



Filial mistletoes: the functional morphology of moss sporophytes

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1 ORIGINAL ARTICLE

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3 **Filial mistletoes: alternation and altercation**
4 **of generations in mosses**

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20 Running Title: Parent–offspring conflict in mosses

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1 *Background* A moss sporophyte inherits a haploid set of genes from the maternal
2 gametophyte to which it is attached and another haploid set of genes from a paternal
3 gametophyte. Evolutionary conflict is expected between genes of maternal and paternal
4 origin that will be expressed as adaptations of sporophytes to extract additional resources
5 from maternal gametophytes and adaptations of maternal gametophytes to restrain
6 sporophytic demands.

7 *Interpretation* The seta and stomata of peristomate mosses are interpreted as sporophytic
8 devices for increasing nutrient transfer. The seta connects the foot, where nutrients are
9 absorbed, to the developing capsule, where nutrients are needed for sporogenesis. Its
10 elongation lifts stomata of the apophysis above the boundary layer, into the zone of
11 turbulent air, thereby increasing the transpirational pull that draws nutrients across the
12 haustorial foot. The calyptra is interpreted as a gametophytic device to reduce
13 sporophytic demands. The calyptra fits tightly over the intercalary meristem of the
14 sporophytic apex and prevents lateral expansion of the meristem. While intact, the
15 calyptra delays the onset of transpiration.

16 *Predictions* Nutrient transfer across the foot, stomatal number, and stomatal aperture are
17 predicted to be particular arenas of conflict between sporophytes and maternal
18 gametophytes, and between maternal and paternal genomes of sporophytes.

19

20 Key words: moss; calyptra; seta; stomata; transpiration; parent–offspring conflict

21

1 Sporophytes of mosses, liverworts, and hornworts are often described as parasites on the
2 gametophytes to which they are attached and from which they are nourished (Haberlandt,
3 1886; Vaizey, 1888; Goebel, 1905; Jennings, 1928; Raven, 2002b). Roth (1969) rejected
4 this label because gametophyte and sporophyte were two stages of a single life history
5 that underwent coordinated growth whereas parasitism was properly an antagonistic
6 interaction between individuals of different species. He preferred to describe relations
7 between haploid and diploid generations as gonotrophy (nutrition from a progenitor).
8 Matrotrophy (nutrition from a mother) is a term of similar meaning (Graham and Wilcox,
9 2000). Whatever label is used, relations between diploid progeny (sporophytes) and
10 haploid progenitors (gametophytes) are expected to be neither perfectly harmonious nor
11 purely antagonistic whenever sporophytes possess paternal alleles that are absent in
12 maternal gametophytes (Haig and Wilczek, 2006).

13 There are two ways to conceptualize genetic individuals (genets) when a
14 sporophyte grows attached to a gametophyte. The more familiar is to recognize the two
15 generations as distinct individuals. The less familiar is to recognize the maternal haploid
16 genet as extending across the gametophyte-sporophyte boundary into the sporophyte. In
17 the orthodox account, the boundary between genets separates diploid from haploid
18 tissues. In the heterodox account, two haploid genets (mum and dad) are physically fused
19 in the sporophyte but nevertheless maintain distinct genetic interests. All mum's genes
20 are present in both generations and benefit from the same outcomes whether a particular
21 gene is expressed in the gametophyte or sporophyte. By contrast, paternal genes are
22 absent from mum and, for this reason, are subject to different selective forces from those
23 experienced by maternal genes. Here, and in the remainder of this paper, I adopt the

1 convention that haploid parents are mums and dads (monosyllabic) to distinguish them
2 from diploid mothers and fathers (bisyllabic) of tracheophytes.

3 A sporophyte's maternal genome is transmitted in its entirety to all other sexual
4 and asexual offspring produced by its mum, but the sporophyte's paternal genome may
5 be absent from the mum's other offspring, either because these are produced asexually or
6 because they are sired by a different dad. Therefore, genes of maternal origin will favor
7 allocations of limited resources among multiple offspring that maximize mum's fitness,
8 whereas genes of paternal origin will favor increased investment in their particular
9 sporophyte at the expense of other sporophytes or asexual propagules produced by mum.
10 Interactions between the generations are expected to exhibit a high degree of
11 coordination, because a sporophyte and its mum have a mutual interest in each other's
12 well-being, on account of the genes they share, but conflicts arise nevertheless because
13 sporophytes also inherit genes from their dads (Haig and Wilczek, 2006).

14 Conflict between genes of mums and dads can be illustrated by considering the
15 selective forces acting on X-linked and Y-linked genes of mosses with XY sporophytes
16 (Ramsay and Berrie, 1982). Sporophytes always inherit X chromosomes from their
17 mums. Therefore, X-linked genes will favor a distribution of resources among a mum's
18 asexual and sexual progeny that maximizes the mum's fitness. By contrast, Y-linked
19 genes are always inherited from a sporophyte's dad and will be absent from a mum's
20 asexual offspring and from sexual offspring sired by other dads. Therefore, Y-linked
21 genes will favor their sporophyte receiving more maternal resources than the amount
22 favored by X-linked genes.

1 Half the time an autosomal gene will be derived from a sporophyte's mum and
2 subject to the same selective forces as an X-linked gene. Half the time it will be derived
3 from a sporophyte's dad and subject to the same selective forces as a Y-linked gene.
4 Therefore, unimprinted autosomal genes will evolve phenotypic effects that are a
5 compromise between maternal and paternal optima, but imprinted autosomal genes will
6 evolve effects that enhance maternal fitness when inherited from mums but paternal
7 fitness when inherited from dads (Haig, 1997).

