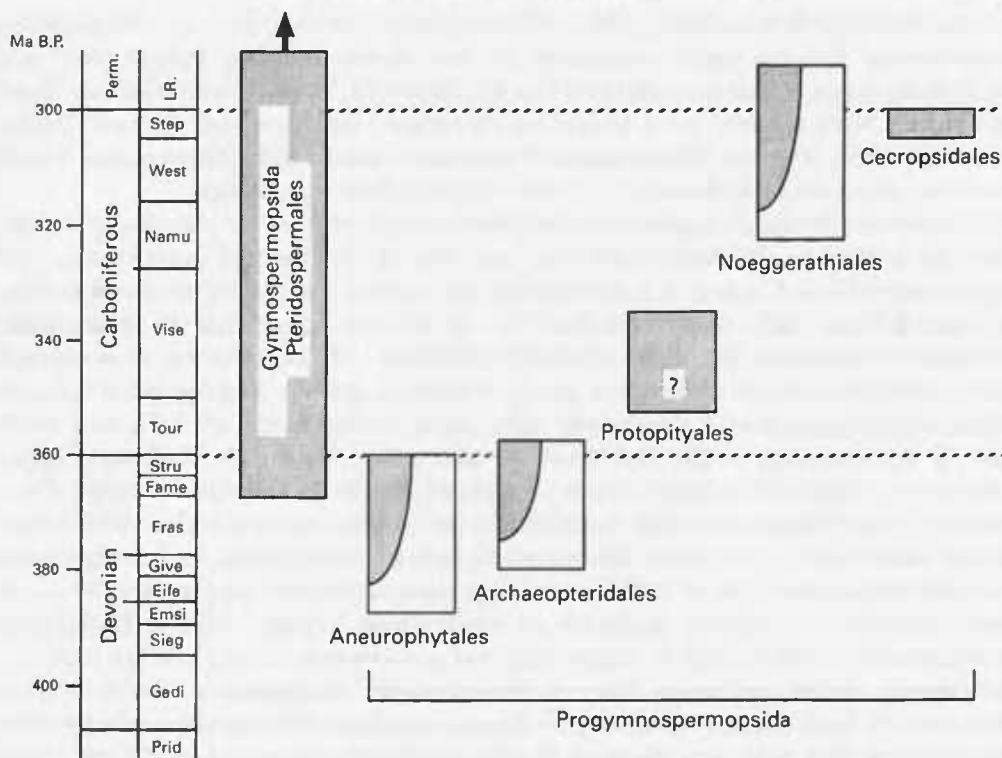
Fig. 12. Tentative non-numerical phylogeny and known stratigraphic ranges of the five progymno-spermopsid orders plus the gymnospermopsids, with heterospory indicated by stippling. The uncertain phylogenetic relationships of these lineages prevent direct assessment of the number of origins of heterospory within the group.

evidence is ambiguous and in fact only the Aneurophytales contains any homosporous species, and (2) the three Carboniferous orders all radiated from the Archaeo-pteridales, despite the apparent stratigraphic discontinuities above and below the Protopityales (Fig. 12) (cf. Beck, 1981), then in theory one origin in the Aneurophytales could explain heterospory throughout the Progymnospermopsida and Gymnospermopsida. Admittedly, this most parsimonious scenario is improbable.

The Gymnospermopsida is here delimited unusually broadly to encompass all seed-plants, including the angiosperms; it is equivalent to the Spermatophyta of Donoghue & Doyle (1989). A vigorous, long-running debate on whether the Gymnospermopsida *sensu lato* is monophyletic (Long, 1966, 1975; Rothwell, 1985, 1986; Crane, 1985 *a*, *b*; Doyle & Donoghue, 1986; Rothwell & Scheckler, 1988; DiMichele *et al.*, 1989; Patterson, Williams & Humphries, 1993; Rothwell & Stewart, 1993; Stevenson, 1993) or polyphyletic (Andrews, 1961; Smith, 1964; Chaloner, Hill & Lacey, 1977; Beck, 1981, 1985; Stewart, 1981; Meyen, 1984; Beck & Wight, 1988; Galtier & Rowe, 1989; Chaloner & Hemsley, 1991) has been further fuelled by recent discoveries of small pteridospermalean ovules in the Famennian stage of the Upper Devonian (e.g. Pettitt & Beck, 1968; Chaloner *et al.*, 1977; Gillespie *et al.*, 1981; Fairon-Demaret & Scheckler, 1987; Galtier & Rowe, 1989; Rowe, 1992) that imply a Frasnian origin for

the clade (Rothwell & Scheckler, 1988). With regard to ovule morphology, the strongest synapomorphy for the early seed-plants is the pollen-receiving lagenostome and associated hydrasperman reproduction (Fig. 8f; Rothwell, 1986). Competing assertions of polyphyly have focused on a perceived divergence between radiospermic ovules possessing three or more integumentary vascular strands and platyspermic ovules possessing only two such strands (cf. Meyen, 1984; Rothwell, 1986).

All of the competing phylogenetic hypotheses concurred that the Archaeopteridales is derived relative to the Aneurophytales, and that one or both of these two earliest progymnospermopsid orders is implicated in the origin(s) of the Gymnospermopsida (e.g. Stein & Beck, 1987, fig. 3) (see also Fig. 12). All also agreed that the lyginopterid pteridospermaleans are the most primitive members of the putative radiospermic lineage. Several authors favoured a single transition from a homosporous aneurophytalean to a lyginopterid (Rothwell, 1982, 1985, 1986; Rothwell & Erwin, 1987; Rothwell & Scheckler, 1988; DiMichele *et al.*, 1989; Stewart & Rothwell, 1993), whereas two cladistic analyses (Crane, 1985*a, b*; Doyle & Donoghue, 1986, 1992; Donoghue, 1989) implied a single transition from a heterosporous archaeopteridalean ancestor. Beck (1976, 1981, 1985) advocated diphyly for seed-plants, suggesting that an aneurophytalean gave rise to radiospermic gymnospermopsids and an archaeopteridalean generated a separate ginkgoalean–coniferalean lineage. Meyen (1984) also hypothesized seed-plant diphyly, suggesting that pteridospermaleans bearing cupulate, radiospermic ovules and those bearing non-cupulate, platyspermic ovules evolved independently from separate archaeopteridalean ancestors; the radiospermic pteridospermaleans in turn generated the more derived orders of seed-plants (cf. Crane, 1988).

Table 3 shows that a positive correlation has yet to be demonstrated between platyspermy and direct, non-cupulate attachment to the parent frond; we suspect that the early radiation of ovule morphologies was more complex and less linearly directional than a single radiospermic–platyspermic divergence (Rothwell, 1986; DiMichele *et al.*, 1989; *contra* Andrews, 1963; Meyen, 1984). Other probable red herrings introduced into recent debates include the appearance in the fossil record of platyspermic ovules soon after radiospermic ovules (e.g. Chaloner *et al.*, 1977; Thomas & Spicer, 1987), and the discovery of a single ovule with a non-functional, parenchyma-filled beak rather than a well differentiated lagenostome (*Coumiasperma remyi*: Galtier & Rowe, 1989, 1991; Fig. 8*g*). First, further specimens of *Coumiasperma* are needed to demonstrate that it is not teratologous, analogous to the abnormally bisexual *Pullaritheca* cupule described by Long (1977*a*) (Fig. 9). Secondly, the morphology of *Coumiasperma* may be derived despite its simplicity (i.e. paedomorphic), merely reflecting the ecologically specialized aquatic pollination inferred for the ovule by Galtier & Rowe (1989, 1991). Thirdly, even if *Coumiasperma* proved to be primitive, it could be readily intercalated between a progymnospermopsid ancestor and the more derived lagenostomalean ovules listed in Table 3. Although *Coumiasperma* is somewhat younger than several other ovule genera, first appearances in the fossil record have proved to be poor indicators of phylogenetic relationships at narrow time-scales (e.g. Doyle & Donoghue, 1986; Bateman *et al.*, 1992). Thus, these recent discoveries are consistent with seed-plant monophyly. Assertions of polyphyly should focus less on relationships among seed-plants and more on demonstrating that they are linked to more than one progymnospermopsid ancestor. To date, this question has not been

properly tested cladistically. The progymnospermopsids were treated as outgroups, being included primarily to polarise the far more numerous seed-plant OTUs; the full range of potential gymnospermopsid ancestors was not made available for comparison. Also, no Devonian or Lower Carboniferous pteridospermalean has yet been fully reconstructed; satisfactory phylogenies cannot be obtained from data describing only partial plants (Bateman, 1992*b*, *c*, 1994).

Some authors (e.g. Doyle & Donoghue, 1986) argued that the aneurophytaleans are uniformly homosporous, and that the Rothwell hypothesis therefore requires that the origin of seed-plants should coincide with yet another origin of heterospory. However, low-level heterospory has been inferred in some putative aneurophytaleans, such as *Chaleuria* (Fig. 6*a*; Andrews *et al.*, 1974; Gensel & Andrews, 1984; Taylor & Taylor, 1992; Stewart & Rothwell, 1993) and *Tetraxylopteris* (Bonamo & Banks, 1967; Thomas & Spicer, 1987), rendering feasible the inheritance of heterospory by the seed-plants from an aneurophytalean ancestor. The argument for the inheritance of heterospory by the earliest seed-plant is stronger for the Beck hypothesis, as many *Archaeopteris* species show clear-cut heterospory (Fig. 6*d*; Arnold, 1939; Beck, 1960; Pettitt, 1965, 1970; Phillips *et al.*, 1972; Chaloner & Pettitt, 1987; Chaloner & Hemsley, 1991). In summary, the Gymnospermopsida is the only uniformly heterosporous class. The origin of the class could have coincided with an independent origin for heterospory, but it is more likely that heterospory was inherited from a progymnospermopsid ancestor.

To conclude, of the ten tracheophyte classes shown in Fig. 11, four (the two earliest classes of tracheophyte, plus the two earliest classes of the non-lycophyte eutracheophyte clade) appear to be uniformly homosporous and one (the uniformly heterosporous Gymnospermopsida) probably inherited heterospory rather than acquiring it *de novo*. Heterospory originated at least once in each of the five remaining tracheophyte classes (Zosterophyllopsida, Lycopsida, Sphenopsida, Pteropsida, Progymnospermopsida), though it does not delimit any of them; all include many homosporous species. We are confident that there were at least four separate origins of heterospory in the Pteropsida, giving an *absolute* minimum number of independent origins of heterospory in tracheophytes of *eight*. At least two origins are also highly likely in the Sphenopsida and three in the Progymnospermopsida, yielding a more realistic minimum of *eleven* origins.

Each future discovery of a new heterosporous species could in theory either increase these figures (if the new species is only distantly related to known heterosporous groups) or decrease these figures (if the new species ties together two or more heterosporous groups previously regarded as polyphyletic, thereby giving them a common origin; the most promising example would be the future discovery of a heterosporous trimerophytopsid). Decreased estimates of the number of origins are unlikely, because (1) heterospory consistently appears *within* major clades rather than coinciding with their origin (i.e. it does not delimit those clades as a ubiquitous synapomorphy), and (2) no evidence (phylogenetic or otherwise) has accrued to suggest that heterospory is wholly reversible; once a lineage becomes heterosporous it stays heterosporous (but see below). Moreover, the current popularity of phylogenetic analyses will eventually allow sufficient cladograms to accrue to assess not the *minimum* number of origins but the *actual* number, as heterospory-related characters are forced to compete with other characters for the privilege of being depicted as non-homoplastic

in the most parsimonious overall solutions to character conflicts. We predict that considerably more than eleven independent origins of heterospory will eventually be inferred among the tracheophytes.

V. INTER-CLADE COMPARISON OF LEVELS OF HETEROSPORY

Thus far, we have fragmented heterospory into a suite of more narrowly defined evolutionary innovations, outlined several methods of detecting such innovations, and noted their highly iterative evolution across the plant kingdom. Here, we integrate those themes in order to compare the ranges of heterosporous phenomena exhibited by different lineages, paying particular attention to the members of each lineage that show the greatest number of derived reproductive features. Brief reviews of many of the following heterosporous taxa are presented in texts on comparative plant morphology, both palaeobotanical (Andrews, 1961; Emberger, 1968; Meyen, 1987; Thomas & Spicer, 1987; Taylor & Taylor, 1992; Stewart & Rothwell, 1993) and neobotanical (Corner, 1964; Bierhorst, 1971; Sporne, 1974, 1975; Bold et al., 1987; Gifford & Foster, 1989; Bell, 1992).

(1) Zosterophyllopsida

Evidence of heterospory in the wholly extinct zosterophyllopsids is confined to a few barinophytaleans from the Upper Devonian of Euramerica (Meyen, 1987; Taylor & Taylor, 1992), notably Protobarinophyton pennsylvanicum (Brauer, 1981; Cichan et al., 1984), Barinophyton richardsonii (Pettitt, 1965), and B. citrulliforme (Fig. 6c; Arnold, 1939; Pettitt & Beck, 1968; Pettitt, 1970; Brauer, 1980; Taylor & Brauer, 1983; Cichan et al., 1984; Thomas & Spicer, 1987; Stewart & Rothwell, 1993). They share similarly low levels of megaspore–microspore differentiation. Several megaspores and many microspores coexist in the same sporangium (category 1), typically separated by a five- to twenty-fold difference in size. Differences in morphology and wall ultrastructure reported by Cichan et al. (1984) do not appear especially profound.

Thus, the only concrete evidence of heterospory in the zosterophyllopsids is category (1) anisospory; the group has not developed heterosporangy. It has been assumed that the presence of heterospory implies the presence of dioicy and the absence of heterosporangy implies the absence of endospory, so that the barinophytaleans have become recognized as one of the classic examples of 'incipient heterospory' (e.g. Pettitt, 1970; Cichan et al., 1984). However, this group cannot be used to demonstrate that the development of dimorphic spores preceded the development of dimorphic sporangia, as (1) no known barinophytalean successfully evolved such sporangia and (2) the group is not believed to have generated any heterosporous descendants.

(2) Lycopsida

In contrast, with one notable (and almost certainly derived) example described below, category (1) heterospory is absent from the lycopsids, despite their remarkably good fossil record and the survival to the present day of three major lineages (Fig. 10). Rather, a clear-cut transition from homospory to category (2) heterospory separates the most derived homosporous lycopsid, Leclercqia complexa (Banks et al., 1972; Grierson & Bonamo, 1979) from the most primitive heterosporous lycopsids of the Selaginellales (cf. Bateman, 1992a; Gensel, 1992; Thomas, 1992).

