True kin recognition, in the form of somatic incompatibility, has multiple independent origins

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Grafen (1990) distinguished between 'true kin recognition' and other types of recognition (see also Barnard 1991). He argued that the term true kin recognition has a special meaning and that only one case of claimed kin recognition, that of clonal fusion in the ascidian, *Botryllus schlosseri*, qualifies. This possible true kin recognition system is an example of so-called 'somatic incompatibility' (alias allorecognition): the tendency selectively to accept or reject extended intimate contact with conspecifics. Here we argue that, if *B. schlosseri* exercises true kin recognition, then many other examples of 'somatic incompatibility', distributed through diverse taxa, are also instances of true kin recognition. Hence, true kin recognition may have multiple independent origins.

Grafen argued that any process of true kin recognition must not only permit an organism to discriminate kin from non-kin, but must also be maintained because of advantages accruing from this discrimination. Importantly, these advantages must be dependent on the discrimination being based on ancestral relatedness. A true kin recognition system can then be contrasted with examples of other recognition systems that are based on matching and that might have the effect of enabling an organism to distinguish between what is kin and what is non-kin but do not base this distinction on ancestral relatedness. Such recognition systems can be regarded only as 'kin bias' (Barnard 1991) and include species recognition, group recognition and individual recognition. True kin recognition systems can also be contrasted with those systems that make an accurate assessment of ancestral relatedness but in which relatedness is not important to the maintenance of the system. We conclude this note by arguing that graft rejection is an example of this form of recognition.

The evolution of a true kin recognition system depends upon three kinds of loci (Grafen 1990): detection, matching and using (see also Hamilton 1964). Advantages accrued from the action of the user loci (kin selective or avoiding inbreeding depression) must be dependent upon ancestral relatedness. It is hence critical to Grafen's definition of true kin recognition that the matching locus distinguishes on the basis of ancestral relatedness. Polymorphism of rare alleles at the matching loci is essential for the effective discrimination of kin. In sum, to qualify a system as one of true kin recognition, this polymorphism at the matching loci must allow an accurate assessment of ancestral relatedness in which the relatedness is important to the maintenance of the polymorphism.

Aggregated settlement of fusible larvae of *B. schlosseri* (Grosberg & Quinn 1986) may involve a true kin recognition system under the above stipulations (Grafen 1990). Adjacent colonies of *B. schlosseri* grow into each other and can fuse to form a chimera. In so doing they may benefit from increased size, lower age of first reproduction and tolerance of a wider range of environmental variables. Colonies that enter a chimeral alliance are, however, threatened by the costs of 'somatic cell parasitism' in which one member increases its contribution to overall reproduction relative to the other (see Buss 1982). The transfer of conventional parasites may represent a further cost. *Botryllus schlosseri* possesses a genetically based histocompatibility system in which fusion is restricted almost entirely to closely related individuals on the basis of the sharing of at least one allele at a highly polymorphic matching locus. Similarity at this polymorphic locus is a reliable indication of ancestral relatedness. Further, by fusing predominantly with kin, inclusive fitness advantages (avoiding the costs of somatic cell parasitism and reaping the benefits of chimera formation) can be accrued (but see Barnard 1991). These inclusive fitness benefits hence constitute a selective force for the maintenance of the polymorphism at the matching locus.

Table I. Phyletic survey of examples of chimera formation, somatic incompatibility and somatic cell parasitism