8 Three genetic factions can be identified, with distinct interests (Haig, 2006). The
9 first contains genes that are selected to maximize maternal fitness. These include genes
10 that are expressed in the maternal gametophyte and maternally-inherited genes expressed
11 in the sporophyte, including genes on X chromosomes or in the genomes of maternally-
12 inherited organelles (Natcheva and Cronberg, 2007; McDaniel *et al.*, 2007). Maternally-
13 expressed imprinted genes of the sporophyte also belong to this faction. The second
14 contains genes that are selected to maximize paternal fitness. These include Y-linked
15 genes and paternally-expressed imprinted genes. The third contains unimprinted
16 autosomal genes of the sporophyte. These genes evolve to favor a compromise between
17 maternal and paternal interests.

18 From a genetic perspective, conflict between genes of maternal and paternal
19 origin will be played out partly between haploid and diploid tissues at the gametophyte-
20 sporophyte interface and partly within diploid tissues of the sporophyte. From a
21 phenotypic perspective, sporophytes are predicted to exhibit paternally-encoded
22 adaptations for overcoming maternal constraints on nutrient transfer and maternal
23 gametophytes are predicted to possess adaptations for regulating resource transfer to

1 sporophytes. These predictions extend the theory of parent-offspring conflict (Trivers,
2 1974; Westoby and Rice, 1982; Queller, 1983) to the case of a diploid offspring
3 nourished by a haploid parent (Trivers and Burt, 1999; Haig and Wilczek, 2006).

4

5 **Gametophyte–sporophyte relations**

6 This section sketches the range of relations between haploid and diploid generations in
7 extant embryophytes (land plants) together with the phylogenetic distribution of stomata.
8 Subsequent sections will focus on peristomate mosses (including taxa that have
9 secondarily lost a peristome) and will emphasize the roles of stomata and calyptras in
10 sporophyte nutrition. The most recent common ancestor of mosses, and the most recent
11 common ancestor of liverworts, are much older than the most recent common ancestor of
12 angiosperms. By this criterion, mosses and liverworts each encompass much greater
13 phylogenetic diversity than flowering plants, including substantial variation in relations
14 between gametophytes and sporophytes. This paper cannot adequately review that
15 diversity. Therefore, I will often make general statements that are true of many mosses
16 but not of all. Comparative studies, especially studies that seek to understand exceptions
17 to general rules, will be an important means of testing ideas about intergenerational
18 conflict presented in this paper.

19 Figure 1 presents a phylogenetic hypothesis of relations of major taxa discussed in
20 this paper (based on Chang and Graham, 2011) onto which the presence of stomata are
21 mapped. Liverworts form a clade sister to all other embryophytes with mosses sister to a
22 hornwort–tracheophyte clade, and hornworts sister to tracheophytes (Qiu et al., 2007).
23 Molecular data suggest *Oedipodium* is the sister group to the peristomate mosses (Cox et

1 al., 2004) although this has been disputed on morphological grounds (Ligrone and
2 Duckett, 2011).

3 Diploid development begins when an egg is fertilized and the resulting zygote
4 divides to produce an embryo enclosed within the haploid epigonium. Sporophytes of
5 liverworts complete spore maturation while enclosed within the epigonium, close to the
6 source of maternal nutrients. Mature capsules of most species are then elevated on a
7 short-lived sporophytic seta. In the process, the epigonium is ruptured and the capsule's
8 contents exposed for spore dispersal. Neither gametophytes nor sporophytes of liverworts
9 possess stomata.

10 Sporophytic stomata are a general feature of the hornwort–tracheophyte clade.
11 Sporogenous tissues of hornworts are produced progressively from an intercalary
12 meristem. Older spores are found toward the apex, with newer spores toward the base, of
13 the linear capsule. In most hornworts, the sporophyte emerges from the epigonium while
14 spore production is ongoing, with exposed parts of the capsule bearing stomata. Stomata
15 have been lost independently from sporophytes of *Notothylas* and from sporophytes of a
16 clade containing *Megaceros*, *Nothoceros* and *Dendroceros* (Renzaglia *et al.*, 2009).
17 Sporophytes of *Phaeoceros laevis* exhibit high rates of photosynthesis but nevertheless
18 rely on organic molecules supplied by mum (Thomas *et al.*, 1978). Nutrients may also
19 flow in the other direction: nitrogen fixation by symbiotic cyanobacteria housed in
20 gametophytes of *Anthoceros punctatus* was supported by sporophytic photosynthesis
21 when gametophytes, but not sporophytes, were kept in the dark (Stewart and Rodgers,
22 1977).

1 Embryos of modern tracheophytes develop enclosed by maternal gametophytic
2 tissues (or by endosperm in flowering plants), but then produce a shoot and root that
3 emerge from the enclosing tissues and enable the sporophyte to become nutritionally self-
4 sufficient. Stomata are present on aerial parts of sporophytes. Maternal gametophytes are
5 usually short-lived relative to their sporophyte progeny.