Indeed, heterosporous reproduction in the uniformly non-woody Selaginellales and

more primitive portion of the uniformly wood-producing Rhizomorphales (up to and including the tree *Paralycopodites* on Fig. 10) can be generalized. This group includes the earliest heterosporous lycopsids such as the Upper Devonian *Barsostrobus famennensis* (Fairon-Demaret, 1977) and *Cyclostigma kiltorkense* (Chaloner, 1968). Sporangia are aggregated into bisexual cones, typically with basally concentrated megasporangia (though segregation from microsporangia is imperfect in some species, e.g. Fig. 7a). Spore size, ornamentation and ultrastructure vary greatly among species, but all show strong dimorphy in all of these parameters (cf. Figs 6e, f). Several megaspores occur in each megasporangium, though in many species only one survives to generate a tetrahedral tetrad of megaspores (Figs 8a–b). Extant selaginellaleans are generally regarded as generating a single tetrad of viable spores per megasporangium (e.g. Fig. 6f), though detailed studies (e.g. Duerden, 1929; Hemsley, 1993) show that more than one tetrad can reach maturity in some sporangia (over 20 % in *S. lobbii*), whereas in other species apparently *ad hoc* abortions within tetrads typically leave only one (*S. willdenowii*) or two (*S. lobbii*, *S. erythropus*) viable megaspores per megasporangium.

The Selaginellales includes species that together possess several specialized mechanisms for active dispersal of microspores (Koller & Scheckler, 1986) and megaspores (Page, 1989). Megagametophytes are largely endosporic, relying on food reserves traceable to the parental sporophyte, though archegonia and/or rhizoids often project through the triradiate suture. Megaspore wall ornamentation in general and laesural ornamentation in particular often allows the entrapment and transport of microspores produced by the same sporophyte, thereby increasing the chances of pollination but at the expense of probable autogamy (Phillips, 1979; Bateman, 1992a). Once fertilized by a biflagellate spermatozoid, the embryonic sporophyte develops rapidly.

Subsequent evolution within the rhizomorphic lycopsids led to progressively increased reproductive sophistication (Fig. 10) (Phillips, 1979; Bateman *et al.*, 1992). Segregation of megasporangia and microsporangia into separate unisexual cones allowed modification of the megasporophyll–megasporangium complex without necessarily including potentially maladaptive, developmentally parallel changes in the microsporophylls. *Sigillaria*, the most primitive genus in this group, shed several megaspores within the megasporangium, which in turn remained attached to the megasporophyll. This aggregate dispersal unit may subsequently have fragmented (Phillips, 1979). Access of spermatozoids to the female gametophyte was blocked by subarchesporial parenchyma adhering to the proximal pole of the megaspore; thus, the presence of putative embryos in plugged megaspores led Phillips & DiMichele (1992) to infer apoximis.

The remainder of the clade is characterized by retention of the megaspore in the megasporangium during pollination, fertilization and embryogeny as well as dispersal. This strategy required abortion not only of all but one megasporocyte but also of three of its four meiotic products, leaving a single functional megaspore plus three abortive megaspores in a tetrahedral tetrad (Pettitt, 1970, 1971; Phillips, 1979; Chaloner & Hemsley, 1991; Hemsley, 1993). The abortive megaspores are very small in the genera included in Figure 10, but somewhat larger in *Caudatocorpus* (Brack-Hanes, 1981; Hemsley & Bartram, 1991). Even less well understood but even more intriguing are

isolated tetrads of putative lycopsid megaspores assigned to the Lower Carboniferous spore-species *Subcystosporites barbatus* (Hemsley, 1993). These apparently show the two fertile plus abortive megaspore pattern that is characteristic of the early pteropsid *Stauropteris* (see section V4), but with the added complexity of a size disparity between the two putatively fertile spores in each tetrad. It is tempting to place *Subcystosporites* between *Sigillaria* and *Caudatocorpus* in a linear evolutionary sequence (Hemsley, 1993). However, this cannot be justified in the absence of further knowledge of the parent plants of *Subcystosporites* and *Caudatocorpus* (Bateman, 1992 b, c). Also, the rarity of *Subcystosporites* implies that it may be a developmental anomaly, analogous to those described above for extant selaginellaleans (Hemsley, 1993).

Once megaspores had been reduced to a single functional unit per megasporangium, their ornamentation no longer served any adaptive function and was lost in at least most derived species (Bateman *et al.*, 1992; Hemsley, 1993); similarly, megaspore wall thickness decreased despite concomitant increases in megaspore size that reached 10 mm in some species (Chaloner & Hemsley, 1991, fig. 8.6). The proximal portions of the sporophylls expanded laterally, eventually becoming enrolled around the megasporangium to form an integumentary structure in the most reproductively sophisticated genus, *Lepidophloios* (Fig. 8 a). Spermatozoids were permitted access to the megaspore only by a linear micropylar aperture (Scott, 1901; Phillips, 1979; Thomas, 1981; Stewart & Rothwell, 1993). The resulting disseminule, termed an aquaearp by Phillips & DiMichele (1992), strongly resembles early pteridospermalean ovules (cf. Figs 8 a, f; see below). However, unlike *bona fide* ovules, aquaearps were probably pollinated after dispersal rather than retained on the parental sporophyte; they are well adapted for aquatic pollination and dispersal of the resulting embryo (Phillips, 1979; Chaloner & Pettitt, 1987). The less well known *Miadesmia membranacea* (Fig. 8 b; Benson, 1908; Hemsley, 1993) provides an interesting comparison with *Lepidophloios*. It also possessed a single unornamented megaspore in each megasporangium, in turn encased by lappet-like and filliform elongations of both the proximal and distal portions of the sporophyll. Together, these elongations formed a micropylar structure that probably evolved independently of the superficially similar structure in *Lepidophloios*. The small size of the megaspores (*ca.* 800 μm) compares more closely with selaginellaleans than *Lepidophloios*. Overall, the most derived Upper Carboniferous lycopsids were at least as reproductively advanced as contemporaneous seed-plants (Chaloner & Pettitt, 1987).

The extant *Isoetes** is generally regarded as a descendant of Carboniferous tree lycopsids (Mägdefrau, 1956; Bateman *et al.*, 1992; Pigg, 1992; Bateman, 1994). Most species of *Isoetes**, like their putative progenitors such as *Chaloneria* (Pigg & Rothwell, 1983), are strongly heterosporous. Moreover, megasporangia and microsporangia are usually segregated both spatially and temporally; the microsporangia mature later in the season, encouraging allogamy. However, at least two extant species of *Isoetes** reputedly show category (1) anisospory; megaspores and microspores develop in the same sporangium (Goswami & Arya, 1968; Thomas & Spicer, 1987). If so, this almost certainly represents reversal of the more sophisticated reproductive strategy evident in most isoetaleans; these species merit further study.

(3) *Sphenopsida*

The earliest heterosporous equisetalean is the Tournaisian *Protocalamostachys farringtonii*, an archaeocalamitacean cone (Bateman, 1991 *a*; Hemsley *et al.*, 1994). Several megaspores and many microspores developed in different sporangia but on the same sporangial cluster (Fig. 7*c*). There is a five- to ten-fold size difference between the two spore genders (Fig. 4), though the megaspores are relatively small, variable in size within sporangia, and in morphology are broadly similar to the microspores. Thus, heterosporangy was attained, but it is unlikely that the female gametophytes were endosporic or dispersed within the sporangium.

Several calamitacean cones from the Upper Carboniferous of Euramerica show evidence of low-grade heterospory (Good, 1975): examples include *Calamostachys americana* (Fig. 7*a*; Arnold, 1958), *C. casheana* (Williamson & Scott, 1894; Lacey, 1941), *C. thompsonii* (Darrah, 1936), *Paracalamostachys* (? = *Calamostachys*) *spadiciformis* (Thomas, 1969), and *Palaeostachya andrewsii* (Baxter, 1955, 1962). They resemble *P. farringtonii* in having limited differentiation between megaspores and microspores; typically, both have triradiate sutures and perispores but little surface ornamentation. Elaters are reliably absent from megaspores but have been reported on microspores of three of the species listed above. Megaspores are two to four times the diameter of the microspores (typically 60–120 μm: 150–400 μm, e.g. Fig. 3*b*) and show greater intrasporangial variation in size. Several megasporocytes produce viable megaspore tetrads in each megasporangium, and megasporangia are far less common than microsporangia. Unlike *P. farringtonii*, each sporangiophore typically bears only one gender of sporangium (Fig. 7*a*). Most cones show segregation (albeit sometimes imperfect) of basally concentrated megasporangiophores and apically concentrated microsporangiophores, though Good (1975) suggested that *C. thompsonii* and *P. andrewsii* were capable of generating unisexual cones. Considered together, these calamitaceans show heterosporangy but not monomegaspory; thus, endospory and endomegasporangy are also unlikely. A similarly low level of heterospory has been reported in the Mid-Permian schizoneuran cone *Echinostachys cylindrica* (Grauvogel-Stamm, 1978; Meyen, 1979).

The one intriguing exception to low level heterospory is the much-discussed *Calamocarpon insignis* (Fig. 8*e*; Baxter, 1963, 1964; Leisman & Bucher, 1971; Good & Taylor, 1974; Good, 1975). This also has elater-bearing microspores that otherwise broadly resemble the megaspores. However, each megasporangium contains only one large (2–3 mm), elongate viable megaspore, whereas the microspores are unusually small for a calamitacean (30–60 μm). The two genders of sporangium were usually but not invariably borne separately on unisexual cones (Good, 1975). Some dispersed megasporangium–megaspore units contain well developed megagametophytes (Baxter, 1964), implying that they were not only monomegasporangiate but also endomegasporangiate, and thus broadly comparable in sophistication with contemporaneous rhizomorphalean lycopsids such as *Lepidodendron* (Figs 10, 13) (Baxter, 1963).

Authors have long speculated on possible heterospory in Upper Carboniferous sphenophyllaleans. Noting wide intraspecific ranges for spore sizes and upper limits of *ca.* 150 μm, approaching the 200 μm lower size threshold for megaspores, Thomas & Spicer (1987) hypothesized that low-grade heterospory may have occurred in

Sphenophyllum tenerrimum and *Bowmanites dawsonii*. The original case for low-grade heterospory in *B. dawsonii* was made by Thoday (1906, fig. 14), who noted mean spore diameters of 83 μm and 106 μm in adjacent sporangia; individual spores reached 135 μm. Thoday also reported that the largest spores shared sporangia with many abortive spores, and occurred towards the base of the cone – features that indicate megaspore development. However, Taylor & Taylor (1992: 312) argued that the larger spore measurements misleadingly included the perispore (see also T. Taylor, 1969; W. Taylor, 1986). Superficially, much the most convincing example of a heterosporous sphenophyllalean was *Bowmanites delectus* (Arnold, 1944, 1947). Unfortunately, this cone proved to belong to a noeggerathialean progymnosperm, and so was transferred to the cone-genus *Discinites* in 1949 by Arnold. Although ' *B.* ' *delectus* continues to be cited erroneously as a clearly heterosporous sphenophyllalean (e.g. Sporne, 1975; apparently also Meyen, 1987), the present case for heterospory in the group must be deemed credible but unproven.

(4) *Pteropsida*

The earliest heterosporous pteropsids were extinct stauropteridalean 'pre-ferns'. The Upper Devonian *Gillespiea randolphensis* (Erwin & Rothwell, 1989) bore fusiform eusporangia both laterally and terminally. Microsporangia have not been found; megasporangia are 0·4–1·0 mm long and are believed to contain one or two viable megaspores *ca.* 160 μm in diameter. By the Lower Carboniferous, *Stauropteris berwickensis* (Long, 1966; Bateman & Rothwell, 1990) and *S. burntislandica* (Fig. 8c; Surange, 1952; Chaloner, 1958; Chaloner & Pettitt, 1987; Hemsley, 1990; Chaloner & Hemsley, 1991) had evolved a unique megaspore configuration that is best understood from dispersed tetrads (Chaloner, 1958). Within each megasporangium, a single megasporocyte produced a tetrad of spores surrounded by a tapetal membrane (Hemsley, 1990, 1993), but rather than all four megaspores being viable or three being aborted, two viable megaspores developed, ten times the diameter of their adherent aborted sisters. Developmental control was imperfect, as occasionally three megaspores remained viable. Reports of larger spore numbers (Sporne, 1975; Meyen, 1987) are doubtful (Taylor & Taylor, 1992). Relative to *S. berwickensis*, *S. burntislandica* had larger megasporangia (*ca.* 0·5 mm: 1·3 mm), larger megaspores (*ca.* 175 μm: 225 μm), and possessed abundant parenchyma in the proximal portion of the sporangium. The much less common microsporangia attributed to *S. burntislandica* are smaller (*ca.* 0·6 mm), globose, and contain many triradiate microspores *ca.* 30 μm in diameter. The rarity of dehisced megasporangia, apparent lack of an obvious dehiscence mechanism, and tendency of functional and non-functional megaspores to persist as dispersed tetrads are circumstantial evidence of megaspore retention (Chaloner, 1958; Long, 1966; Haig & Westoby, 1989; *contra* Taylor & Taylor, 1992).

Even more attention has been paid to the phylogenetically ambiguous and ecologically specialized water-ferns of the Salviniales and Marsileales. The former in particular are well represented in the fossil record following their first appearance in the Upper Cretaceous (Collinson, 1990, 1991). The Salviniales are represented by the extant genera *Salvinia** and *Azolla**. Sporophytes of both genera are adapted for flotation on the surface of freshwater bodies, and both protect the subaqueous sporangia in sterile

laminae that are termed sporocarps. In these genera, the sporocarp is regarded as the homologue of the soral indusium of terrestrial leptosporangiate ferns (Gifford & Foster, 1989).

A single leaf of *Azolla** generally bears both small sporocarps containing a single megasporangium and large sporocarps containing several microsporangia (Figs 7*h–i*). Occasional bisporangiate sporocarps also occur (Sporne, 1975), notably in the Upper Cretaceous *Azinia* (Balueva, 1964) and Eocene *Azolla primaeva* (Hills & Gopal, 1967). Only one megasporocyte develops in each megasporangium and three of the four meiotic products abort to leave a single megaspore that is typically 300–400 μm in diameter (Fig. 7*h*). Both genders of spore mass are surrounded by tapetally derived mucilagenous periplasmodium. In the megasporangium this becomes localized into several proximally concentrated massulae that delimit a central cylindrical cavity and act as buoyancy aids. These in turn are enclosed by the distal portion of the sporangium, which dehisces along with the megaspore–massular unit and protects the female gametophyte. Each microsporangium releases several spherical massulae that bear both microspores and hook- or anchor-like glochidia. Once dispersed in the water column, *ad hoc* encounters of a microsporangial mass and a megasporangial unit lead to their adhesion via the glochidia (Fig. 7*i*) and subsequent fertilization by motile spermatozoids.