Group	Mechanism of chimera formation	Evidence of somatic incompatibility	Evidence of somatic cell parasitism
Protoctista			
Myxomycota	e.g. *Physarum polycephalum*. Fusion of plasmodia (acellular mass of protoplasm derived from growth of a zygote formed from syngamy of two amoebae; Carlile 1973). Protoplasmic streaming along 'veins' along the fusion margin unites the plasmodia to a chimera	Failure of plasmodia of *P. polycephalum* to fuse unless genetically identical. Genetic basis: fusion is under the control of several polymorphic loci of which two, *f* and *n*, are best understood (Carlile 1973), i.e. complete matching necessary for fusion to occur	Fusion of incompatible strains of *P. polycephalum* is rare in nature but can be induced under laboratory conditions. In some cases a post-fusion reaction may proceed in which a 'killer' phenotype eliminates the nuclei of the other 'sensitive' phenotype hence attaining complete dominance of the chimera (Lane & Carlile 1979)
Acrasiomycota	e.g. *Dictyostelium mucoroides* (1) Coaggregation of amoebae to a multi-cellular grex. The grex transforms into a stalked fruiting body which exhibits cell differentiation into germ-line and somatic (stalk) cells (Buss 1982). (2) Formation of somatic variants within a grex by mutation of the cellular components (see Buss 1982)	Failure of genetically different amoebae to coaggregate, e.g. *D. mucoroides* (Buss 1982). Genetic basis: not known but given that only genetically identical amoebae aggregate, it appears as if complete matching is necessary for fusion to occur	*D. mucoroides* has a mutant cell type that, following aggregation, forms a stalkless fruiting body. In chimeras with normal stalked cell types, the mutant cell type plays no part in stalk formation and hence contributes a disproportionately high fraction of the chimera's germ-line cells (Buss 1982)
Fungi			
Ascomycota	e.g. *Neurospora crassa* (1) Fusion of hyphae (hyphal anastomosis) followed by extensive exchange of nuclei to form a heterokaryon (see Buss 1987). (2) Formation of somatic variants within a mycelia by mutation (see Buss 1987)	Failure of hyphal anastomosis unless mycelia are genetically identical, e.g. *N. crassa*. Genetic basis: fusion allowed only if both mycelia are identical at highly polymorphic loci (see Mylyk 1975), i.e. complete matching necessary for fusion to occur	If one nuclear type of chimeric mycelium of *N. crassa* contributes to more than 30% of the total it suppresses the reproductive activity of the other nuclear type (see Buss 1987)
Animalia			
Porifera	(1) Fusion of gemmules (asexual propagules consisting of amoeboid cells inside epithelial package) or larvae, e.g. freshwater sponge *Ephydatia fluviatilis* (see Simpson 1973). (2) Fusion of adults, e.g. boring sponge *Cliona* (see Simpson 1973). Free migration of cells derived from fusion partners occurs throughout the chimera	(1) Failure of fusion between gemmules or larvae (see Grosberg 1988). (2) Failure of adults to fuse (see Simpson 1973). (3) Strain-specific reaggregation of cells following break up of a sponge (e.g. De Sutter & Van de Vyver 1979). (4) Graft transplantation (see Grosberg 1988). Genetic basis: full identity at polymorphic loci required for fusion of gemmules/larvae but only partial matching required for graft acceptance (see Grosberg 1988)	In the strain-specific reaggregation of homologous cell fractions of *E. fluviatilis*, the cells from each strain coexist without conflict. Sometimes, however, one strain attains dominance and hence assumes a larger role in reproduction relative to the other strain in the chimera (De Sutter & Van de Vyver 1979)

Table I. Continued

Group	Mechanism of chimera formation	Evidence of somatic incompatibility	Evidence of somatic cell parasitism
Animalia			
Cnidaria	e.g. colonial hydroid *Hydractinia echinata*. Fusion of colonies to form a chimera which shares a common gastrovascular system (see Buss 1990). See Grosberg (1988) for other examples	(1) Failure of fusion between colonies of *H. echinata* by passive means (no growth) or through aggression mediated by nematocyst bearing hyperplastic stolons (2) Fusion for a transitory period followed by rejection. Genetic basis: partial matching at polymorphic loci required for permanent fusion (with clone mates, siblings and half-siblings). Whether rejection is passive or aggressive is under complex ontogenetic control (see Grosberg 1988)	Gametes produced in the chimera of *H. echinata* may be formed disproportionately by one of the fusion pair. Only colonies that fuse permanently are susceptible to such somatic cell parasitism. Transitory colonies are not (see Buss 1990)
Bryozoa	Fusion of colonies of zooids (see Grosberg 1988) to share a common vasculature and sensory system	Failure of colonies to fuse. Sibling colonies of *Thalamoporella californica* are generally fusible whilst non-siblings are not (see reference in Grosberg 1988). Genetic basis: not known although the above example shows that only partial matching is required for fusion to occur	Zooids exhibit polymorphism with some specialized for reproduction and others for somatic functions. It is conceivable that the zooids of one fusion partner might attain dominance of the reproductive roles in the chimera. There is, as far as we know, no documented evidence for this
Urochordata	e.g. colonial ascidian *Botryllus schlosseri* (Grosberg & Quinn 1986). Fusion of colonies derived from aggregated settlement of larvae near histocompatible larvae. Chimeral colonies are united by a common vasculatory system. See Grosberg (1988) for other examples	Fusion only between close kin. Genetic basis: fusibility controlled by identity at one locus with multiple co-dominant alleles (see reference in Grosberg & Quinn 1986). Fusion restricted to clone mates and siblings, i.e. partial matching only required for fusion to occur	One genotype contributes disproportionately to the germ line of the chimera relative to its contribution to the soma (see Buss 1990)

Multi-allelic self incompatibility in plants manifest as failure of selfed pollen grains to adhere to, germinate on or penetrate through the stigma (see Richards 1986) may constitute a further example of true kin recognition. Since these systems involve failure of kin to fuse, as a form of inbreeding avoidance, they are hence mechanistically distinct to the true kin recognition systems of the above organisms.