6 Arrangements vary among mosses. Sporophytes of *Sphagnum*, *Andreaea*, and
7 *Andreaeobryum* develop enclosed within the epigonium until late in spore maturation.
8 Mature capsules of *Sphagnum* and *Andreaea* are elevated on a gametophytic
9 pseudopodium whereas mature capsules of *Andreaeobryum* are elevated on a short seta
10 that resembles the setae of liverworts (before cell elongation) more than the setae of other
11 mosses (Steere and Murray, 1976; Murray, 1988). By contrast, capsules of *Takakia*
12 rupture the epigonium and are elevated on a sporophytic seta before meiosis (Renzaglia
13 *et al.*, 1997). Sporophytes of *Takakia*, *Andreaea* and *Andreaeobryum* lack stomata
14 whereas *Sphagnum* capsules bear numerous pseudostomata. Whether pseudostomata are
15 homologous to stomata is disputed because they lack open pores and do not function in
16 transpiration (Boudier, 1988; Cox *et al.*, 2004; Duckett *et al.*, 2009a).

17 In peristomate mosses, an intercalary meristem produces a seta between the foot
18 and precursors of the future capsule (Fig. 1a). Setal elongation causes the epigonium to
19 rupture into an upper portion known as the calyptra and a lower portion known as the
20 vaginula. The calyptra remains tightly appressed to the apex of the sporophyte.
21 Sporogenesis occurs after the calyptra is shed (Fig 1b), exposing stomata at the base of
22 the developing capsule in a region known as the neck or apophysis. *Oedipodium* is
23 possibly the sister group of peristomate mosses (Cox *et al.*, 2004). Its sporophytes

1 possess numerous stomata on an elongated neck, or pseudoseta, and a capsule that is
2 exposed prior to maturity (Crum, 2007; Shimamura and Deguchi, 2008).

3 The calyptra of peristomate mosses is typically a robust, tightly-fitting structure
4 that covers the capsule-forming part of the sporophyte. A structure that corresponds to a
5 calyptra (i.e., an upper detached part of the epigonium) has a variable form in other
6 mosses. Calyptras of *Sphagnum* and *Andreaea* are relatively flimsy whereas calyptras of
7 *Andreaebryum* and *Takakia* are more substantial structures; the former covering the
8 entire capsule, the latter the upper part of the capsule only. Calyptras of *Andreaebryum*
9 and *Takakia* can be removed without adverse effects on sporophyte development
10 (Murray, 1988; Renzaglia *et al.*, 1997). The calyptra of *Oedipodium* is small and readily
11 detached (Crum 2007).

12 There are at least three competing scenarios of the evolutionary origin of stomata.
13 (1) Stomata have a single origin in a common ancestor of mosses and the hornwort-
14 tracheophyte clade (Ligrone *et al.*, 2012). Recent discoveries of shared mechanisms of
15 stomatal control in mosses and tracheophytes have been interpreted as supporting this
16 hypothesis (Bowman, 2011; Chater *et al.*, 2011; Fig. 2a). This scenario implies secondary
17 loss of stomata in *Takakia*, *Andreaea*, and *Andreaebryum*, and loss of a stomatal role in
18 transpiration in *Sphagnum*. (2) Stomata evolved twice; once in an ancestor of peristomate
19 mosses and once in an ancestor of hornworts and tracheophytes (Cox *et al.*, 2004;
20 Duckett *et al.*, 2009a; Fig 2b). In this scenario, pseudostomata of *Sphagnum* and stomata
21 of other mosses are not homologous. (3) Stomata of hornworts and tracheophytes are not
22 homologous (Pressel *et al.*, 2011). This implies at least three origins of stomata. The

1 resolution of this question—of one or more origins of stomata—does not substantially
2 affect the functional arguments of subsequent sections.

3 Stomata are absent in taxa with sporophytes that are enclosed in the epigonium
4 until after meiosis (liverworts, *Andreaea*, *Andreaebryum*, *Sphagnum*) but are present in
5 most taxa with sporophytes that emerge from the epigonium before meiosis (Fig. 2). This
6 association has exceptions. Capsules of *Takakia* lack stomata but are exposed before
7 meiosis (Renzaglia et al. 2007) whereas capsules of *Bryobartramia* possess stomata
8 despite enclosure of the sporophyte in a persistent epigonium (Stone 1977). Stomata have
9 been secondarily lost in many peristomate mosses, hornworts, and tracheophytes.
10 Gametophytic enclosure of the sporophyte until maturity has been conjectured to be
11 ancestral for embryophytes (Murray 1988). As an addendum, ‘escape’ from the
12 epigonium can be conjectured to have evolved independently in *Takakia*, peristomate
13 mosses, and the hornwort-tracheophyte clade, with two of these ‘escapes’ associated with
14 independent origins of stomata.

15

16

Food and water

17 Church (1919) proposed that transpiration evolved to promote parasitic absorption of
18 food from gametophytes. His hypothesis is worth quoting at length:

19

20 “Why should the diploid sporophyte initiate a transpiration current, and its associated stomatal
21 mechanism, when the homologous gametophyte, which started on equal terms failed to do so? A
22 little consideration, however, suggests that such a current was never initiated directly for the
23 purpose of absorbing water; that any elementary organism can recognize the nature of its
24 physiological problems and solve them directly is too much to expect. The successful solution of

1 any problem, as in the case of all biological mechanism, is always of the nature of an adaptation
2 of something pre-existing. The transpiration-current, in other words, traces its origin to the
3 haustorial absorption of food rather than water ... food-supply direct from the gametophyte is the
4 first need of a parasitic zygote; and in so inducing a haustorial drain, an upward current may be
5 initiated which may continue to take water. ... [The] transpiration-current which marks the
6 essentially new physiological mechanism allowing existence in less and less saturated air was
7 never 'invented' *de novo* for its special purpose; it began as a mechanism of parasitic nutrition,
8 and has been adapted to its special purpose ...” (pp. 71–72).