In *Salvinia**, both genders of sporocarp are of equal size (Fig. 7*d*). Several sporocarps are borne on each modified leaf; the most proximal contains several large megasporangia, whereas the remainder contain many smaller microsporangia borne on a repeatedly dichotomous framework (again, some bisexual sporocarps have been reported: Bierhorst, 1971; Meyen, 1987). Each megasporangium contains only one viable megaspore (Fig. 7*e*; typically the surviving product of eight megasporocytes: Bierhorst, 1971), surrounded by a thick cellular perispore that bears a remarkable resemblance to the integument of a pteridospermalean ovule (*q.v.*). Each microsporangium encloses a single massula containing the products of 8–16 microsporocytes. The microspores produce spermatozoids while still enclosed by the sporangium; similarly, the female gametophyte eventually protrudes from the megasporangium but remains enclosed during fertilization and the subsequent development of the sporophyte. Sporocarps are eventually released by passive tissue decomposition (e.g. Hossain, 1971).

The three extant genera of the Marsileales, *Marsilea**, *Regnellidium**, and *Pilularia**, are typically rhizomatous freshwater marginals rather than true aquatics. They share a similar productive biology. Like the Salviniales, they bear several unisexual sporangia encased in sterile laminae that are termed sporocarps (Fig. 7*g*). However, the marsilealean sporocarp appears an unlikely homologue with the indusium-derived salvinialean sporocarp – rather, it is homologous with either a pinna (Bower, 1923) or an entire megaphyll (Eames, 1936). Bierhorst (1971) offered a more complex explanation for the origin of the marsilealean sporocarp that involved a saltational change in its developmental trajectory. Similar structures were reported in an apparently more primitive heterosporous water-fern by Rothwell & Stockey (1993). Marsilealean sporocarps are borne singly or in a small cluster on a non-laminate framework that is attached at or near the base of a petiole. The adaxial surface of each modified pinna encloses several more-or-less paired elongate sori. Each sorus is in turn

enclosed by a membranous indusium attached to the gelatinous sporophore, and supplied by vascular traces emitted from the mid-vein of the sporocarp, which overlies the sporophore. Within the sorus, the linear receptacle bears several small lateral microsporangia and a smaller number of much larger terminal megasporangia, all leptosporangiate. As in the Salviniales, both genders of sporangia contain the meiotic products of 8–16 sporocytes. Only one large megaspore remains viable in each megasporangium (Fig. 7h), bearing a proximal gelatinous mass that channels spermatozoids to the single prominent archegonium (Fig. 7f). The sclerotic sporocarps are well adapted for long-term desiccation resistance (Bierhorst, 1971). Upon rehydration, the sporophore expands greatly and unequally, curving back on itself. This action drags the sori out of the sporocarp and into the water column (the sporocarps of *Pilularia** merely fragment), allowing fertilization of the archegonia by large motile spermatozoids from adjacent microsporangia (Myles, 1978). The zygote develops on the female gametophyte, which remains within the megasporangium wall.

The sophisticated heterospory evolved by these low-diversity ecological specialists contrasts strongly with the homosporous tendencies of the filicaleans that dominate modern pteridophytic floras, though admittedly the life histories of few species have been investigated in detail (e.g. Lloyd, 1974; Bell, 1979; Dyer & Page, 1985; Haig & Westoby, 1988b; Karpelainen, 1994). Where heterospory has been detected it is low-grade and subtlely expressed. In the best known example, *Platyzoma microphylla**, spore gender differentiation occurs among rather than within sporangia (*contra* Thomas & Spicer, 1987). Some sporangia produce *ca.* 32 spores that average *ca.* 85 μm in diameter and consistently generate exclusively antheridial, filiform gametophytes. Although spore size ranges are large (Andrews *et al.*, 1974), other somewhat larger sporangia contain *ca.* 16 spores that average *ca.* 175 μm in diameter and consistently generate sequentially monoicous, spathulate gametophytes (Fig. 6b; Tryon, 1964; Tryon & Vida, 1967; Bierhorst, 1971; Andrews *et al.*, 1974; Sporne, 1975; Duckett & Pang, 1984). We strongly believe that other filicaleans possess similarly subtle heterospory or, even more problematically, dioicy that does not reflect spore bimodality (analogous to that observed in *Ceratopteris**: Schedlbauer, 1976; Duckett & Pang, 1984).

(5) *Progymnospermopsida*

The extinct progymnospermopsids are more effectively discussed in the relative order of appearance in the fossil record of five constituent orders (Fig. 12).

The earliest heterosporous species attributed to the aneurophytaleans is the Eifelian *Chaleuria cirrosa* (Fig. 6a; Andrews *et al.*, 1974), arguably the oldest evidence of heterospory in any plant lineage (Fig. 11). Reported spore size distributions are so complex that a more rigorous statistical analysis is desirable. The fusiform sporangia often contain a mixture of putative microspores and megaspores, though one gender dominates each sporangium. Microspores range from 30–48 μm in diameter. Megaspores are 60–156 μm in diameter; within this range they are bimodal, peaking at 60–75 μm and 120–130 μm (Andrews *et al.*, 1974). Morphological differences between megaspores and microspores appear relatively trivial; most may merely reflect the greater ontogenetic expansion of the megaspores. Interpretation of the development of such a complex distribution of spore sizes is problematic, and the correct identification

of any inviable spores becomes crucial. *Chaleuria* presumably exhibited free-sporing heterospory analogous to that of *Platyzoma**.

The penecontemporaneous *Enigmophyton superbum* (Høeg, 1942; Vigran, 1964) is also a putative aneurophytalean, though the associated heterosporous sporangia have not been found in organic connection with the rather incongruent foliar organs and may instead belong to the co-occurring heterophyllous zosterophylopsid *Barinophyton* (Andrews, 1961; Pettitt, 1970). Megasporangia contain several megaspores up to 250 µm in diameter, whereas microsporangia contain many spores 60–85 µm in diameter. The wide range of spore sizes (73–176 µm) recorded in another, better known aneurophytalean, *Tetraxylopteris schmidtii* (Bonamo & Banks, 1967), led Thomas & Spicer (1987) to infer low-grade heterospory (though this interpretation was questioned by Taylor & Taylor, 1992). Thus, all records of heterospory in the Aneurophytales are equivocal, due to inconclusive evidence for either heterospory itself or the taxonomic assignment of the heterosporous species.

No such ambiguities surround the occurrence of heterospory in the Upper Devonian archaeopteridaleans. These include *Archaeopteris latifolia* (Fig. 6*d*; Arnold, 1939; Pettitt, 1965; Chaloner & Pettitt, 1987; Chaloner & Hemsley, 1991), *A. halliana* (Arnold, 1939; Phillips *et al.*, 1972), *A. macilenta* (Beck, 1960; Phillips *et al.*, 1972), and *A.* cf. *jacksonii* (Pettitt, 1965, 1970; Phillips *et al.*, 1972). All have adaxial fusiform eusporangia averaging 2–3 mm long. Medyanik (1982, fig. 1) inferred anisospory akin to that of *Chaleuria* in his *Archaeopteris* sp. C on the basis of a single sporangium containing both megaspores and microspores, but Chaloner & Pettitt (1987) suggested that Medyanik's observation reflects only post-mortem infiltration of microspores into a dehisced megasporangium; all other known archaeopteridalean sporangia contain only one spore gender. Megasporangia and microsporangia are typically equal in average length, though the former can be distended radially by the enclosed expanding megaspores. Microsporangia contain several hundred microspores, ranging in average size from *ca.* 30 µm in *A. halliana* to *ca.* 60 µm in *A.* cf. *jacksonii*. Again, megaspores and microspores differ only trivially in morphology. In all species, both spore genders show very broad size distributions, with the smallest megaspore being approximately one third the diameter of the largest (Phillips *et al.*, 1972; Chaloner & Pettitt, 1987). In contrast, variation in spore size ranges among these species is remarkably low; the smallest megaspores occur in *A.* cf. *jacksonii* (9–48 per megasporangium, 110–370 µm in diameter) and the largest in *A. halliana* (8–16 per megasporangium, 180–470 µm in diameter). Surprisingly, at least two megasporocytes yield viable tetrads in all species, and megaspore abortion is both infrequent and *ad hoc*. This weakens (but by no means disproves) the conjecture of Pettitt & Beck (1968) and Gensel & Andrews (1984) that other apparently homosporous species of *Archaeopteris* could have borne *bona fide* seeds. The suggestion of Phillips *et al.* (1972) that all *Archaeopteris* species were heterosporous is more credible, though equally speculative; most reviewers continue to recognize some homosporous species. The most remarkable feature of the order is the consistent expression of low-grade heterospory throughout the Late Devonian without an obvious transition to a more sophisticated mode of reproduction.

The Lower Carboniferous *Protopitys scotica* (Fig. 6*g*; Walton, 1957; Smith, 1962*a*) is the only recorded fertile member of the Protopityales. Walton (1957) reported little intrasporangial variation in spore size but considerable intersporangial variation, with

Table 3. *Characteristics of Upper Devonian and selected Lowermost Carboniferous ovules*

Species	Location(s)	Age	Preservation	Cupulate	Integumentary lobes				Key references
					Number	Fusion ($\%$)	Winged	Overarching	
Elkinsia polymarpha	Elkins W Virginia	Fa2b-c	Adpression (Petrifaction)	Yes	4-5	30	No	No	Gillespie *et al.*, 1981; Rothwell *et al.*, 1989; Serbet & Rothwell, 1992
Moresnetia zalesskyi	Belgium (several)	Fa2c	Adpression (Petrifaction)	Yes	8-10	< 10	No	No	Fairon-Demaret & Scheckler, 1987
Archaeosperma arnoldii	Port Allegeny Pennsylvania	Fa2d	Adpression	Yes	5-6	80	No	Yes	Pettitt & Beck, 1968; Pettitt, 1970
Unnamed	Oesel C Germany	Tn1a-b	Adpression	?	?3-4	80	Yes	No	Rowe, 1992, in prep.
Xenotheca devonica	Baggy Point SW England	Tn1a-b	Adpression	Yes	?4-5	70	No	No	Rogers, 1926; Fairon-Demaret & Scheckler, 1987
Spermalithus devonicus	Kiltorcan S Eire	Tn1a-h	Adpression	?	?2	80	Yes	No	Chaloner *et al.*, 1977
Hydrasperma tenuis	Ballyheigue W Eire	Tn1a-h	Petrifaction	Yes	8-12	50	No	No	Matten *et al.*, 1980, 1984
Coumiasperma remyi	Coumiac S France	Tn2c-3a	Petrifaction	?	*ca.* 8	20	No	Yes	Galtier & Rowe, 1989, 1991
Eosperma oxroadense	Oxroad Bay SE Scotland	Tn3	Petrifaction	?	2	100	No	No	Barnard, 1959
Lyrasperma scotica	SE Scotland (several)	Tn3	Petrifaction	?	2	50	Yes	No	Long, 1960

Notes to Table 3. Age: The Famennian (Fa) precedes the Tournaisian (Tn); the Devonian-Carboniferous boundary lies within the Tn1b. Integumentary lobes: Two lobes is equivalent to platyspermy, greater than two to radiospermy (cf. Meyen, 1984; Rothwell, 1986). Lateral fusion into a continuous integumentary sheath is measured relative to the total length of the lobes rather than of the nucellus, and values are very approximate. Lobe radial diameter must exceed 20% of the nucellar diameter in order to qualify as wings. Overarching is defined loosely to encompass any substantial constraint on access to the lagenostome caused by incurved integumentary lobes forming 'pseudomicropyles'. Putatively primitive integumentary character states are large numbers of unfused, unwinged, spreading lobes. Ovules morphologically identical to the Ballyheigue *Hydrasperma tenuis* also occur in the Tn3 of southeast Scotland (Long, 1977a; Rothwell & Wight, 1989). *Spermalithus devonicus* is not universally recognized as an ovule as the presence of a megaspore membrane has not yet been demonstrated (e.g. Rothwell & Scheckler, 1988); this reservation also applies to the unnamed German ovule. More detailed reviews of ovules are available for the Upper Devonian (Fairon-Demaret & Scheckler, 1987; Rothwell & Scheckler, 1988) and for the more diverse Lower Carboniferous assemblages (Andrews, 1963; Long, 1966, 1975; Rothwell, 1986). Another ovule-species of Tn1a-b age has been located in the Taff Gorge, near Cardiff (J. Hilton, personal communication, 1993).

means for sporangial populations ranging from *ca.* 80–150 μm (cf. *Bowmanites dawsonii*, described above). Aggregating the contents of several sporangia, Smith (1962a) described a size range of 75–355 μm; the apparently bimodal distribution shows a large peak at *ca.* 120 μm and a smaller, flatter peak at *ca.* 270 μm (Fig. 3a). Yet again, morphological differences between putative megaspores and microspores were trivial, and even the largest megaspores occur as substantial intrasporangial populations. Although *P. scotica* was deemed homosporous by Stubblefield & Rothwell (1989), the inference of free-sporing heterospory by Walton (1957) and Smith (1962a) appears justified by available data. However, Andrews *et al.* (1974) and Bateman & Cleal (1994) noted that similar patterns of spore size variation characterize fertile organs that co-occur with *P. scotica* but are attributed to the seed-bearing Pteridospermales, namely *Staphylotheca kilpatrickensis* (Smith, 1962a) and *Alcicornopteris hallei* (Smith, 1962b).

The Noeggerathiales first appeared in the Namurian and extended into the Lower Permian. Taxonomists have placed the order in several classes (e.g. Bierhorst, 1971); it was transferred to the Progymnospermopsida by Beck (1981), a decision tentatively endorsed by subsequent authors (Meyen, 1987; Thomas & Spicer, 1987; Taylor & Taylor, 1992). The cones superficially resemble sphenophyllalean sphenopsids (*q.v.*); sporophylls are paired in the cone-genus *Noeggerathiostrobus* but occur singly as fused whorls in *Discinites*. Only putatively megasporangiate cones of *N. bohemicus* (Halle, 1954; Andrews, 1961; Němejc, 1963) have been found, with each megasporangium containing *ca.* 16 triradiate megaspores. *Noeggerathiostrobus vicinalis* (Němejc, 1928; Remy & Remy, 1956; Taylor, 1981) bore microsporangia containing many microspores 60–100 μm in diameter and megasporangia containing a few megaspores *ca.* 800 μm in diameter. *Discinites delectus* (Arnold, 1944, 1947, 1949; Andrews, 1961) has similar spore sizes; microspores are *ca.* 80 μm, whereas megaspores are *ca.* 700 μm and occur in intrasporangial populations of *ca.* 16 (occasional abortions were reported by Arnold, 1947). Although similar spore dimensions characterize *D. major* (Němejc, 1928; Andrews, 1961) – microspores are *ca.* 100 μm and megaspores *ca.* 1000 μm – only a single functional megaspore occupies each megasporangium. More information is needed on these enigmatic fossils.

