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11. THE OCHLOSPECIES CONCEPT

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Abstract

A review is presented of White's ochlospecies, which represents a particular type of species problem distinct from those resulting from familiar complications of hybridisation, autogamy or apomixis. An ochlospecies is a polymorphic species with chaotic infraspecific variation which is intractable to formal taxonomic treatment; ten criteria are suggested for recognising ochlospecies. Two hypotheses are presented as possible explanations for this type of variation pattern. One, the 'Prance hypothesis', refers to processes of isolation and refusion driven by Pleistocene climatic change. The other, the 'rapid expansion hypothesis', proposes that genetic processes associated with the rapid population expansion of a colonising generalist could result in the observed patterns without an allopatric phase. A test of these hypotheses is suggested.

> *Species such as these are a nightmare to the taxonomist, though when aspects of their biology other than taxonomy are considered they may have much to offer to general, and, in particular, to evolutionary studies.*
>
> White, 1998.

Introduction

It is the common experience of the monographer of a large genus of plants that the entities recognised as species are not homogeneous with respect to their variation patterns, and cannot be made so. They differ both with respect to their infraspecific variation and in their relations to other species. This has been expressed as follows by Hilliard & Burtt (1971) in their monograph of *Streptocarpus*: "Discussions on species often seem to imply that species in, say, orchids are rather different from those of grasses or oaks. Is this true? We think not. Of course, there are special situations that occur in one group but not in another. In the main, however there is more evidence that any group of adequate size will contain species of many different kinds than that different groups will have different sorts of species".

At a meeting of the Systematics Association on Taxonomy and Geography, White (1962) reported on this phenomenon, as revealed by his studies of African Ebenaceae. Of 90 species of *Diospyros*, most were monotypic, seven polytypic and three polymorphic (i.e. ochlospecies, to be discussed here). Forty-eight species were taxonomically isolated: clearly distinguishable from other species by a number of *diagnostic* characters. In contrast 36 species belonged to groups of two to five closely related species, and these could further be divided into allopatric (for which White used the term 'superspecies' of Mayr) or sympatric groups. Species belonging to these species groups could only be distinguished from one another by *differential* characters (White's term).

The three polymorphic species, *Diospyros ferrea, D. natalensis* and *D. mespiliformis,* were quite different from the others in that while the total amount of variation within these species was equivalent to that of a polytypic species, or even a superspecies or species group, the variation pattern proved utterly intractable to strict taxonomic treatment (Fig. 1). Consequently the taxonomist has no recourse other than to recognise a single variable species with no formal variants. For these species White introduced the term 'ochlospecies' from the Greek root, *ochlos,* meaning an irregular crowd or a mob (with an apposite secondary meaning of trouble or annoyance).

Plants have many well documented sources of taxonomic complexity, mainly due to cytological complexity, hybridisation, apomixis or autogamy. These classes of species problem have recently been reviewed by Mayr (1992). White did not intend the term ochlospecies to be used for these cases, for which, in general, other terminologies are available. If putative ochlospecies resolve themselves as hybrid swarms or apomictic groups, then the term ochlospecies is not applicable. When these other types of species problems are separated, the sexual, outbreeding ochlospecies becomes another class of species problem. As such, ochlospecies have a number of characteristic and curious features (see below), but they have never been subject to experimental study, mainly because most of the recognised examples are long-lived tropical trees and large herbs, unsuited to life on the laboratory bench. Nevertheless, as White himself recognised, they still offer interesting opportunities for evolutionary studies.

Definition

A general definition of an ochlospecies would be (after White, 1998):