9

10 In many cases, description of sporophytes as parasites is probably intended as no more
11 than a rhetorical flourish but the theory of parent-offspring conflict suggests the epithet is
12 more than a trope. Sporophytic fitness is usually maximized by transfer of more resources
13 than maximizes maternal fitness. If transpiration has a major role in sporophytic nutrition,
14 then sporophytes should possess adaptations to increase transpiration and maternal
15 gametophytes adaptations to reduce transpiration.

16 Modern tracheophytes produce sporangia only after a sporophyte is nutritionally
17 self-sufficient and no longer receiving nutrients from its mum. Thus, adult transpiration
18 cannot constitute parasitism on maternal gametophytes. Ancestral tracheophytes however
19 may have possessed permanently-dependent sporophytes. Aerial axes of *Cooksonia*, and
20 other early vascular plants, possess stomata concentrated at the base of sporangia
21 (Edwards *et al.*, 1996), an arrangement compatible with apoplastic delivery of nutrients
22 to the sporangial base followed by symplastic transport to spore-forming tissues
23 (Edwards *et al.*, 1998). Boyce (2008) calculated that *Cooksonia* stems are often too
24 narrow to have been photosynthetically self-sufficient once allowance is made for

1 cuticular, transport, and support functions. Therefore, he concluded that *Cooksonia*
2 fossils are the remains of dependent sporophytes of unpreserved gametophytes and that
3 stomata functioned in transpiration-driven transport of solutes to sporangia. Church's
4 hypothesis thus receives some support from early tracheophytes. Below I will consider a
5 possible role of transpiration in 'parasitic' nutrition of moss sporophytes.

6

7

Stomata and setae

8 The mature sporophyte of a peristomate moss can be divided into four functional regions:
9 foot, seta, apophysis, and capsule. Sporophytes produce a single capsule and then die.

10 Therefore, the functions of foot, seta, and apophysis are to be sought in services provided
11 to the capsule's spores. The apophysis is formed by terminal differentiation of the cells of
12 the intercalary meristem (Kreulen, 1975; French and Paolillo, 1975a) and has been
13 variously interpreted as part of the seta or part of the capsule, but I will treat it as a fourth
14 region, distinct from seta or capsule. Stomata are restricted to the apophysis in many
15 peristomate mosses (Valentine, 1839; Haberlandt, 1914; Paton and Pearce, 1957).

16 Mitotic divisions of the intercalary meristem of peristomate mosses promote
17 elongation of the embryonic axis and thereby facilitate penetration of the foot into
18 gametophytic tissues (Vaizey, 1888; Uzawa and Higuchi, 2010). Downward penetration
19 requires that the sporophyte elongates faster than the epigonium and that gametophytic
20 tissues provide less resistance to expansion in the downward than upward direction. Setal
21 elongation eventually causes the epigonium to rupture into two parts, an upper calyptra
22 and lower vaginula. Subsequent elongation results in upward growth of the sporophyte

1 carrying the calyptra aloft. Capsule maturation and sporogenesis occur only after the
2 calyptra is split or shed.

3 Sporophytes of liverworts, *Sphagnum*, and *Andreaea* develop enclosed within the
4 epigonium until immediately prior to spore dispersal. Mature capsules of most liverworts
5 are then elevated on a sporophytic seta produced by elongation of existing cells without
6 cell division, whereas capsules of *Sphagnum* and *Andreaea* lack a seta and are elevated
7 on a gametophytic pseudopodium. By contrast, setae of peristomate mosses and *Takakia*
8 elongate before meiosis. Setae position capsules above the boundary layer of still air and
9 thereby facilitate long-distance dispersal of spores (Niklas, 2000; Raven, 2002a).

10 Why should peristomate mosses elongate their seta before spore maturation,
11 distancing the developing spores from their source of nutrition, placing them in a more
12 desiccating environment and exposing them to grazers? The paradox deepens when it is
13 noted that the ephemeral seta of liverworts is produced at less cost than the more robust
14 seta of mosses. The paradox is resolved if setal elongation enhances spore nutrition. The
15 moss seta can be compared to a waxed drinking straw that functions as a low resistance
16 conduit for water transport from the foot, where nutrients are absorbed, to the developing
17 capsule, where nutrients are unloaded for sporogenesis. Setal elongation lifts the stomata
18 of the apophysis above the boundary layer, into the zone of turbulent air, thereby
19 increasing evaporative water loss and strengthening the transpirational pull that draws
20 maternal nutrients across the haustorial foot. Sporophytes suck.

21 Stomatal function is commonly viewed as mediating a tradeoff between influx of
22 CO₂ (benefit) and efflux of water vapor (cost). However, evaporative water-loss may
23 benefit sporophytes if transpiration brings nutrients to the developing capsule (Ligrone

1 and Gambardella, 1988). Transpiration could serve both functions, delivery of nutrients
2 and maintenance of high rates of carbon fixation, but one can ask what is the relative
3 importance of these processes in any particular case. If the principal function of
4 transpiration is to replace water lost as a side-effect of photosynthesis, then natural
5 selection will promote efficient use of water relative to amount of carbon fixed. If on the
6 other hand, its principal function is to draw nutrients from the maternal gametophyte,
7 then water use will be profligate relative to photosynthetic carbon gain.