The Stephanian *Cecropsis luculentum* (Stubblefield & Rothwell, 1989) is attributed to the monotypic Cecropsidales. It shares with *Archaeopteris* the possession of adaxial eusporangia, but here they are globose (*ca.* 2 mm in diameter) and borne in sorus-like clusters. Megasporangia and microsporangia are similar in size and morphology, and probably co-existed in the same clusters. The unusual unornamented microspores are elongate and asymmetrically triradiate (*ca.* 55 × 27 μm). The megaspores are generally similar to the microspores but are symmetrical and *ca.* 500 μm in diameter. As in *Discinites major*, they were reduced to a single functional megaspore per megasporangium (Fig. 8d), presumably by abortion of megasporocytes and subsequently of megaspores. Given the lack of megasporangial specialization, it seems unlikely that the megaspore was dispersed intrasporangially. Nonetheless, this last of the progymnosperms to appear in the fossil record is also arguably the most reproductively derived, narrowing the evolutionary gap from the progymnosperm-derived seed-plants.

(6) *Gymnospermopsida (including Angiospermales)*

Unlike the aforementioned groups, the gymnospermopsids are by definition heterosporous, and their identification rests primarily on demonstrating the presence of a megaspore membrane within putative ovules (e.g. Rothwell & Scheckler, 1988; Chaloner & Hemsley, 1991). In dispersed spore assemblages, morphology and ultrastructure are insufficient to reliably distinguish megaspores of the earliest seed-plants from those of their putatively ancestral progymnospermopsids (Hemsley, 1993). The seed-plant ovule is typically defined as an indehiscent integumented mega-sporangium and a seed as a fertilized ovule containing a megagametophytic embryo (e.g. Stewart & Rothwell, 1993: 279). However, careful scrutiny of the earliest putative ovules challenges these definitions.

Borne by the extinct Pteridospermales, these ovules are characterized by hydra-sperman reproduction (Rothwell, 1986; Fairon-Demaret & Scheckler, 1987; Rothwell & Scheckler, 1988). Although invariably present, the integumentary lobes are numerous, narrow, unfused and spreading in genera such as *Moresnetia*, *Elkinsia* and *Genomosperma* (Table 3, Fig. 8*f*). Even allowing for the ontogenetic changes inferred by Rothwell & Scheckler (1988), the role of the integument in either megaspore protection or microspore capture is questionable. Other early ovules such as *Archaeosperma* and *Coumiasperma* (Fig. 8*g*) possessed fewer, larger integumentary lobes that overarched the lagenostome, but the 'micropyle' thus formed is rudimentary and unlikely to have co-opted the prepollen-capturing role of the lagenostome (see below). The essentially non-micropylar indehiscent megasporangia of these early pteridospermaleans have therefore been termed preovules (e.g. Rothwell & Scheckler, 1988; Galtier & Rowe, 1991; Stewart & Rothwell, 1993). The concept of indehiscence has been treated ambiguously in the literature; the term could refer to retention of the megaspore in the megasporangium (our endomegasporangy), retention of the megasporangium on the sporophyte until the ovule has been pollinated, or complete failure of the megasporangium to dehisce, thereby requiring the microgametophyte to penetrate the megasporangium wall (presumably by generating a pollen tube). All these phenomena are difficult to demonstrate in fossil material.

With one possible exception discussed below, all of the earliest well documented seed-plants possessed hydrasperman reproductive biology (Fig. 8*f*). Prepollen capture was primarily the responsibility of a bilayered elaboration of the distal apex of the megasporangium (nucellus) that delimited a domed chamber (pollen chamber) subtending a narrow apertural cylinder (lagenostome = salpinx). The precise method of pollen capture, and the possible roles of integumentary and cupular lobes in both pollen capture and megaspore protection, have been vigorously debated (cf. Andrews, 1963; Taylor & Millay, 1979; Niklas, 1981; Taylor, 1982; Rothwell, 1986; Rothwell & Scheckler, 1988; Stewart & Rothwell, 1993). Much depends upon the orientation of the ovules; if upright, passive capture of airborne prepollen is possible, but if pendent a pollen-drop mechanism would be required to draw the prepollen through the narrow aperture of the lagenostome. Once within the subtending pollen chamber, the prepollen by definition germinated proximally (Fig. 2: Schopf, 1938; Chaloner, 1970). It is assumed to have liberated motile spermatozoids, though pollen tube formation cannot be ruled out – both pollen drops and pollen tubes have been demonstrated in the more derived Upper Carboniferous pteridospermalean *Callospermarion* (Rothwell,

1972, 1979). The megaspore membrane within the nucellus was expanded into an apical 'tent-pole', which often bore the three abortive members of the megaspore tetrad (Pettitt, 1969, 1970; Long, 1975; Chaloner & Hemsley, 1991). Up to three archegonia developed in a shallow annular depression surrounding the tent-pole (Matten *et al.*, 1980, 1984), as in extant cycadaleans and ginkgoaleans. Subsequent expansion of the megagametophyte sealed the entrance to the pollen chamber by driving a tapered central column attached to the pollen-chamber floor into the often similarly tapered lagenostome (Fig. 8*f*). Simultaneous rupturing of the pollen chamber floor presumably enabled the spermatozoids to access the archegonia. Seeds were probably shed soon after pollination; the rarity of preserved embryos implies immediate embryogeny rather than dormancy (e.g. Long, 1975; Chaloner & Pettitt, 1987).

Reproductive evolutionary trends among these early pteridospermaleans include increased megaspore size and decreased thickness of the megaspore membrane (Chaloner & Hemsley, 1991), presumably facilitating nutrient transfer from sporophyte to female gametophyte. Also, ovule release switched from passive senescent fragmentation to active physiological abscission (Rothwell & Scheckler, 1988). The Upper Carboniferous Medullosaceae apparently possessed fully functional micropyles, revealing transfer of function of prepollen capture from the nucellus to the integument. They also reflect a transition from triradiate to monolete microspores, though germination remained proximal. Comparison of medullosaceans with extant cycadaleans reveals transitions from tetrahedral to linear development of megaspore tetrads, and from proximal to distal microspore germination via a single sulcus (e.g. Chaloner, 1970) (Fig. 2). Pollen tube formation facilitated endosporic microgametophyte nutrition, rather than the transfer of gametes (siphonogamy) that characterizes more derived seed-plants. The frequent assumption that pollen tube formation evolved synchronously with the monosulcate aperture is difficult to justify. Indeed, the relative sequence and phylogenetic positions of acquisition of reproductive characters peculiar to seed-plants remain ambiguous (cf. Chaloner, 1970; Doyle & Donoghue, 1986; Haig & Westoby, 1989; Crane, 1990; Doyle & Hotton, 1991; Friedman, 1993).

Having briefly considered derivatives of hydrasperman reproduction, we will now speculate on what might have preceded this condition but post-dated the free-sporing heterospory of putatively ancestral progymnospermopsids. Recent discussions have focused on the ovule *Conniasperma remyi*. Although somewhat younger than the oldest pteridospermaleans and possessing relatively derived integumentary characters (Table 3), *Conniasperma* is characterized by a massive parenchymous beak rather than a pollen chamber–lagenostome apparatus (Fig. 8*g*). The thick nucellus and presence of a cellular gametophyte imply that the ovule was both mature and viable, causing Galtier & Rowe (1989, 1991) to suggest either a remarkably early occurrence of siphonogamy or, more likely, water-borne pollination followed by lysigenous dissolution of the nucellar break to allow fertilization. Aquatic pollination could have preceded ovule abscission if the sporophyte grew in standing water – otherwise, abscission would presumably have preceded pollination in a reproductive strategy reminiscent of rhizomorphaleans, salvinialeans and marsilealeans. Although there is no evidence of a functional triradiate suture in the *Conniasperma* megaspore, Thomas & Spicer (1987) speculated that such sutures could have allowed fertilization in the earliest preovules.

Thus, our knowledge of the origin(s) and reproductive biology of pteridospermaleans

is constrained by lack of close extant relatives of either the potential seed-plant ancestors or the earliest seed-plants, lack of reconstructions of these pivotal fossils that would enable meaningful cladistic analysis, and the difficulty of detecting in fossils transient and/or microscopic characteristics of seed-plant reproduction. Without knowledge of the sequence of acquisition of these key characters, we cannot successfully interpret the biology of potentially intermediate fossil forms. Nonetheless, present evidence is sufficient to show that the transition from free-sporing heterospory to the seed habit could have been gradual and virtually indefinable. Overall, the reproductive biologies of the most derived genera of heterosporous pteridophytes (e.g. *Lepidophloios*, *Marsilea**, *Salvinia**) are more sophisticated than those inferred for the earliest seed-plants; the apparent distinctness of seed-plants, reflecting many putative synampomorphies, actually represents later evolutionary innovations. Indeed, reliable synapomorphies of the Gymnospermopsida are surprisingly elusive.

(7) *Summary : patterns of character acquisition*

Figure 13 lists 12 heterosporic features in their approximate order of appearance in conventional interpretations of the evolution of heterospory and the seed habit. We do not believe that any other suite of reproductive innovations has evolved as frequently as heterospory *sensu lato*. The emergence of at least low-grade heterosporic phenomena in several different lineages can be viewed as a series of natural long-term experiments in the attainment of similar evolutionary 'goals' by modification of radically different genomes at different times and presumably in different habitats. The repeatability of the evolutionary process in different lineages, and consequent iterative acquisition of series of convergent but non-homologous characters, offers an unparalleled opportunity to infer the mechanisms that drove the evolution of a major evolutionary innovation. Careful comparison of the sequence of acquisition of these characters across lineages offers the best approach in seeking generalizations about the evolutionary mechanisms that underlie heterospory. Key questions include: (1) Did the various facets of heterospory evolve in the same order in each lineage? Students of heterospory (including ourselves) tend to view the sequence of acquisition of heterosporic phenomena as broadly predictable, typically using anthropocentric logic of gradual evolutionary progression from homospory towards the 'ultimate goal' of the historically successful seed habit. (2) Were all of these characters essential, or could some be bypassed? (3) Could heterosporic phenomena be lost – in other words, is progressive reproductive sophistication reversible? (4) Did each heterosporic character evolve individually and independently, or could two or more of these characters evolve simultaneously (saltationally *sensu* Bateman & DiMichele, 1994)? One of our main objectives in making this comparison was to seek perturbations of previous gradualist evolutionary scenarios (cf. DiMichele *et al.*, 1989; Chaloner & Hemsley, 1991). (5) Why did reproductive evolution in several highly disparate lineages stop at highly sophisticated heterospory, leaving only the arguably monophyletic seed-plants to exploit the full evolutionary and ecological benefits by adding other more derived reproductive characters to their basic heterosporic repertoire?

Comparison of heterospory across lineages is handicapped to some extent by the inability to detect in fossils transient phenomena that can only be demonstrated conclusively by direct observation of living species (even when such information *is* evident in fossils it can pass unrecorded). Authors tend to observe one of the more

Class Order	Heterospory*	Dioicy	Heterosporangy*	Endospory	Monomegaspory*	Endomegasporangy	Integumentation*	Lagenostomy*	*In situ* pollination	*In situ* fertilization	Pollen tube formed	Siphonogamy
Zosterophyllopsida† Barinophytales†	X	X?	O	O?	O	O	O	O	O	O	O	O
Lycopsida (Clubmosses) Selaginellales	X	X	X	X	O	O	O	O	O	O	O	O
Rhizomorphales[1]	X	X	X	X	X	X?	X	O	O	O	O	O
Sphenopsida (Horsetails) Equisetales	X	X?	X	X?	X	X?	O	O	O	O	O	O
Sphenophyllales†	X?	X?	O	O?	O	O	O	O	O	O	O	O
Pteropsida (Ferns) Stauropteridales†	X	X?	X	X?	O[2]	X?	O	O	O	O	O	O
Salviniales	X	X	X	X	X[3]	X	O	O[4]	O	O	O	O
Marsileales	X	X	X	X	X	O	O	O	O	O	O	O
Filicales (*Platyzoma*)	X	X	X	O	O	O	O	O	O	O	O	O
Progymnospermopsida† Aneurophytales†	X	X?	O[5]	O?	O	O	O	O	O	O	O	O
Archaeopteridales†	X	X?	X	O?	O	O	O	O	O	O	O	O
Protopityales†	X?	X?	X?	O?	O	O	O	O	O	O	O	O
Noeggerathiales†	X	X?	X	X?	X	X?	O	O	O	O	O	O
Cecropsidales†	X	X?	X	X?	X	X?	O	O	O	O	O	O
Gymnospermopsida (Seed-plants)	X	X	X	X	X	X >	X	X	X	X	X	X

Fig. 13. Maximum numbers of heterosporic characters acquired by specific orders, listed in *approximate* sequence of acquisition (see Table 2). Origins of characters are phylogenetically independent except for some progymnospermopsid orders and the gymnospermopsids (see Fig. 11). Daggers indicate extinct higher taxa, asterisks indicate heterosporic characters most likely to be detected in fossils. Enboldened entries indicate the maximum number of characters exhibited by extant members of the orders. Footnotes: [1]Lepidodendrales plus Isoetales of most authors (DiMichele & Bateman, 1994), [2]Strictly, reduction in *Stauropteris* is to two viable megaspores rather than one (e.g. Chaloner & Hemsley, 1991), [3]*Salvinia** only, [4]*Salvinia** possesses a cellular perispore that superficially resembles a pteridospermalean nucellus, [5]Sporangia of *Chaleuria* contain spores that are dominantly but not exclusively of one gender.

reliable features of a fossil (asterisked in Fig. 13) and then infer the presence in that fossil of other phenomena usually associated with that feature in extant species; examples are heterospory and dioicy, heterosporangy and endospory, monomegaspory and endomegasporangy, and lagenostomy and *in situ* pollination. Unfortunately, it is difficult to justify such biological extrapolations, given that one of the great successes of comparative palaeontology has been the repeated demonstration of character combinations in fossils that have *not* been recorded in their closest extant relatives (e.g. Oliver & Scott, 1904; Thomas, 1915; Florin, 1951; Beck, 1960; Banks, 1975; Grierson & Bonamo, 1979; Rothwell & Erwin, 1985, 1987). We cannot, for example, rule out the possibility of *in situ* pollination in some of the more derived heterosporous pteridophytes, notably rhizomorphalean lycopsids such as *Lepidophloios* (Fig. 8a).