The histocompatibility reaction of *B. schlosseri* is an example of 'somatic incompatibility'. Many other organisms have somatic incompatibility. The capacity for apparently independent organisms to form chimeral alliances between cells or individuals of the same species is widespread amongst the true (acellular) slime moulds (Myxomycota), cellular slime moulds (Acrasiomycota), ascomycete fungi and a range of clonal animals (see Grosberg 1988) including sponges, cnidarians, bryozoans and ascidians (see Table I). All of the above organisms can benefit from amalgamation. However, as with

B. schlosseri, intimate fusion leaves the individual vulnerable to somatic cell parasitism (or related phenomena) by their conspecific fusion partner(s). Again as with *B. schlosseri* this problem is minimized by the action of recognition systems which typically prevent amalgamations between non-relatives. In Table I we detail the occurrence of chimera formation, the evidence for somatic incompatibility, the evidence for somatic cell parasitism and, where known, the genetic basis of somatic incompatibility for examples from the taxa listed above. The recognition systems described in Table I appear to be directly analogous to that described for *B. schlosseri*. Furthermore, the form of the costs and the benefits appear to be phenomenologically comparable.

In many of the above examples fusion mediated by a somatic incompatibility system occurs only between individuals that are genetically identical at all of the histocompatibility loci. This we refer to as complete matching. In others it occurs between conspecifics which share some but not necessarily all of the histocompatibility alleles (partial matching). Complete matching could be thought of as a form of self recognition but can equally well be considered an extreme form of kin recognition. That somatic incompatibility systems might vary in the degree of relatedness required for fusion was predicted by Buss (1982). He argued that the higher the costs of chimera formation relative to the benefits, the more related one should expect organisms to have to be in forming a chimeral alliance. This would have the kin-selected effect of reducing the inclusive fitness losses incurred by somatic cell parasitism whilst at the same time accruing the fitness advantages of chimera formation. This model could also be viewed as a formalization of the optimal degree of fussiness that a true kin recognition system should display. Indeed, the three variables of benefits (b), costs (c) and relatedness (r) correspond to those in Hamilton's (1964) rule that a kin-selected trait will spread according to the manner in which b and c are dependent on r. Under conditions of extreme somatic cell parasitism, the costs may be so high as to allow inclusive fitness to be increased only when the relatedness between the two fusion partners is very high.

The examples of somatic incompatibility given in Table I suggest that true kin recognition has multiple independent origins. The precise number of origins is unclear because phylogeny is uncertain, because further examples are likely and

because the phenomenon may have been lost on several occasions. It is predicted that the phenomenon should be absent from non-colonial organisms (colonial here is defined as an intimate association involving tissue contact). Non-colonial organisms never fuse and are hence never exposed to the threat of somatic cell parasitism. Buss (1987) argued that, as predicted, the majority of non-colonial organisms do not possess genetic somatic incompatibility mechanisms. His assertion is based on the ease with which tissue grafts can be transplanted between unrelated conspecifics of many non-colonial organisms. In contrast, in colonial organisms tissue grafting is usually possible only between very close relatives (see Grosberg 1988).

As exceptions to the above rule, vertebrates, echinoderms and a few other non-colonial mobile invertebrates do have the ability to reject grafts from non-relatives (Buss 1987). Graft rejection in these organisms is certainly evidence of somatic incompatibility/allorecognition and hence of an ability to discriminate kin from non-kin by genetic matching (as in the colonial organisms). Furthermore, matching involved in graft rejection involves highly polymorphic loci. However, evidence of a highly polymorphic matching locus capable of distinguishing kin from non-kin does not constitute full evidence for a true kin recognition system (Grafen 1992). Hence, can graft rejection be regarded as true kin recognition? Returning to Grafen's (1990) stipulation, if the polymorphism of the matching locus allows an accurate assessment of ancestral relatedness but the relatedness is not important for the maintenance of the system then the answer must be no (Grafen 1990; Barnard 1991). There are adequate reasons to suspect that this may be the case. Graft rejection may be an artefact of recognition systems that are employed as a defence mechanism against invasive pathogens. This is supported by the finding that the MHC in humans is involved in conferring malarial resistance (Hill et al. 1992) and yet is also involved in graft rejection. An alternative possibility is that allorecognition evolved in proto-echinoderms of a colonial nature and was then carried through the radiation of non-colonial echinoderms and vertebrates as an artefact (Buss 1987). If graft rejection is an epiphenomenon of a highly polymorphic matching locus maintained by selective forces in which ancestral relatedness is not important, then the allorecognition systems involved in graft rejection qualify as examples of highly discriminatory

true genetic matching system which are not true kin recognition.

Can we be sure that the instances of somatic incompatibility detailed in Table I are not also of the above designation and hence not true kin recognition? Barnard (1991) points out that it is possible that the matching in *Botryllus* is not to achieve estimation of ancestral relatedness but rather to obtain some direct fitness advantage. Whether Barnard is correct will be amenable to experimental investigation. It is, however, reasonable to suggest that if Grafen's claimed incidence of true kin recognition is just that, then there exist multiple independent origins of such recognition, each one associated with somatic incompatibility.

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