8 All moss sporophytes depend on their mum for inorganic nutrients but vary,
9 among species, in their dependence on maternal sources of fixed carbon. In some species,
10 almost all organic molecules are supplied by mum. In others, a substantial proportion is
11 supplied by sporophytic photosynthesis (Haberlandt, 1886; Rastorfer, 1962; Krupa, 1969;
12 Proctor, 1977). Net sporophytic photosynthesis occurs in *Funaria hygrometrica* but not
13 in *Polytrichum juniperinum* (Paolillo and Bazzaz, 1968) Despite this difference, *Funaria*
14 and *Polytrichum* sporophytes have similar numbers of similar-sized stomata (Paton and
15 Pearce, 1957).

16 A cuticle is present on all surfaces of moss sporophytes except the foot (Vaizey,
17 1887). Stomata regulate the exchange of gases between the atmosphere and internal
18 spaces of the apophysis by opening and closing pores in this otherwise impermeable
19 epidermis. Even if the support of photosynthesis is a major function of transpiration, the
20 theory of parent-offspring conflict predicts that moss sporophytes should maintain open
21 stomata beyond the point that is optimal for maternal fitness. An analogy with
22 hemiparasitic angiosperms and their hosts is useful. Stomata of hemiparasites are able to
23 remain open when host stomata close because the costs of parasite transpiration are borne

1 by the host. In this way, a hemiparasite can continue to photosynthesize when its host's
2 stomata close to cope with parasite-exacerbated water stress. Parasites gain additional
3 advantages of maintaining open stomata if nutrients are obtained via the transpiration
4 stream (Press *et al.*, 1988; Shen *et al.*, 2006). Moss stomata, like the stomata of
5 hemiparasites (Press *et al.*, 1988), are often open at night (Paton and Pearce, 1957;
6 Garner and Paolillo, 1973; Renzaglia *et al.*, 2007) and close only when the capsule itself
7 starts to dehydrate (Paton and Pearce, 1957). Moss sporophytes remain turgid as
8 gametophytes wilt (Vaizey, 1887).

9 The proportion of permanently-open stomata increases as capsules of *Funaria*
10 *hygrometrica* mature, contributing to the desiccation of the capsule that occurs prior to
11 release of spores (Garner and Paolillo, 1973). Pseudostomata of *Sphagnum* capsules are
12 the primary site of water loss before discharge of the desiccated capsule (Duckett *et al.*,
13 2009a). Hornwort stomata open once and then remain open as the capsule desiccates
14 (Lucas and Renzaglia, 2002; Duckett *et al.*, 2009b; Pressel *et al.*, 2011).

15 Desiccation of the capsule in preparation for spore dispersal has been proposed to
16 be the original function of stomata with regulation of gas exchange acquired as a
17 secondary function early in the history of land plants (Duckett *et al.*, 2009a). Capsule
18 desiccation could remain the primary function of stomata of hornworts and
19 pseudostomata of *Sphagnum* because vapor loss in these taxa is not replaced by
20 transpiration. Stomata may also play an important role in desiccation during the final
21 stages of capsule maturation of peristomate mosses. This process would be facilitated by
22 interruption of transpiration. However, the maintenance of transpiration at earlier stages
23 of development suggests stomata serve some other function at these stages.

1

2

Border zones

3 There are two disjunct interfaces between maternal and offspring tissues after rupture of
4 the epigonium. At one end of the sporophyte, the foot is embedded in the vaginula (basal
5 interface) whereas, at the other end, the future capsule and intercalary meristem are
6 enclosed by the calyptra (distal interface). Interactions at both interfaces are expected to
7 show traces of a mixed history of conflict and collaboration, analogous to the interplay of
8 conflict and cooperation in mammalian placentas (Haig, 1993, 2010).

9

10

Basal interface

11 Moss placentas have attracted much recent interest with particular attention paid to the
12 distribution of ‘transfer cells’ (Ligrone and Gambardell, 1988; Ligrone *et al.*, 1993; Frey
13 *et al.*, 2001). Transfer cells are defined by the presence of wall ingrowths that increase a
14 cell’s surface area to volume ratio (i.e. the ratio of plasma membrane to cytoplasm) and
15 are believed to facilitate rapid secretion into, or rapid absorption from, the placental space
16 (Gunning and Pate, 1969; Browning and Gunning, 1979a). Most mosses have transfer
17 cells on both sides of the placenta. Placentas of *Andreaea*, *Andreaeobryum*, and
18 Polytrichales possess sporophytic transfer cells, but not gametophytic transfer cells, and
19 *Sphagnum* has transfer cells on neither side of the placenta. Ligrone *et al.* (1993)
20 commented that this variation “has no obvious (or even obscure) functional meaning.”

21 Without knowing what transfer cells secrete, and what they absorb, their function
22 is difficult to interpret in terms of either intergenerational cooperation or conflict. The
23 theory of parent–offspring conflict suggests sporophytic transfer cells might be expected

1 to secrete substances that increase sporophytic access to maternal resources whereas, in
2 some circumstances, gametophytic transfer cells might be expected to secrete substances
3 that inhibit the actions of sporophytic factors.

4 Limited data exist on the function of sporophytic transfer cells. The gradient of
5 cellular degeneration in advance of the foot of *Funaria hygrometrica* suggest the
6 secretion of hydrolytic enzymes. Excised sporophytes of this species absorb sucrose and
7 glucose from the medium, and rapidly convert glucose to sucrose (Browning and
8 Gunning, 1979a, b, c). Excised haustoria of *Polytrichum formosum* acidify the medium,
9 generating a proton gradient, which is used to drive uptake of amino acids (Caussin *et al.*,
10 1983; Renault *et al.*, 1989).