Moreover, satisfactory answers to questions (1)–(5) require a detailed phylogeny encompassing many species of all major land-plant clades; the present information (Fig. 13) is further weakened by potential non-independence of character acquisitions among (1) the two lycopsid orders (Fig. 10), (2) the five progymnospermopsid orders, and (3) the gymnospermopsids and their putative progymnospermopsid ancestor (Fig. 12). Also, the phylogenetic positions of ecologically specialized, highly apomorphic clades that lack known intermediates with any potential ancestors, such as the Salviniales and Marsileales, will be impossible to resolve convincingly using morphological data alone; comparable molecular phylogenies are desirable to resolve both these 'long-branch' problems and potential examples of paedomorphosis (e.g. Bateman, 1994). Admittedly, pteridophytes are proving relatively recalcitrant to many of the molecular techniques that have been successfully applied to seed-plants (J. Pahnke, personal communication, 1992; M. W. Chase, personal communication, 1993).

A detailed land-plant phylogeny would provide explicit hypotheses of both the number of origins of heterospory and the pattern of character acquisition in each heterosporous lineage. Revised distinctions of homologous from analogous heterosporic features in different lineages would allow further clarification of present terminological ambiguities. A good example is Schopf's (1938) concept of 'seed-megaspore': 'the large functional and three small aborted megaspores which formed the unequal tetrads produced by certain specialized free-sporing pteridophytes in the Palaeozoic' (Hemsley, 1993: 136). In practice, this term has been both inflated beyond this definition and applied inconsistently to different taxonomic groups. First, the dispersed spore-genus *Subcystosporites* with two putatively viable megaspores is included but the similar megaspore tetrad of *Stauropteris* (Fig. 8c) is excluded. Secondly, among the more derived taxa, some spores that apparently did not retain the three aborted members of the tetrad are included (e.g. *Calamocarpon*) but others are excluded (e.g. *Cecropsis*; Fig. 8d). Thirdly, the 'seed-megaspore' category includes the megaspore membranes of some but not all of the earliest seed-plants (e.g. *Spermatosporites*, a spore-genus that includes the megaspore membrane of *Archaeosperma*). As Hemsley (1993) recognized, the term 'seed-megaspore' currently encompasses an ill-defined grade that includes few *bona fide* seeds. A suggested alternative term, 'preovule megaspores', is no more helpful; if seed-plants are monophyletic, only one of the many lineages that produced 'preovule megaspores' actually gave rise to the ovule. Full exploitation of the valuable data summarized by Hemsley (1993) requires a phylogenetic context.

Even more importantly, combining a phylogeny with knowledge of the ecological preferences of the analyzed species offers the best hope of elucidating the evolutionary mechanisms that underlie the observed patterns of character distributions. Given that a rigorous land-plant phylogeny remains a distant goal, we will illustrate the principles of the argument using the lycopsid phylogeny (Fig. 10). As a null hypothesis this implies simultaneous (saltational) evolution of heterospory, dioicy, heterosporangy and endospory (between *Leclercqia* and *Stachygynandrum*), followed by gradual, stepwise acquisition of endomegasporangy (*Chaloneria* to *Sigillaria*), monomegaspory (*Sigillaria* to *Diaphorodendron/Synchysidendron*), and integumentation (*Lepidodendron* to *Lepido-phloios*). Within the Lycopsida, low-level anisosporous heterospory is found only in two Asian species of *Isoetes**, which almost certainly evolved from a more strongly heterosporous *Chaloneria*-like ancestor. Although we have not encountered any other reports of evolutionary losses of heterosporic phenomena, we suspect that they have not been sought, given the broad appeal of the 'ladder of progression' as an evolutionary model. The genesis of additional cladograms is likely to reveal other 'retrograde' events that further challenge gradualist, unidirectional (and typically strongly adaptationist) models.

It is a moot point whether heterospory, dioicy, heterosporangy and endospory actually evolved saltationally in the Lycopsida, as implied by the cladogram. However, this certainly did not occur in some other lineages. For example, all known members of the exclusively fossil Barinophytales and Aneurophytales failed to advance beyond anisosporous heterospory and presumed dioicy. The wide range of degrees of heterospory evident among different species within the Equisetales and Progymno-spermopsida would in theory allow gradual, unidirectional evolution, whereas other groups such as the stauropteridalean, salvinialean and marsileaean pteropsids resemble the Lycopsida in lacking known species that show low-level heterospory.

Moreover, some heterosporous species appear to defy theoretical evolutionary optima. For example, conventional wisdom requires the reduction of a megasporangial population to a single viable megaspore prior to the evolution of megaspore dispersal within the sporangium; it is both redundant and a waste of resources to distribute more than one energetically expensive megaspore within a single disseminule. However, this did not prevent the evolution of a propagule containing two apparently viable megaspores in some *Stauropteris* and lycopsid species (Fig. 8c), and a propagule containing several putatively apomictic megaspores in the lycopsid *Sigillaria*. In contrast, the specialized water-fern *Marsilea** possesses only one viable megaspore per megasporangium but generally releases it into the water column prior to pollination. Thus, monomegaspory and endomegasporangy are not necessarily evolutionarily coupled. A further example of contrasting evolutionary trajectories is evident among species showing low-grade heterospory. *Barinophyton* and *Chaleuria* possess the supposedly relatively derived character of large size differences between microspores and megaspores but the primitive character of anisospory, whereas *Platyzoma** produces megaspores and microspores in separate sporangia but the two spore genders differ far less radically in relative size.

In summary, current (albeit inadequate) evidence suggests that the sequence of acquisition of heterosporic characters is indeed *broadly* predictable. The sequence of acquisition differs only in detail among lineages, implying that particular stages can

only be temporarily by-passed during evolution. However, it is also clear that heterosporic phenomena could evolve saltationally and also be lost during evolution, though loss of heterospory *sensu stricto* (i.e. spore size bimodality) has not been suggested for any lineage. Saltation and character loss both imply a substantial *ad hoc* element to the evolution of heterospory. Phylogenetic loss of heterosporic characters also suggests that they are not necessarily adaptively advantageous, emphasizing previous arguments that in most ecological settings heterospory may represent an adaptive valley rather than an adaptive peak (e.g. Chaloner & Pettitt, 1987; DiMichele *et al.*, 1989). The questions of if, when, and where heterospory is adaptively advantageous are critical to understanding its evolution in general and the evolution of the seed habit in particular. We will return to this topic in the final section of the paper, after briefly reviewing the physiological control of heterospory.

VI. PHYSIOLOGICAL CONTROL OF HETEROSPORIC PHENOMENA

Based on the above evidence, there can be little doubt that gender expression in heterosporous plants is determined epigenetically. We assume that heterospory is controlled hormonally via nutrient clines, and involves competition between mega-spores and microspores for resources. Competition occurs irrespective of physical scale. For example, in *Protocalamostachys farringtonii*, microsporangia that are closely juxtaposed to megasporangia generate larger numbers of smaller megaspores than those associated only with other microsporangia (Fig. 4; Bateman, 1991 a). A more extreme form of competition is evident in the salvinialean pteropsid *Azolla**, where a vascularized papilla within the sporocarp generates either a single terminal mega-sporangium (Fig. 7 h) or several lateral microsporangia; suppression of primordia for one gender of sporangium is necessary to allow the expression of the other gender (or, more probably, is caused by the other gender). Megaspores develop in the more nutrient-rich microenvironments of the sporophyte, which typically occur closest to the most active vascular supply; for example, megasporangia are concentrated toward the base of most bisexual pteridophyte cones (Figs 7 a–b).

Apparent deviations from this pattern can still be explained in metabolic terms. Most isoetalean lycopsids lost their ancestral ability to generate cones along with the loss of the ability of the stem to branch, so that the sporophylls were expressed directly on the stem (Bateman, 1994). In *Chaloneria* this led to expression of megasporangia higher on the stem than microsporangia, as they were closer to the metabolically active stem apical meristem. Moreover, many species of *Isoetes** show seasonal temporal separation of gender, first producing megasporangia and then microsporangia later in the season as the metabolic activity of the sporophyte declines (Bierhorst, 1971).

Perturbations of gender expression in contrasting lineages provide further evidence of epigenetic control. Examples include occasional bisexual sporocarps of *Azolla**, and occasional bisexual cones in derived lycopsids and equisetaleans that typically bear unisexual cones (e.g. *Calamocarpon*). Moreover, spatial orientation apparently influences the positional expression of megasporangia relative to microsporangia in some selaginellalean cones. More striking is a perturbation of the stronger gender differentiation in early pteridospermalean seed-plants. Although no early pterido-spermalean has yet been fully reconstructed, current evidence suggests that clusters of ovule-bearing cupules and prepollen-bearing synangia (microsporangial clusters) reliably developed on separate branching systems, attached either directly to the stem

or to the median rachises of megaphyllous fronds (e.g. Walton, 1931; Long, 1977*b*; Retallack & Dilcher, 1988; Rowe, 1988). Gender separation across the architecture of the sporophyte was sufficiently great that no-one has yet demonstrated that any early pteridospermalean was monoecious rather than dioecious. Despite this evidently well entrenched gender separation, Long (1977*a*) discovered a single bisexual specimen among many ovulate cupules of *Pullaritheca longii* (see also Rothwell & Wight, 1989; Bateman & Rothwell, 1990). This genus typically bore many crowded *Hydrasperma* ovules (Fig. 8*f*) on a highly vascularized 'placental' disc at the base of the cupule (Fig. 9*c*), but in Long's developmentally anomalous specimen microsporangia developed along one sector of the periphery of the disc (Fig. 9*a*). Moreover, between the ovule-bearing and microsporangia-bearing regions of the placenta occur two hybrid organs (Fig. 9*b*). One more closely resembles an ovule and the other a sporangium, but both developed over-proliferated walls. This observation not only supports the long-held assertion of homology between the microsporangium wall and ovulate nucellus, but also indicates that control of gender is subtle and tenuous even in these reproductively derived plants. We suspect that the sporangia and hybrid structures developed in a marginal zone of the placenta that was inadequately vascularized and thus failed to provide sufficient nutrients for the expression of femaleness.

The complex, epigenetic nature of gender control has important implications for developmental canalization. Control of spore size (and presumably therefore of gender) is lax in examples of low-grade heterospory such as *Protopitys scotica* (Figs 3*a*, 6*g*), *Calamostachys americana* (Figs 3*b*, 7*b*), *Protocalamostachys farringtonii* (Figs 4, 7*c*) and *Archaeopteris latifolia* (Figs 5, 6*d*). Size spectra are broad for microspores and especially for megaspores; the two modes are poorly defined and the two distributions often overlap. Also, megaspores resemble microspores in morphology and wall ultrastructure. Such systems offer a great deal of flexibility in gender expression, in terms of the relative proportions of megaspores and microspores generated at any one moment during the ontogeny of the sporophyte. Further flexibility of gender occurs in subtly heterosporous plants such as *Platyzoma**, where gametophyte gender is not firmly fixed during sporogenesis and can be modified by environmental factors. More derived modes of heterospory (e.g. rhizomorphaleans, *Calamocarpon*, pteridospermaleans) result in increasingly disparate megaspore and microspore development as the two genders diverge in size, shape, ornamentation, wall thickness and wall ultrastructure. With the attainment of monomegaspory and monomegasporangy, gender expression became so strongly canalized in the sporophyte that it was also fixed in the ensuing gametophytes. The reproductive strategy of the gametophyte was irrevocably determined by differential resource allocation in the sporophyte. It now becomes crucial to determine under what (if any) circumstances this strategy is evolutionarily advantageous.

VII. HOW THE SPOROPHYTE PROGRESSIVELY GAINED CONTROL OVER THE GAMETOPHYTE: A 'JUST-SO' STORY

(1) *Introduction: evolutionary antagonism between sporophyte and gametophyte*

The biphasic life history of embryophytic plants permits the conspecific sporophyte and gametophyte to have independent ecological preferences and fates, albeit linked by a shared genome. The strongly heteromorphic alternation of generations in most land-

plants accentuates this independence and leads to different preferences for physical conditions on the part of sporophyte and gametophyte, particularly in the free-sporing life histories that characterize lower vascular plants. Furthermore, in many species each life-history phase can reproduce asexually, by-passing the alternate phase and thereby evading many selective constraints. Superimposed on this ecological dichotomy is a common genome that must be differentially expressed in order to generate two distinct morphologies, a process requiring complex epigenetic control of developmental pathways. Meiosis is the responsibility of the sporophyte, and gametogenesis–syngamy the responsibility of the gametophyte (Fig. 1). Profound differences between sporophyte and gametophyte in development and ecology are therefore inevitable. The two life-history phases are best viewed as having experienced long-term co-evolution. As in interspecific co-evolutionary relationships, responses can be either antagonistic or co-operative. Thus, the long-term survival of a species of free-sporing plant is a complex venture that depends on the ability of the two phases to maintain a successful balance between sexual reproduction and the vegetative (economic) survival of the individual. Even the morphology of angiospermaleans can be determined in part by sporophyte–gametophyte antagonism (e.g. Till-Bottraud *et al.*, 1993).

Throughout land-plant history there have been numerous evolutionary excursions that allowed one of the two phases to establish some degree of dominance. The dominant phase exerts principal influence on the sexual reproductive function of the other, reducing the ecological disparity between them by compressing their aggregate life history. In extreme dominance one phase assumes nutritional support of the alternate phase and thereby presents natural selection with a functionally unitary individual; this is most evident today in the sporophyte of the seed-plants and in the gametophyte of the bryophytes, though examples abound in other clades that were ecologically important in times past (see Kenrick, 1994). Several phylogenetically disparate lineages have independently undergone life-history compression, suggesting that a more unitary individual can confer significant ecological (and hence selective) advantages over a life history characterized by two fully independent, free-living phases.