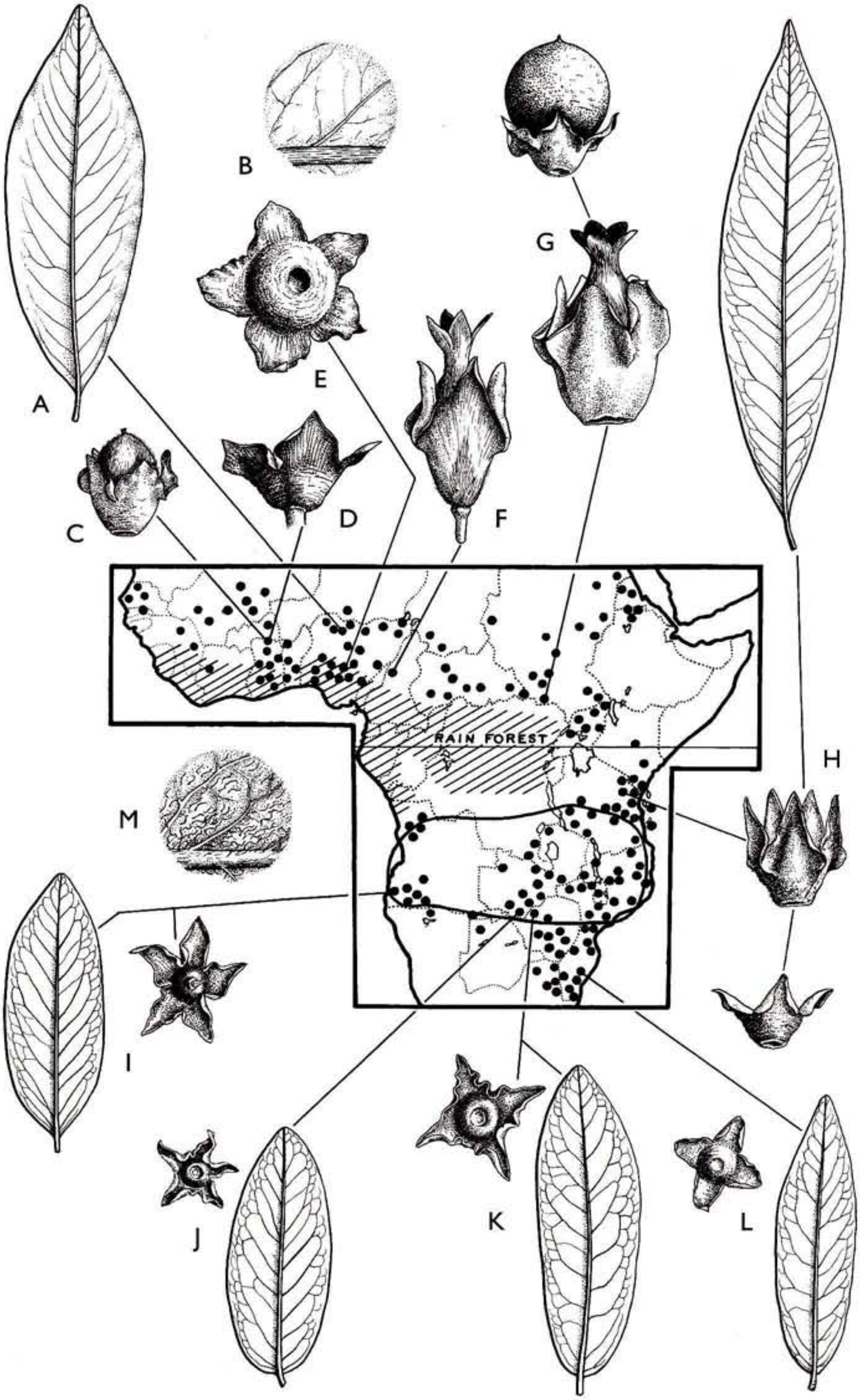
"A very variable (polymorphic) species, whose variation, though partly correlated with ecology and geography, is of such a complex pattern that it cannot be satisfactorily accommodated within a formal classification".

However, this would be too broad a category, as ochlospecies have some highly characteristic traits and can be rather narrowly defined (as was done by White) to give a rather homogeneous set of problem species. We can recognise four *strong traits* which are essential to the concept, and six *weaker traits* which are usual or common in ochlospecies but not essential.

Strong traits

1. Species which show variation that is strongly polymorphic but only weakly polytypic (i.e. non-hierarchical).
2. Character-state distribution shows only partial correlation with geography and ecology (checkerboard variation).
3. Characters vary independently, and not in a correlated fashion.
4. Complexity of variation is not due to hybridisation between currently recognisable species, or to a specialised breeding system (i.e. an ochlospecies is not a hybrid swarm or an aggregate of apomictic microspecies).

FIG. 1. Pictorialized distribution map of *Diospyros mespiliformis* from F. White (1962) showing the main features of variation. **A** leaf (*Conservator of Forests s.n.*); **B** indumentum of lower leaf surface (*Conservator of Forests* 208); **C** immature fruit (*Andoh* FH 5173); **D** calyx of mature fruit (*Nortey* 103); **E** calyx of mature fruit (Conservator of Forests 208); **F** female flower (*Ledermann* 2958); **G** female flower and mature fruit (*Hoyle* 761); **H** leaf, calyx of female flower and calyx of mature fruit (*Semsei* FH 2900); **I** leaf and calyx of mature fruit (*Santo* 2219); **J** ditto (*White* 2993); **K** ditto (*Lovemore* 76); **L** ditto (*Torre* 2669); **M** indumentum of lower leaf-surface (*Santo* 2219). The continuous line demarcates the distribution of *D. kirkii.* Reproduced with permission from the Systematics Association.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Weak traits

5. Ochlospecies are usually geographically and ecologically widespread, occurring in several climatic and vegetation zones ('ecological and chorological transgressors' of White). An exception is the ochlospecies *Trichilia micrantha* which, while geographically widespread, is not an ecological or chorological transgressor (Pennington, 1981).

6. Distinct variants are recognisable locally but not globally. At a particular locality two distinct and non-intergrading forms may be found, and other forms may be found at other localities, but taken together all the forms intergrade and the classification breaks down.