11 If the principal function of sporophytic transfer cells is to extract resources from
12 maternal gametophytes then one might predict conflict between maternal and paternal
13 genomes within sporophytes over their development. Transfer cells however are reported
14 from apogamous sporophytes of *Physcomitrium coorgense* (Lal and Narang, 1985). This
15 seems to argue against a major role of imprinted genes in the development of sporophytic
16 transfer cells because apogamous sporophytes develop without a paternal genome.

17 Even less is known about the function of gametophytic transfer cells. The
18 vaginula of *Funaria* fills with water when the sporophyte is removed (Bopp and Weniger,
19 1971), possibly an osmotic response to solutes secreted by gametophytic transfer cells.
20 Auxotrophic mutants of *Physcomitrella patens* growing on supplemented media provide
21 evidence of a barrier to free transport of metabolites from maternal gametophytes to early
22 embryos (Courtice *et al.*, 1978). In these experiments, mutants growing on supplemented
23 media were vigorous and cross-fertile but self-sterile. Therefore, metabolites moved

1 freely from the medium into gametophytes but not from gametophytes to young embryos.
2 Cross-fertility showed that viable gametes were formed and that sporophytes could
3 develop if the mutant maternal allele of sporophytes was complemented by a wild-type
4 allele from dad.

5 The placental space is littered with cellular debris as cell walls disintegrate in
6 advance of the sporophytic foot (Browning and Gunning, 1979a; Frey *et al.*, 2001;
7 Uzawa and Higuchi, 2010). This gross morphology suggests the aftermath of a struggle
8 between the generations. One might argue that maternal gametophytes facilitate ‘creative
9 destruction’ to nourish their offspring, but similar cell death is not observed when
10 gametophytes supply nutrients to asexual propagules such as gemmae (Ligrone *et al.*,
11 1996) nor in the placenta of ferns where cells of the two generations are closely
12 interdigitated (Ligrone *et al.*, 1993; Duckett and Ligrone, 2003). Haig and Wilczek
13 (2006) have suggested this difference may be explained by reduced intergenerational
14 conflict in ferns (relative to mosses) because a fern mum is committed to a single
15 sporophyte and lacks other options for reproductive investment, whereas a moss mum
16 may invest in multiple sporophytes as well as asexual progeny.

17 Considerable variation exists in the depth to which the sporophytic foot penetrates
18 maternal tissues (Roth, 1969; Ligrone *et al.*, 1993; Uzawa and Higuchi, 2010). The
19 presence or absence of barriers to unfettered flow between maternal and offspring tissues
20 is also variable. Apoplastic continuity between gametophytic and sporophytic hydroids is
21 present in *Bryum capillare* (Ligrone and Gambardella, 1988) and *Funaria hygrometrica*
22 (Browning and Gunning 1979c) whereas the two sets of hydroids are separated by a layer
23 of sporophytic transfer cells in *Timmiella barbulooides* (Ligrone *et al.*, 1982). The foot

1 does not penetrate as far as the maternal vascular strand in other mosses (Uzawa and
2 Higuchi, 2010).

3 The foot of *Funaria hygrometrica* is regionally differentiated with a basal part,
4 consisting of an epidermis with weakly-developed wall ingrowths plus a central core of
5 hydroids, embedded in the central vascular strand of the gametophyte. This region
6 appears specialized for water uptake and apoplastic transport. Above this region,
7 epidermal cells have strongly-developed wall ingrowths and lie adjacent to vaginular
8 cells with similar ingrowths. At this level, plasmodesmata connect epidermal cells of the
9 foot to each other and to the parenchymatous cortex present between epidermis and
10 hydroids. This region appears specialized for nutrient uptake from the vaginula and
11 symplastic transport. As the foot grades into the basal part of the seta, epidermal cells
12 lose wall ingrowths and surround a core of stereids, leptoids, and hydroids (Wiencke and
13 Schulz, 1975, 1978; Schulz and Wiencke, 1976).

14

15 *Distal interface*

16 The upper part of the epigonium of *Sphagnum* is torn irregularly as the capsule expands
17 (Valentine, 1837; Boudier, 1988). The calyptra of most peristomate mosses, by contrast,
18 is a robust structure that separates from the vaginula along a regular line of abscission. In
19 *Funaria hygrometrica*, the calyptra remains alive for months after its separation from the
20 rest of the maternal gametophyte (True, 1906). This section will discuss protective and
21 morphogenetic roles that have been ascribed to the calyptra, before considering how
22 these purported functions interact with the conflicting interests of maternal and paternal
23 genomes.

1 Sporophyte development takes place partially or completely enclosed within the
2 epigonium and its descendant parts, the calyptra and vaginula. Earlier separation of the
3 calyptra would result in shallower penetration of the foot into maternal tissues, and setal
4 elongation accelerates once the calyptra separates from the vaginula, just as capsule
5 expansion accelerates once the constraining bonds of the calyptra are broken. Thus, a
6 sporophyte's external form can be moulded by variation in the resistance of gametophytic
7 tissues to sporophytic expansion.

8 *Funaria hygrometrica* is by far the best-studied species with respect to calyptral
9 effects on development. Its calyptra is 2–5 mm long with a distal rostrum, an enlarged
10 sac-like middle, and a short basal collar that clasps the seta tightly. The intercalary
11 meristem of the sporophyte is initially located within the close-fitting rostrum. Apical
12 expansion begins when the sporophytic apex is withdrawn from the rostrum into the
13 calyptral sac. The apophysis expands first, with differentiation of stomata, followed by
14 expansion of the capsule and rupture of the calyptra (True, 1906; Garner and Paolillo,
15 1973; Paolillo, 1968; French and Paolillo, 1975*a, b, c*, 1976; Budke *et al.*, 2011).