The morphological and ecological complexities of the primitive embryophyte life history induce an inherent antagonism between the sporophytic and gametophytic phases, which reflects their potential to experience the physical environment in profoundly different ways. The sporophyte can gain control over gametophytic functions during spore development. Meiosis and sporogenesis occur within the sporangium; thus enclosed by sporophytic tissue, the spores develop within the metabolic microenvironment of the parent sporophyte (Shattuck, 1910; Bell, 1979; Näf, 1979; Willson, 1981, 1983), though recent observations suggest that developing spores can also influence the metabolism of surrounding sporophytic tissues (P. R. Bell, personal communication, 1993). Later in ontogeny, the economic dependency of the archegonium offers the gametophyte an opportunity to influence the early metabolic microenvironment of the resulting embryo and juvenile sporophyte. Thus, metabolic linkages inherent in the alternation of generations in theory permit either of the generations to gain significantly greater control over its own fitness, through compression of the life history and domination of the physiology of the alternate generation (Willson, 1981; Haig & Westoby, 1988*a*, *b*).

Sex determination in plants is strongly environmentally controlled; examples range bryophytes (e.g. Shaw & Gaughan, 1993) to reproductively complex angiosperms (e.g. Diggle, 1993). Possible reasons for this dominantly epigenetic determination of gender in plants, rather than the sex chromosome systems prevalent among animals, have received surprisingly little attention in the literature. Epigenetic systems allow more flexible responses to environmental cues and the redistribution of resources among genders. In contrast, sex chromosome systems in plants would be prone to disruption during polyploid speciation events, which are common among plants but rare among animals (e.g. Stace, 1993). Nonetheless, it is noteworthy that ploidy levels among extant plants tend to be lower among heterosporous than homosporous groups (e.g. Löve, Löve & Pichi-Sermolli, 1977; Stebbins, 1992). Environmental sex determination is most strongly favoured when (1) the 'offspring' enters an environment other than that occupied by the 'parent' (in this case, gametophyte = offspring and sporophyte = parent, although the concept applies more directly to seed-plants), and (2) neither the offspring nor the parent can control or predict the environmental conditions encountered by the offspring (cf. Williams, 1975; Charnov & Bull, 1977; Charnov, 1993; Roff, 1993). In the primitive alternation of free-living generations that characterized early vascular land-plants, the gametophyte is much better positioned than the sporophyte to be the arbiter of gametogenesis and syngamy, because of the environmental unpredictability inherent in the random broadcast of spores. For those spores that successfully generate mature gametophytes, syngamy necessitates release of spermatozoids into the environment in order to locate a receptive ovum. To be successful in a terrestrial setting, this system requires surficial moisture and gametophyte populations that are either sufficiently dense or sufficiently structured to offer a high probability of successful syngamy. The gametophyte can respond rapidly to environmental variation, produce spermatozoids and ova when conditions are suitable for reproduction (Voeller, 1971), and in some instances communicating chemically with other gametophytes (Näf, 1979; Haig & Westoby, 1988*b*).

In contrast, a homosporous sporophyte is poorly positioned to exert direct control over sex ratio and the processes that precede syngamy. Sporogenesis and spore dispersal must precede gametophyte growth and development (Fig. 1). The sporophyte is temporally distant from the point of syngamy, so that significant changes in environmental conditions can occur between the onset of sporogenesis and gamete production. Despite these constraints, in all heterosporous life histories the sporophyte dictates the sex ratio through its ability to influence spore developmental patterns. There are two conditions under which the sporophyte can most successfully control sex ratio. It can occupy conservative environments that offer a relatively low probability of significant environmental changes occurring between sporophytic determination of sex ratio and subsequent gamete release. The most typical such habitats are aquatic and semi-aquatic (e.g. DiMichele *et al.*, 1989). Alternatively, the environment can be by-passed by the evolution of structural modifications that eliminate the need for free water, namely the seed habit (e.g. Chaloner & Pettitt, 1987). We emphasize the importance of considering in detail the role of environment as a selective filter; free-sporing heterospory is successful in only a narrow spectrum of environments. Evolutionary scenarios (especially those formulated by palaeobotanists) consistently fail to address the ecological consequences of heterospory, treating life-history evolution as

a straightforward structural problem readily solved by adaptive responses (e.g. Tiffney, 1981; Chaloner & Hemsley, 1991).

(2) *Homosporous systems*

As the undoubted antecedent of heterospory, homospory is generally treated as a simple life history; these primitive ancestral species are isosporous, their gametophytes are bisexual, and the potential for intra-gametophytic selfing is omnipresent (e.g. Tiffney, 1981). This view underestimates the collective diversity of homosporous systems. Both sporophytes and gametophytes can exhibit complex arrays of developmental and biochemical controls of sex ratio and gamete production. Credible evolutionary scenarios must presume that such complexities evolved early in land-plant history and existed in the immediate ancestors of at least some heterosporous lineages. Willson (1981), Haig & Westoby (1988b) and Korpelainen (1994) argued that gametophytes of homosporous systems determine their sex ratio in response to a combination of environmental signals and metabolic vigour. Within a population of conspecific gametophytes, the larger individuals tend to develop archegonia first and only later develop antheridia. In contrast, smaller gametophytes tend to generate only antheridia (Klekowski, 1979; Näf, 1979). This strategy is economically sound. The larger gametophytes have more rapid rates of growth, greater resources, and thus greater ability to support a juvenile sporophyte. Although smaller gametophytes cannot successfully support a sporophyte, by producing numerous male gametes they increase their individual potential to participate in the process of genetic recombination. Thus, there is a clear evolutionary basis for gender differentiation among populations of gametophytes that are derived from homosporous sporophytes; small gametophytes maximize fitness by being male, large gametophytes by being female or sequentially bisexual. Once dispersed from the sporophyte, gametophytic gender is determined by the interaction of the gametophytic genome, the internal metabolic microenvironment of the gametophyte, and the external microenvironment.

Certainly, the gametophyte is the optimal phase of a primitive vascular plant life history in which to determine sex ratio and the timing of gamete production – a key factor rarely discussed in the context of plant life-history evolution. Only the gametophyte has direct access to information about the local microenvironment during gametogenesis (Voeller, 1971; Charnov & Bull, 1977). Nonetheless, gametophyte gender is related to metabolic vigour, which partly reflects the initial size and stored resources of the spore. The sporophyte can directly influence initial spore size, and thus indirectly influence the sex ratio in a population of gametophytes. Spores that develop and mature in favourable metabolic microenvironments on the parent sporophyte will tend to be larger and hence more likely to express the female phenotype than spores developing in less favourable sporophytic microenvironments (Bell, 1979). This potential constraint on gametophyte population dynamics is inconsequential if gametophyte populations are dense (Haig & Westoby, 1988b), a common phenomenon among lower vascular plants such as *Equisetum* (Duckett & Duckett, 1980).

Many pteropsid species have evolved biochemical signalling systems that permit them to 'communicate' when determining the *timing* of gamete production (Näf, 1979; Willson, 1981, 1983; Haig & Westoby, 1988b), which in turn influences sex ratio. Antheridiogens produced by rapidly growing female gametophytes induce antheridial

formation in adjacent gametophytes that are smaller and slower growing. Haig & Westoby (1988*b*) argued that these 'signalling molecules' benefit both male and female gametophytes. Willson (1981) presented two models. In the first model, the antheridiogens gave the sporophyte even greater control of gametophytic sex expression in populations with high levels of inbreeding, thereby maximizing the probability of inter-gametophytic fertilization (Klekowski, 1969, 1979). The second model resembled that of Haig & Westoby in focusing on dominantly outbreeding populations, where antheridiogens permitted female gametophytes to both control the source of spermatozoid donors and reduce the growth rates of competing gametophytes; antheridiogens in such populations would also benefit undifferentiated gametophytes by signalling them that receptive females were present and that a male-biased strategy was at least momentarily advantageous (see also Stevens & Werth, 1993; Wellings & Haufler, 1993; Karpelainen, 1994).

Antheridogen-mediated systems permit gametophytes to by-pass the influence of the parental sporophyte on sex ratio and hence to maximize their individual probability of contributing to the next sporophytic generation. The fitness of individual gametophytes is thus increased by returning to the gametophyte generation a measure of the environmental interpretation lost during phylogeny through sporophyte intervention in sex-ratio determination. When viewed in the overall context of plant life-history evolution, the sporophyte and gametophyte clearly co-evolve.

Most of the emphasis in models of the evolution of homosporous (and heterosporous) mating systems has been placed on control of sex ratio (Charnov, 1981; Willson, 1981; Goldman & Willson, 1986; Haig & Westoby, 1988*a*, *b*). However, sex ratio is only the first step on the path to syngamy; it must be followed by gametangial development and subsequent production of spermatozoids and ova. In homosporous systems, the sporophyte can influence the sex *ratio* but the gametophytes remain the direct interpreters of environmental conditions and thus determine *when* gametes are produced. The distinction between sex ratio determination and timing of gamete production is particularly important for interpreting transitions from homosporous to heterosporous systems. The life-history compression that is characteristic of heterosporous plants with free-sporing endospory severely limits gametophyte flexibility and gives the sporophyte much greater control over the entire productive process, from meiosis to syngamy. However, free-sporing heterospory only gives the sporophyte partial control over the timing of gamete production. Gametes must still be released into the environment, placing strong limitations on the ecological conditions that can be exploited; life-history compression became complete only with the evolution of the seed habit. The implications of the differences between homosporous and heterosporous systems are central to the development of evolutionary scenarios, particularly the interpolation of supposed 'intermediate' stages between the two 'classic' life histories illustrated in Figs 1*a*, *b*. Are putative morphological intermediates actually functionally and ecologically intermediate, or are they functionally homosporous (e.g. *Platyzoma**) and hence poor candidates for evolutionary intermediacy? Given the significant differences between the optimal environmental conditions for the two life-history phases, the 'gap' between free-sporing homospory and free-sporing heterospory may in fact be unbridgeable by unidirectional evolution driven by vectorial 'selective pressures'.

(3) *Heterosporous systems*

(a) *Previous scenarios*

Most major lineages of primitively homosporous plants have experimented with heterospory to various degrees, reaching extremes in the seed habit and in the aquaearps of derived rhizomorphalean lycopsids (Phillips, 1979; Chaloner & Pettitt, 1987; Phillips & DiMichele, 1992). As one of the three principal life histories of extant vascular plants (free-spring homospory, free-sporing heterospory, seed habit), numerous evolutionary scenarios have been offered to explain the origin of heterospory, most as part of broader models encompassing the origin(s) of seeds.

We have already reviewed in detail the fossil record of heterospory. This clearly shows that morphological homospory preceded morphological heterospory, and suggests that anisosporous species existed alongside more strongly heterosporangial species in the Middle and Late Devonian. However, this observation tells us nothing about (1) the exosporic or endosporic nature of gametophytes relative to fossil spore sizes, (2) the timing and morphological transitions of the origin of endospory, or (3) which, if any, of the sexual determination systems available to extant plants operated in ancestral homosporous species.

Fossil patterns have been given life by several assumptions drawn from studies of extant plants. The following scenario, well summarized by Tiffney (1981), has become a conventional wisdom in palaeobotany. First, ancestral homosporous species are assumed to have possessed monoicous gametophytes that reliably expressed both male and female traits. Secondly, anisospory (two spore sizes in one sporangium) is assumed to precede heterosporangy (separate microsporangia and megasporangia). Thirdly, an exosporic, sexually differentiated gametophyte modelled on *Platyzoma** is interpolated between homospory and endosporic dioicy. Fourthly, it is taken as axiomatic that evolution occurs through insensibly gradual and progressive transformation of morphology. In many lineages this assumption requires that known species should be linked by hypothetical intermediate forms yet to be discovered. This morphological transformation series is driven by 'selection pressures'; the larger spores of a population produce more robust gametophytes and hence more successful sporophytes. In this economically oriented scenario, selection 'would favor the gradual restriction of the antheridiate and archegoniate conditions to small and large gametophytes, respectively' (Tiffney, 1981: 208). Selection would then eliminate intermediate-sized spores, leaving only large and small forms that produced sexually differentiated exosporic gametophytes.

This model does not account for the origin of endospory, which is assumed to follow the origin of heterosporangy. Endospory has profound ecological consequences – notably greater unity of the individual in the face of selection – that should be considered independently of the origin of epigenetic control of gender differentiation. Similar evolutionary models have been proposed for the origin of complex mating systems in *homosporous*, exosporic vascular plants (e.g. Willson, 1981; Haig & Westoby, 1988b), where sporophytes and gametophytes have battled for sex ratio control. Without explicit models for the origin, control and ecological consequences of

endospory, this scenario cannot cross the barrier between homospory *sensu lato* (exosporic gametophytes) and heterospory *sensu stricto* (endosporic gametophytes).

Studies of development in heterosporous plants (e.g. Smith, 1900; Shattuck, 1910; Sussex, 1966) have revealed different patterns among the major clades, thereby supporting palaeobotanical inferences of many independent origins of heterospory. The model developed by Haig & Westoby (1988a) and formalized by Charlesworth (1988) is broadly similar to that elaborated by Tiffney (1981) but designed specifically to explain the origin of heterospory. It stipulates that selection drove gradual increases in the minimum spore size necessary for female reproduction, due principally to competition among gametophytes from different sporophytes; the model assumes little necessary size increase for male function, although in the population of isospores a general increase in mean spore size is assumed. The progressive increase in isospore size eventually transcends a threshold where the cost of producing small, obligately male spores is less than that of producing larger, potentially bisexual isospores. At this point the gametophytic population becomes 'vulnerable to invasion by smaller male specialist spores' (Haig & Westoby, 1988a: 265). The result is an evolutionarily rapid differentiation of the gametophyte populations into male and female specialists, with strong selection against intermediate hermaphroditic forms. This model conforms to the observations of Turnau & Karczewska (1987), who reported many examples of size differentiation among Middle Devonian spores of similar morphology and suggested that the key innovation leading to heterospory was the evolution of obligately male microspores from populations of large bisexual isospores.

Like the scenario of Tiffney (1981), the Haig & Westoby (1988a) model does not explicitly consider the origin of endospory, and thus accounts more for the origin of complex homosporous mating systems and the origin of obligate anisospory such as that documented in *Platyzoma**. Haig & Westoby (1988a: 264, 268) argued that selection will favour endospory when juvenile sporophyte development is dependent on pre-existing spore food reserves, a consequence of life under conditions unfavourable for the growth of gametophytes. They envisioned co-option of large spore reserves that evolved principally to support the expense of large, rapidly growing, exosporic female gametophytes, thus implicitly accepting that the transition to endospory was driven by selection and occurred via a free-living, unisexual phase. However, we believe that the ecological constraints on the success of heterosporous plants render such stepwise progression untenable. The need for water to facilitate fertilization, the lack of gametophytic flexibility in responding to environmental vagaries, and the time lag between sporophytic determination of sex ratio and syngamy, all require a highly predictable aqueous environment. Given the independent existence of free living gametophyte and sporophyte and their vast differences in morphology, it is unlikely that aquatic or amphibious habits could be occupied gradually by imperceptible transformation of terrestrial ancestors. Even if one generation evolved traits that permitted it to cross the profound aquatic–terrestrial barrier, the other generation, handicapped by an entirely different growth habit and morphology and ill-equipped for its new habit, would be obliged to follow. Not surprisingly, extant examples of aquatic, homosporous, free-sporing plants are confined to a few liverworts. Only a selectively unitary individual can readily cross this evolutionary–ecological boundary.