16 The seta of *Funaria* bends to gain leverage for withdrawal of the sporophytic
17 apex from the calyptral rostrum (True, 1906; Paolillo, 1968; similar bending of the seta
18 accompanies rupture of the calyptra of *Pohlia nutans*, see Fig. 4 of Kreulen, 1975).
19 Interactions between the calyptra and sporophyte may not be purely physical however.
20 Oehlkers and Bopp (1957) isolated mutants causing premature withdrawal of the
21 sporophyte from the rostrum. This effect was determined by the calyptra's genotype, not
22 the sporophyte's, and was absent when calyptras were killed and then replaced.

1 Experimental manipulations provide direct evidence of a morphogenetic role of
2 the calyptra in shaping young sporophytes. Bopp (1957) reported extensive experiments
3 on the removal and replacement of the calyptra of *Funaria hygrometrica*. The intercalary
4 meristem of the sporophyte was closely appressed to the inner surface of the calyptra.
5 When the calyptra was replaced by a slightly larger calyptra from the same or a different
6 species, the meristem broadened until it tightly fitted the calyptra. Setal thickening was
7 similarly inhibited by calyptras that had been boiled in alcohol or distilled water before
8 being replaced on the sporophyte. When the tip of a calyptra was cut off, the setal
9 meristem broadened as soon as it had been pushed through the open end of the calyptra.
10 Growth-inhibitory substances were also detected in calyptras, but Bopp's experiments
11 indicated that the mechanical constraint provided by the calyptra was sufficient to prevent
12 setal thickening. Removal of the calyptra and broadening of the seta increased
13 transpiration through the seta (Bopp and Stehle, 1957).

14 Bopp's experiments were replicated by French and Paolillo (1975*b, c*, 1976), with
15 similar results and conclusions. Capsule expansion was accelerated when calyptras were
16 removed from older sporophytes whereas removal from younger sporophytes resulted in
17 prolonged intercalary growth without differentiation of a capsule. The meristem
18 expanded laterally when the calyptra was removed with an increase in the number of
19 meristematic cells in transverse sections. Stomata are usually oriented with their long
20 access parallel to the sporophytic axis but stomatal orientation was random when
21 calyptras were removed before division of guard cell mother cells. These effects of the
22 calyptra were determined largely by mechanical restraints on sporophyte development

1 because substitution of killed, chemically extracted, calyptras allowed normal growth and
2 capsule expansion.

3 Experimental results in *Funaria* cannot be generalized to all peristomate mosses.
4 Removal of the calyptra has variable effects among species (Bopp, 1956). *Physcomitrella*
5 *patens* and *Pyramidula tetragona* both belong to the Funariaceae and both possess short
6 setae. The calyptra of *Physcomitrella* is loosely connected to the sporophyte and easily
7 removed without morphogenetic effects (Hohe *et al.*, 2002) whereas the inflated calyptra
8 of *Pyramidula tetragona* never separates from the vaginula and the sporophyte matures
9 within an intact epigonium (Kara *et al.*, 2008). Excised sporophytes of *Mnium*
10 *cuspidatum* never form capsules if the calyptra is retained but often form capsules if the
11 calyptra is removed (Lowry, 1954). The calyptra of *Polytrichum juniperinum* splits along
12 one side and thus determines the plane of bilateral symmetry of the capsule. If the
13 calyptra is prematurely removed, there is minimal thickening of the seta but capsules
14 develop with radial symmetry (Paolillo, 1968). Capsules of *Atrichum rhystophyllum* are
15 malformed when the calyptra splits at atypical locations (Suzuki, 1982).

16 The calyptra has been proposed to protect the sporophytic apex from desiccation
17 (Goebel, 1895; True, 1906; Zielinski, 1909; Irmscher, 1912; Janzen, 1917; Bopp and
18 Stehle, 1957). From this perspective, the thick cuticle of the calyptra of *Funaria*
19 *hygrometrica* has been interpreted as a form of maternal care to prevent drying of the
20 sporophyte's tender tip (Budke *et al.*, 2011). The sporophytic tip wilts if the calyptra is
21 prematurely removed because the sporophyte only develops an effective cuticle on
22 surfaces as they are exposed during the course of normal development (Budke *et al.*,

1 2012). Parental care enabling offspring helplessness is a recurring theme in evolutionary
2 biology.

3 Normal sporophyte development depends on the presence of the calyptra and its
4 premature removal has adverse consequences for sporophyte fitness. But some effects of
5 the calyptra seem ‘designed’ to restrict nutrient transfer to the sporophyte. More copious
6 transpiration, and greater flow of nutrients, could be maintained through a thicker seta but
7 the calyptra tightly constrains lateral expansion of the intercalary meristem and limits
8 setal thickness. Moreover, transpiration is strongly inhibited while the calyptra covers the
9 apophysis. Such a mixture of maternal solicitude and restraint is precisely what is
10 predicted by modern evolutionary theory (Haig, 2010).

11

12

Biphasic nutrition

13 The properties of the calyptra suggest that postembryonic nutrition of the sporophyte is
14 biphasic. Most nutrients are probably transported by a symplastic route while the calyptra
15 occludes stomata of the apophysis. Once stomata are exposed, apoplastic transport via
16 hydroids is predicted to become a major route by which nutrients are translocated to the
17 developing capsule.