(b) *The key role of endospory*

Endosporic gametophyte development is the key innovation that permits the evolution of heterospory. Understanding the origin and evolutionary fixation of endospory requires consideration of ecology as well as morphology, given the ecological limitations that endospory places on gametophyte function. Furthermore, because of ecological constraints on successful syngamy, early endosporic plants may have been able to survive only under a very narrow range of ecological conditions.

Almost all heterosporous plants (including seed-plants) determine gametophyte gender epigenetically rather than through sex chromosomes, and fix that gender prior to spore release (Sussex, 1966; Bell, 1979, 1989; Chailakhyan & Khryanin, 1980). As in homosporous systems, the sporophyte influences gender through control of the metabolic microenvironment of the developing gametophyte. Spores ultimately destined to be female are usually produced in metabolically favourable positions on the sporophyte relative to positions of male sporogenesis.

Among the modern pteridophytic flora, gametophytes that are obligately unisexual are also inevitably endosporic. Each gametophyte undergoes its entire ontogeny within the spore wall, so that the gametophytes are entirely dependent on the sporophyte for nutritional support. Once released from the sporangium into the environment they indulge in little if any photosynthesis; they either mature rapidly to produce gametes or undergo a period of diapause (developmental stasis).

From an ecological viewpoint, endosporic gametophytes effectively function as gametes rather than as a distinct alternative life-history phase. Consequently, free-sporing heterospory suffers from several serious constraints. Determination of gametophyte gender during sporogenesis minimizes the ability of the reproductive phase to respond to environmental vagaries. However, there is a significant lag time between sporangial initiation and syngamy, entailing sporogenesis, spore dispersal, gametophyte germination and development, gametangial initiation, and gametogenesis. Unable to express both types of sex organ or influence gender expression in the rest of the gametophyte population, diapause in spore germination is then the only response available to the sporophyte under unfavourable physical conditions. Thus, by wresting control of the sex ratio from the gametophyte, the sporophyte became unable to respond to changes in physical conditions affecting gamete (especially spermatozoid) viability. A moist environment is required if spermatozoids are to locate receptive ova.

From first principles alone, sporophytically mandated heterospory can be predicted to be a miserable evolutionary failure without a co-occurring morphological change, namely endosporic gametophyte development (DiMichele *et al.*, 1989). Endospory permits evolutionarily important life-history compression. The sporophyte controls the timing of spore production, spore release, and spore gender. However, syngamy remains an uncontrolled variable, at the mercy of environmental perturbations. Nonetheless, the two life-history phases are virtually joined into a single organism that can experience selection more holistically (DiMichele *et al.*, 1989).

The evolution of endospory – the key innovation on the road to *bona fide* heterospory – can be viewed as a developmental 'hopeful monster' (e.g. Bateman & DiMichele, 1994). In a typical terrestrial free-sporing plant, endosporic megagametophytes with limited food reserves and limited ability to grow independently would certainly be

selected against strongly, even in the most benign environments. However, in aquatic or semi-aquatic environments, the sporophyte can successfully exploit the *happenstance* appearance of gametophytic endospory. Such habitats exert relatively low levels of selection against successful syngamy, which is the key constraint in a system where gametophyte gender is fully predetermined. Furthermore, an endosporic gametophyte eliminates the problem of evolutionarily co-ordinating the adaptation of two free-living phases to the aquatic environment. Hence, most extinct heterosporous plants occur in aquatic–amphibious habitats (DiMichele, Phillips & Peppers, 1985; Thomas & Spicer, 1987; Bateman, 1991 *b*; DiMichele *et al.*, 1992). With the exception of selaginellaleans, most extant heterosporous plants also prefer such habitats. Heterosporous ecological specialists growing in seasonally dry to xeric habitats resort to apomixis (DiMichele *et al.*, 1989); this has been documented for at least some extant species of the Selaginellaceae (e.g. Lyon, 1904; Bruchmann, 1912; Geiger, 1935; Steil, 1939, 1951; Horner & Arnott, 1963), *Isoetes** (Pant & Srivastava, 1965), *Marsilea** (Strasburger, 1907; Gupta, 1962), and the closely related *Regnellidium** (Mahlberg & Baldwin, 1975). These plants exploit the ability of larger, metabolically more active females to express sporophyte genes without syngamy (Bell, 1979, 1989; Sheffield & Bell, 1987). Moreover, an apogamous life history subjects the populations to an ever-increasing load of deleterious mutations – the classic Mullerian ratchet (e.g. Maynard Smith, 1978; Buss, 1987; Stearns, 1992). Consequently, heterospory does not appear to have ever been an effective reproductive strategy in water-limited environments.

Endospory probably evolved by chance, as the result of paedomorphic modifications to the rate of gametophytic growth and the timing of development of sexual organs (DiMichele *et al.*, 1989). More rapid cell division and earlier onset of sex organ production together would produce mature endosporic gametophytes without the need to invoke directional selective pressures. Although the postulated evolutionary event is restricted to the gametophyte, it could also be exploited by the sporophyte.

The evolution of endospory is distinct from the evolution of separate genders. Sporophytes can manipulate gametophytic gender expression epigenetically regardless of whether the gametophytes are endosporic or exosporic. Thus, the developmental machinery necessary to produce sexually differentiated gametophyte populations undoubtedly existed in the ancestors of heterosporous lineages. The more restrictive enforced unisexuality of heterosporous gametophytes may reflect the inability of endosporous gametophytes to supplement the limited food reserves provided by the sporophyte. Bisexual endosporic gametophytes are unnecessary as an intermediate stage in the evolution of heterospory. Chaloner & Hemsley (1991: 153) correctly recognized that such a phase is ecologically implausible (though they incorrectly asserted that its existence was advocated by DiMichele *et al.*, 1989). We agree that bisexual endosporic gametophytes are incompatible with the known mechanisms by which sporophytes manipulate gametophyte gender and hence are developmentally implausible.

The evolution of heterospory is typically envisioned as passing through an 'intermediate' stage stage of free-living but unisexual gametophytes (e.g. Tiffney, 1981), typified by the extant pteropsid *Platyzoma** (Tryon, 1964). However, ecological consideration of this scenario (DiMichele *et al.*, 1989) suggests that free-living but obligately unisexual gametophytes suffer the cumulative negative constraints of both

homospory and heterospory but lack the advantages of either (Chaloner & Pettitt, 1987). As independent phases, the sporophyte and gametophyte remain under separate selective regimes. The sporophyte determines gender, yet is distant from the timing of gametogenesis so that gametophytes cannot control their sex ratio in response to local population structure and environmental conditions. This life history offers no mechanisms to escape sporophytic hegemony, and thus represents an evolutionary regression from the more advanced of the homosporous life histories, wherein gametophytes have regained a measure of control over their own fates. *Platyzoma** is the only known example of this life history, and its evolutionary importance has been grossly inflated; soon after its discovery, Sussex (1966) cautioned against regarding *Platyzoma** as more than an evolutionary novelty. If heterospory routinely evolved via such an 'intermediate' it would have had to pass repeatedly through the eye of the ecological needle. Such improbable scenarios reflect *a priori* acceptance of gradual, adaptively-driven evolution as the only means of morphological change, and the desire to incorporate all known forms into linear, unidirectional patterns of evolution. In a reversal of conventional wisdom, process has been allowed to dictate pattern.

(c) Ecological perspective

Any credible explanation of the evolution of heterospory requires consideration of its ecological consequences. As we have already noted, extant heterosporous lineages are most effective in aquatic and amphibious environments if sexual; exceptions to this rule are dominated by asexual apomictic life histories. Rather than being a consequence of competition with other groups of plants, this restriction reflects the consequences of broadcasting into the environment endosporic gametophytes with predetermined gender; that is, as functional gametes. The ecological restrictions of heterospory are similar to those of fish and amphibians, which release spermatozoa and ova into the environment and require free water for successful reproduction. However, non-motile tracheophytes are even more restricted than non-amniotic vertebrates; they cannot migrate to water bodies during the reproductive season and hence must occupy suitable habitats year-round (e.g. Bateman & DiMichele, 1994).

The unity of the individual in the face of selection may be a key innovation of heterospory, and the feature that permitted the invasion of aquatic and amphibious habitats. However, given the non-functionality of heterospory in dry, *terra firma* settings, the transition to aquatic–amphibious habit cannot realistically be envisaged as gradual and passing through many intermediate stages. Heterosporous free-sporing plants do not have the reproductive adaptations to flourish in dry environments, and homosporous free-sporing plants face strong selective barriers in the transition from terrestrial to aquatic habitats due to the need for co-evolution of independent life-history phases. There is no habitat in which 'intermediate' forms have any advantage over exosporic homospory, and they cannot live in the environments available to endosporic heterospory. Endosporic sexual reproduction is dysfunctional in dry habitats. Thus, we envision the transition to aquatic life-styles as opportunistic – the result of evolutionary happenstance. The basal members of heterosporous lineages passed *selective filters* in their ecological transformation, analogous to those influencing the evolution of modern serpentine and mine-tailing specialists (DiMichele *et al.*,

1987) – either the plant can grow in the habitat or it cannot. High, environmentally induced extrinsic stresses tend to reduce the intrinsic stresses that typically result from biotic competition.

In addressing the critical issue of endospory and its ecological consequences, Haig & Westoby (1988*a*) envisioned a more broadly construed regime, related to xeric environments, that selected against exosporic gametophytes. Although we agree that heterospory is likely to survive in habitats that select against exosporic gametophytes, we note that dry environments also select against endosporic gametophytes. Haig & Westoby's scenario was intended to accommodate formal, population-genetics models that presupposed only gradual neo-Darwinian evolution.

Chaloner & Hemsley (1991: 154) argued that heterospory 'successfully challenged homospory...[and] showed its "competitive edge" most effectively'...'in the late Devonian and early Carboniferous'. Seed-plants are then believed to have 'challenged heterospory in the majority of habitats'. This prevailing view in palaeobotany is again rooted in the acceptance of gradual evolution as axiomatic. Our ecological interpretation suggests that heterosporous plants are unlikely to have competed extensively with homosporous plants. Rather, heterosporous species ventured into under-exploited habitats. Furthermore, although the first seed-plant probably evolved in an aquatic or amphibious setting where it may have competed with its heterosporous ancestor, the radiation of seed-plants occurred largely on the land where most of their serious competitors were probably homosporous.

An ecological perspective resolves an apparent contradiction aptly expressed by Chaloner & Hemsley (1991: 154): 'heterosporous plants seem to represent a kind of valley in the topography of success, between the highlands of homospory on one side and seed plants on the other...'. Rather than an adaptive valley, heterospory is a narrow specialist life history that dominated tropical aquatic and amphibious habitats through most of the Carboniferous (Phillips & Peppers, 1984; DiMichele *et al.*, 1985, 1992). There is no reason to believe that because homosporous plants preceded heterosporous plants morphologically they were also obliged to share specific physical resources. Similarly, there is no evidence that competition with seed-plants drove heterosporous plants from their ecological dominance of the wetlands, where they enjoyed 'home-field advantage' *sensu* Pimm (1991). Rather, palaeoecological patterns suggest that they were eventually removed by profound changes in global climate. Only these extrinsic forces, which precipitated the demise of the entire Carboniferous wetland biota, free niches for subsequent occupation by homosporous pteridophytes and strongly heterosporous seed-plant (DiMichele *et al.*, 1987, 1992).

(4) *Total sporophytic control : seed habit*

Seed-producing plants are heterosporous in both phylogenetic and functional terms. Consequently, heterosporous reproduction *sensu lato* can be described as the dominant mode of reproduction in most extant plant communities. The ecological and taxonomic diversity of seed-plants is unrivalled, and much has been written in attempting to explain their evolutionary success. Many of these ideas were synthesized in a series of detailed adaptive scenarios by Haig & Westoby (1989, fig. 2), who recognized two main suites of evolutionary innovations. The first suite concerned modifications to the megaspore and megasporangium : megaspore abortion and retention on the sporophyte,

integumentation, and improved sporophytic provisioning of the megaspore, reflected in modified megaspore and megasporangium wall structure and thickness. All of these features occur in other clades that show well-developed heterospory (Fig. 13). The second suite of characters concerns pollination biology: modifications of the megasporangial unit for microspore capture, delay of resource commitment until pollination and/or fertilization has occurred, pollen tube formation (initially haustorial but later co-opted for siphonogamy), and exclusion of pathogens following pollination. To these criteria can be added the pre-abscission formation of embryos and acquisition of dormancy mechanisms (Chaloner & Pettitt, 1987; Mapes, Rothwell & Haworth, 1989). Only the first of these six innovations has been unequivocally demonstrated in non-spermatophytes; the remainder are characteristic of the seed-plants and, according to Haig & Westoby (1989), reflect escalation caused by inter-male competition. Evolution of the two suites of innovations was largely independent, although Haig & Westoby perceived both as being driven by a series of positive feedback loops that led inexorably to progressively increased megaspore size (see Heterosporous Systems above).

Here, our primary interest is understanding the origin(s) of the earliest seed-plants, and their evolutionary and ecological relationships with other contemporaneous lineages possessing well developed heterospory. We will therefore emphasize the initial seed-plant radiation of lyginopterid and calamopitid pteridospermaleans during the Upper Devonian and Lower Carboniferous (Gillespie *et al.*, 1981; Knoll, 1986; Niklas, 1986; Scheckler, 1986; Retallack & Dilcher, 1988; Rothwell & Scheckler, 1988; DiMichele *et al.*, 1989, 1992; Bateman, 1991b; Stewart & Rothwell, 1993). If the evidence summarized by Haig & Westoby (1989) is viewed phylogenetically, it becomes obvious that many of the reproductive characters widely believed to delimit seed-plants either occur in the more sophisticated members of several other clades or are confined to the more derived members of the seed-plant clade (Fig. 13). This greatly reduces the ranges of relevant characters and clades. We will briefly consider a few examples of such characters, outlining in passing new angles on a couple of classic evolutionary stories.