18 Such a biphasic pattern has been reported in *Funaria hygrometrica*: setal leptoids
19 degenerate before meiosis but transpiration in hydroids is maintained for another month
20 (Schulz and Wiencke, 1976; Wiencke and Schulz, 1978). Leptoids probably degenerate
21 about the time stomata become functional after calyptral rupture (cf. Garner and Paolillo,
22 1973). Wiencke and Schulz emphasized nutrient transport in the first phase and water

1 transport in the second, but hydroids probably play a role in nutrient transport during the
2 second phase (cf. Ligrone and Gambardella, 1988).

3

4 **Testing the predictions**

5 The major prediction of this paper is that moss sporophytes have evolved to take more
6 nutrients from maternal gametophytes than maternal gametophytes have evolved to
7 supply, resulting in ongoing evolutionary conflict. A major caveat should be mentioned.
8 Mum's haploid genome is conserved in its entirety in the offspring's diploid genome and
9 should act in the sporophyte to restrain excessive demands on mum. Thus, conflict is
10 predicted within sporophyte genomes between genes of maternal and paternal origin but
11 the theory does not predict how this conflict will be resolved.

12 Setal elongation before spore maturation places stomata above the boundary layer
13 and thus increases transpiration and the delivery of nutrients to the developing capsule.
14 Because nutrient translocation is predicted to be an important function of transpiration,
15 moss sporophytes are predicted to exhibit low water-use efficiencies. Open stomata at
16 night are expected. Before stomata are exposed to the atmosphere, however, nutrients
17 must be transferred to the growing tip of the sporophyte by other means. Sporophytes are
18 predicted to maintain lower osmotic potentials than gametophytes to facilitate movement
19 of water and solutes into the sporophyte from the gametophyte.

20 Maternal adaptations are expected at the placental interface to control rates of
21 nutrient transfer. These adaptations will be opposed by sporophytic or paternal
22 adaptations to increase transfer. As yet there have been few studies of placental
23 physiology in mosses. Moss developmental genetics is similarly in its infancy but the

1 theory predicts distinct roles for genes of maternal and paternal origin in placental and
2 stomatal development.

3 Comparative studies hold particular promise for testing the ideas presented in this
4 paper. Information about sporophyte nutrition is missing for key taxa. *Takakia* has
5 capsules borne on setae that elongate before spore maturity (like peristomate mosses) but
6 lack stomata. *Oedipodium* possesses numerous stomata on an elongated ‘pseudoseta’
7 (Crum, 2007; Shimamura and Deguchi, 2008). Hornwort sporophytes possess stomata
8 but exhibit rapid external conduction of water (Isaac, 1941). Studies of sporophytic water
9 relations and nutrition in these taxa will be of particular interest.

10 Considerable diversity exists among peristomate mosses in relations between
11 calyptras and sporophytes, in length of setae, and in number and distribution of stomata.
12 Sporophytes in the Polytrichaceae, for example, typically possess many, large stomata
13 associated with well-developed assimilative tissue in the apophysis, but some members of
14 the family have capsules without stomata (Paton and Pierce, 1957). An understanding of
15 how sporophyte nutrition differs between taxa with and without stomata will be of
16 particular interest. *Archidium* species, to take another example, produce the largest spores
17 of any moss in setaless capsules, without stomata, covered by a flimsy ‘calyptra’ that
18 tears irregularly as the capsule expands (Brown and Lemmon, 1985). Why this
19 combination of unusual features? *Archidium* is monoicous. The answer may, in part, be
20 related to diminished conflict associated with frequent self-fertilization of *Archidium*
21 gametophytes.

22 Dioicous mosses produce unisexual gametophytes, either male or female, whereas
23 monoicous mosses produce bisexual gametophytes. When a bisexual gametophyte

1 fertilizes itself, a sporophyte's dad is also its mum. The sporophyte and its single haploid
2 parent are genetically identical at all loci, except that each locus is present in double dose
3 in the sporophyte. Therefore, the genetic interests of maternal and paternal genes will
4 converge as the frequency of gametophytic selfing increases and the degree of conflict
5 will correspondingly diminish. Other things being equal, sporophytes of monoicous
6 mosses are predicted to have shorter setae, smaller capsules, fewer and smaller stomata,
7 and to be less profligate in their use of water than the sporophytes of dioicous mosses.
8 Bisexual gametophytes are likely to possess life histories and ecologies that differ from
9 unisexual gametophytes in many respects, so other things are unlikely to be equal, but
10 statistical and phylogenetic methods now exist for disentangling complex correlations.

11

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15

16

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1 Figure 1. (a) Longitudinal section of developing sporophyte and associated gametophytic
2 structures (*Phascum cuspidatum*, modified from Roth 1969). Gametophytic structures are
3 labelled on the left and sporophytic structures on the right. (b) Habit of *Polytrichum*
4 *commune* (modified from Goebel 1905). The leafy gametophyte bears two sporophytes.
5 The sporophyte on the left retains its gametophytic calyptra whereas the sporophyte on
6 the right has shed its calyptra.

7 Figure 2. Phylogeny of major groups of mosses with presence of stomata indicated by
8 open circles. Taxa in which the sporophyte is enclosed until after meiosis are underlined.

9 (a) Hypothesis in which there is a single origin of stomata from which pseudostomata of
10 *Sphagnum* were derived. (b) Hypothesis in which stomata evolved twice and with
11 pseudostomata of *Sphagnum* not homologous to stomata.

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