Most studies of seed-plant evolution have focused on progressive elaboration of the integument – in other words, on the development of structurally modern seeds (Thomson, 1927, 1934; Arnold, 1938; Walton, 1953; Andrews, 1963; Smith, 1964; Long, 1966; Pettitt, 1970; Niklas, 1981; Steeves, 1983). However, such studies actually document the Palaeozoic radiation of seed-plants rather than the *origin* of the seed habit (DiMichele *et al.*, 1989; Haig & Westoby, 1989). In relatively derived pteridospermaleans the integument is well adapted to fulfil all three of its presumed functions: protecting the megaspore, limiting the access of the gametophyte to sporophytic resources, and capturing microspores. However, the deeply lobed, 'open' integuments of early seed-plants were at best highly inefficient in all these roles; much less effective than the integuments of the Carboniferous lycopsid *Lepidophloios*, for example. The fully functional integument is less generalized than the seed-plants, and the partially functional integument is far more generalized than the seed-plants as a result of convergence.

Similarly, early seed-plant megaspores share wall ultrastructural traits with the megaspores of putatively free-sporing progymnospermopsids such as *Archaeopteris* (Hemsley, 1990, 1993; Chaloner & Hemsley, 1991). This similarity is not surprising,

assuming that the first seed-plant evolved from an archaeopteridalean ancestor, but it eliminates yet another character as a potential synapomorphy of the spermatophytes. Nonetheless, it is noteworthy that the megaspore exines of other highly heterosporous groups, such as the rhizomorphic lycopsids, are deposited early in ontogeny and therefore designed to expand greatly to accommodate the provisioning of the megaspore. The megaspore exines of progymnospermopsids and early pterido-spermaleans lacked this ability to expand, and presumably were deposited after megaspore provisioning (Hemsley, 1993). These observations indicate delayed onset of sporopollenin deposition – a form of paedomorphosis known as postdisplacement (e.g. Alberch *et al.*, 1979). More importantly, they both imply a more efficient mode of megaspore provisioning in seed-plants and at the same time explain why a new barrier, the integument, may have been required to maintain the nutritional *status quo* between the now economically parasitic megaspore and the host sporophyte.

Abortion of megasporocytes and megaspores to leave only one functional megaspore is also widely discussed as a key feature of seed-plants, but it is in fact highly iterative (Fig. 13). This does not reduce the traditional importance of monomegaspory as a pre-requisite for economically sound seeds, but here we highlight monomegaspory primarily because recent observations on oogenesis and fertilization in mice (Agulnik, Agulnik & Ruvinsky, 1990; Agulnik, Sabantsev & Ruvinsky, 1993; Pomiankowski & Hurst, 1993) suggest that it may have profound genetic implications. Three of the four products of meiosis are aborted during mammalian oogenesis, in parallel with the megasporogenesis of monomegasporic plants. However, studies of Siberian mice have revealed at least one example of powerful meiotic drive – biasing the viable products of meiosis in favour of a particular gene or gene complex. Meiotic drive can result in wildly non-Mendelian genetic behaviour, allowing mutations capable of influencing meiosis to spread rapidly through allogamous populations. We can only speculate on whether meiotic drive occurs in monomegasporic plants and, if so, what kind of advantages (or disadvantages) it might confer.

Returning to potential synapomorphies of the spermatophytes, it seems most likely that the key reproductive breakthrough made by seed-plants was simply effective pollination (Haig & Westoby, 1989). Delivery of the full predetermined, endospermic male gametophyte to the female gametophyte by-passed the physical environment as a selective filter for successful syngamy (even ineffective delivery would have been advantageous in Late Devonian, when there were few if any competitors for resources in water-limited habitats). Sporophyte and gametophyte effectively function as a single organism (note that this feature is convergent between the life histories of seed-plants and higher animals).

However, some of the Devono-Carboniferous plants that we currently consider to have possessed a free-sporing life history may in reality have experienced regular (if not invariable) delivery of microspores to the megasporangia. Even without integuments, or without reduction to a single functional megaspore, plants possessing such systems would acquire the same increased ecological potential to colonize terrestrial habitats as those possessing the *bona fide* seed habit (Pettitt & Beck, 1968; Gensel & Andrews, 1984; Stewart & Rothwell, 1993). Unfortunately, pteridophytes possessing rudi-mentary pollination systems would be morphologically indistinguishable from free-sporing heterosporous lineages.

We do not insist that such primitive pollination systems ever existed; this intellectual exercise merely serves to emphasize that the earliest phases of seed evolution primarily concerned extrinsic ecology rather than intrinsic structure. By evolving *reliable* pollination, seed-plants crossed a critical functional threshold; they were the first clade able to fully exploit the resources of the land surface. In the Late Devonian and Early Carboniferous there would have been little competition for those resources in most habitats with surficial moisture limitation, implying that early seed-plant evolution occurred under low selection pressures (DiMichele *et al.*, 1989, 1992).

Nonetheless, it is difficult to envision a series of functional ecological intermediates between free-sporing heterospory and the seed habit. Allogamous heterospory requires pollination for success in the terrestrial environment. In order to reproduce successfully in surficially dry environments, a heterosporous plant must already possess a system to deliver the microspore to the megasporangium. Thus, there exists an 'adaptive valley' between aquatic–amphibious, free-sporing heterospory and the seed habit (Chaloner & Pettitt, 1987) that no degree of 'intermediate' ovule morphology can effectively bridge. It is therefore logical to assume that seed-plants were pre-adapted for invasion of *terra firma* environments, and that pollination therefore evolved in the aquatic–amphibious settings most effectively occupied by heterosporous pteridophytes.

Lastly, we note that there are dangers in focusing too heavily on selected features of a plant when attempting to explain the relative phylogenetic and ecological success of lineages. Any plant responds to its environment as an integrated holistic organism. Its ability to grow in a particular habitat requires a range of specialized physiological and structural traits distributed throughout the bauplan of the sporophyte (and gametophyte). In the case of seed-plants, much can be learned by briefly comparing an early pteridospermalean such as *Hydrasperma* with the very distantly related but reproductively sophisticated rhizomorphic lycopsid *Lepidophloios*. It is difficult to argue that *Hydrasperma* was reproductively more sophisticated (or better adapted) than *Lepidophloios*, but very easy to argue that it was greatly superior in economic–vegetative terms. Unlike *Lepidophloios*, *Hydrasperma* possessed indeterminate growth, a highly developmentally differentiated rooting system, secondary phloem and megaphyllous leaves. These characters – all probably inherited from its putative progymnospermopsid ancestor, albeit with some modification (e.g. Trivett, 1993) – were at least as important as the seed habit in allowing hydrasperman pteridospermaleans to radiate into water-limited environments (Bateman & Scott, 1990), leaving *Lepidophloios* as a wetland specialist doomed to extinction upon climate change (DiMichele *et al.*, 1985). The resulting rapidly increasing diversity of structural features that accompanied the early seed-plant radiation was curtailed only by the eventual onset of ecological saturation (e.g. Valentine, 1980).

VIII. SUMMARY

(1) In aggregate, past discussions of heterospory and its role in the alternation of generations are riddled with ambiguities that reflect overlap of terms and concepts. Heterospory *sensu lato* can be analyzed more effectively if it is fragmented into a series of more readily defined evolutionary innovations: heterospory *sensu stricto* (bimodality of spore size), dioicy, heterosporangy, endospory, monomegaspory, endomegasporangy, integumentation, lagenostomy, *in situ* pollination, *in situ* fertilization, pollen

tube formation, and siphonogamy (Tables 1, 2, Figs 1, 13). Current evidence suggests that the last five characters are confined to the seed-plants.

(2) The fossil record documents repeated evolution of heterosporous lineages from anisomorphic homosporous ancestors. However, interpretation is hindered by disarticulation of fossil sporophytes, the difficulty of relating conspecific but physically independent sporophyte and gametophyte generations in free-sporing pteridophytes, the inability to directly observe ontogeny, and the rarity of preservation of transient and/or microscopic reproductive phenomena such as syngamy and siphonogamy. Unfortunately, the rarely preserved phenomena are often of far greater biological significance than corresponding readily preserved phenomena (e.g. heterospory versus dioicy, heterosporangy versus endospory).

(3) In most fossils gametophyte gender can only be inferred by extrapolation from the morphology of the sporophyte and especially of the spores. This is readily achieved for species possessing high-level heterospory, when the two spore genders have diverged greatly in size, morphology, ultrastructure and developmental behaviour. However, the earliest stages in the evolution of heterospory, which are most likely to be elucidated in the early fossil record of land-plants, also show least sporogenetic divergence. It is particularly difficult to distinguish large microspores and small megaspores from the large isospores of some contemporaneous homosporous species (Figs 3–6 a, g). Heterospory is best identified in fossils by quantitative analysis of intrasporangial spore populations.

(4) The spatial scale of the differential expression of megaspores and microspores varies from co-occurrence in a single sporangium (anisospory) to different sporophytes (dioecy) (Figs 6–8). Studies of the relative positions of the two spore morphs on the sporophyte, and of developmentally anomalous terata (Fig. 9), demonstrate that gender is expressed epigenetically in both the sporophyte and gametophyte. Hormonal control operates via nutrient clines, with nutrient-rich microenvironments favouring femaleness; megaspores and microspores compete for sporophytic resources. External environments can also influence gender, particularly in free-living exosporic gametophytes.

(5) The evolution of heterospory was highly iterative. The number of origins is best assessed via cladograms, but no current phylogeny includes sufficient relevant tracheophyte species. Also, several extant heterosporous species differ greatly from their closest relatives due to high degrees of ecological specialization and/or saltational evolution; extensive molecular data will be needed to ascertain their correct phylogenetic position. Current evidence suggests a *minimum* of 11 origins of heterospory, in the Zosterophyllopsida (1: Upper Devonian), Lycopsida (1: Upper Devonian), Sphenopsida (?2: Lower Carboniferous), Pteropsida (?4: Upper Cretaceous/Palaeogene) and Progymnospermopsida (?3: Upper Devonian/Carboniferous). The arguably monophyletic Gymnospermopsida probably inherited heterospory from their progymnospermopsid ancestor (Table 3, Figs 11–13). No origin of heterospory coincides with the origin of (and thus delimits) any taxonomic class of tracheophytes. The actual number of origins of heterospory is probably appreciably higher, exceeding that of any other key evolutionary innovation in land-plants and offering an unusually good opportunity to infer evolutionary process from pattern.

(6) Heterospory reflects the convergent attainment of similar modes of reproduction

in phylogenetically disparate lineages. Nature repeated this experiment many times, whereas true phylogenetic synapomorphies evolve only once and require a unique causal explanation. Cladograms also offer the best means of determining the sequence of acquisition of heterosporic phenomena within lineages, here exemplified using the lycopsids (Fig. 10). Comparison of such sequences *among* lineages can potentially allow generalizations about underlying evolutionary mechanisms. Current evidence (albeit inadequate) indicates broadly similar sequences of character acquisitions in all lineages, though they differ in detail. Some logical evolutionarily stages were temporarily bypassed. Other lineages appear to have acquired two or more characters during a single saltational evolutionary event. Heterosporic phenomena can also be lost during evolution. Although no complete reversals to homospory have been documented, this could reflect unbreakable developmental canalization of heterospory rather than selective advantage relative to homospory. Several extant species refute widely held assumptions that certain phenomena, notably heterospory and dioicy, are reliably positively correlated. Moreover, some fossils are likely to possess combinations of heterosporic characters that are not found in their extant descendants. Fossil data have played a crucial role in understanding both the number of origins of heterospory and the ensuing patterns of character acquisition.

(7) Although non-adaptive evolutionary events are likely in at least some lineages, the highly iterative nature of heterospory and similar patterns of character acquisition in different lineages together suggest that its evolution was largely adaptively driven. However, many previous adaptive models of heterosporic evolution confused pattern and process, and paid insufficient attention to the role of the environment as a passive filter of novel morphotypes. Linear gradualistic models were imposed on the data, often intercalating hypothetical intermediates where desired.

(8) The evolution of heterospory is best understood in terms of inherent antagonism between the sporophytic and gametophytic phases of the life history for control of sex ratio and reproductive timing. Control is achieved directly by the gametophyte, via gametogenesis, and indirectly by the sporophyte, via sporogenesis and the ability to determine to varying degrees the environment in which the gametophyte undergoes sexual reproduction. Increasing levels of heterospory (particularly the acquisition of endospory) compress the heteromorphic life history, as the increasingly dominant sporophyte progressively co-opts the sex determination role of the gametophyte. The resulting life history is more holistic, effectively streamlining evolution by offering only a single target for selection.

(9) However, by wresting control of sex ratios from the gametophyte, the ability of the sporophyte to respond rapidly to environmental changes decreases. This competitive weakness is greatest for heterosporous species possessing exosporic but obligately unisexual gametophytes (epitomized by the pteropsid *Platyzoma**). It can be alleviated in endosporic species by occupying favourable environments (e.g. the aquatic Salviniales and Marsileales), switching to an apomictic mode of reproduction (thereby incurring inbreeding depression; e.g. many selaginellaleans), or acquiring more complex pollination biologies (thereby by-passing the environment as a selective filter: the seed-plants).

(10) Lineages differ greatly in the maximum number of heterosporic characters that were acquired by their most derived constituent species. Several Devono-

Carboniferous lineages reached the level of reducing numbers of functional megaspores to one per sporangium (Figs 7*e*,*f*, 8, 13), but only the putatively monophyletic gymnospermopsids broke through this apparent barrier to acquire the increasingly complex pollination biology that characterizes modern seed-plants.

(11) Many theories have been proposed to explain the remarkable success (both in terms of species diversity and ecological dominance) of seed-plants. The majority focus on characters that are absent from the earliest seed-plants (the Devono-Carboniferous lyginopterid pteridospermaleans), which were no more reproductively sophisticated than other penecontemporaneous lineages possessing advanced heterospory (particularly the most derived lycopsids, equisetaleans and progymnospermopsids). Reliable pollination was a key reproductive breakthrough, though the sophisticated economic–vegetative characters inherited by the earliest seed-plants from their putative progymnospermopsid ancestors were probably equally important in ensuring their success in water-limited habitats.

(12) With the exception of some ecologically specialized pteropsids, known heterosporous lineages originated during a relatively short period in the Upper Devonian and Carboniferous (Fig. 11). They exploited a window of opportunity that existed before niches became too finely partitioned and saturated with seed-plant species. This non-uniformitarian ecology renders negligible the probability of new heterosporous lineages becoming *established* today, even though 'hopeful monsters' possessing 'incipient heterospory' are probably constantly being generated from homosporous parents.

IX. ACKNOWLEDGEMENTS

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