7. Ochlospecies sometimes have a closely related, but morphologically distinct and monotypic satellite species. For example *Diospyros kirkii* is the satellite of the ochlospecies *D. mespiliformis, Ficus kamerunensis* is the satellite of *F. thonningii, Heracleum minimum* is the satellite of *H. sphondylium* and *Myrmecodia beccarii* is the satellite of *M. tuberosa.*

8. Similar variants may occur in widely separated localities and appear to be polytopic in origin.

9. An apparently unifying characteristic of ochlospecies is that they tend to occur in medium to large genera usually with more than 50 species, and in such genera tend to occur with a low frequency of 1–8%. No ochlospecies so far definitely known is a member of a monotypic or oligotypic genus.

10. Ochlospecies often have long synonymies: the variation has driven a proliferation of names that eventually prove untenable. Thus ochlospecies are often created by the lumping of a dozen or more species.

Many ochlospecies will display all ten traits, but to qualify as an ochlospecies, a species must have the first four and should have at least the first six.

The tenth criterion is important because it reveals the usual epistemic (rather than evolutionary) route to the formation of ochlospecies. It follows from the incomplete nature of tropical floristics that many ochlospecies may lie unrecognised as a series of poorly collected related 'species' awaiting the attention of a taxonomist. Extreme cases are those of *Vavaea amicorum* where 21 species were reduced to one apparent ochlospecies with no infraspecific variants (Pennington, 1969), and *Allophyllus cobbe* into which a vast amount of variation and names were disposed, somewhat contentiously, by Leenhouts (1994). The three 'Pennington Conditions' used to justify the treatment of *Vavaea* are also, of necessity, ochlospecies conditions, and Mabberley (1979) used the Pennington Conditions to justify treating *Chisocheton lasiocarpus* as an ochlospecies and not recognising formal infraspecific variants. The Pennington Conditions are as follows:

1. None of the variants are well correlated with geography.
2. Different variants may occur in the same locality and in the same habitat.
3. Variants are based on slight vegetative differences, the most striking of which appear to have originated polytopically.

The question of polytopic origins is interesting as they may be characteristic of variation in ochlospecies. White (1998) suggests that extreme variants, particularly the rheophytic and microphyllous forms of *Diospyros natalensis,* have originated more than once. Rheophytes in this ochlospecies occur in widely disjunct places such as Mt. Mulanje and the Dwesa River in South Africa. In these places the rheophytes form part of larger non-rheophytic populations and are likely to be independently locally derived.

A word is appropriate here concerning phenotypic plasticity. There is as yet no evidence that ochlospecies variation is due to exceptional phenotypic plasticity. White himself cultivated ten species of New Caledonian *Diospyros* in Oxford for some 20 years, including the ochlospecies *D. parviflora* (Fig. 1 in Pannell, this volume), and all "retained their species-specific vegetative characters" (White, 1993). Nowhere does he suggest that ochlospecies variation becomes uniform under conditions of uniform cultivation. However, discussing the variation of *D. natalensis* on Mt. Mulanje, White (1988) notes that some of it has been shown to be phenotypic. Whatever the final picture may be, the invocation of phenotypic plasticity does not explain everything about ochlospecies. Phenotypic plasticity is a highly important plant adaptation, under tight genetic control, although it remains a difficult phenomenon to study (Sultan, 1995). There is as yet little clear idea as to why some species have a large phenotypic response and others are invariant with respect to environment, although it has been suggested that evolution in a spatially heterogeneous environment may promote plasticity (Zhivotovsky *et al.*, 1996). It would thus be extremely interesting if all ochlospecies variation was due to phenotypic plasticity, although at present this appears unlikely.

Is the ochlospecies concept really necessary?

In cases where medium to large genera of tropical trees have been recently revised, very often an ochlospecies is proposed. Tables 1 & 2 give the occurences of different species types in 90 species of African Ebenaceae (*Diospyros*) and 67 species of South American Meliaceae (*Trichilia*). Monotypic species, polytypic species and ochlospecies refer to different patterns of infraspecific variation, whereas group species refer to the pattern of variation just above the species level. These two types of variation are largely

TABLE 1. A classification of species types, according to interspecies relationships (group, isolated) and infraspecific variation (monotypic, polytypic, ochlospecies) for 90 African Ebonies of the genus *Diospyros.* Only 86 species are treated as four are too little known (White, 1962).

Species relationship:	*Isolated*	*Group*	Total
Species type:			
Monotypic	46	30	76
Polytypic	2	5	7
Ochlospecies	2	1	3
Total	50	36	86

TABLE 2. A classification of species types, following Table 1, for 67 species of the genus *Trichilia,* after Pennington (1981).

Species relationship:	*Isolated*	*Group*	Total
Species type:			
Monotypic	14	44	58
Polytypic	1	6	7
Ochlospecies	2	0	2
Total	17	50	67

independent, and so most group species are also monotypic. Nevertheless, it is convenient to divide species into these categories, as the species level in one taxon may be equivalent to variation at the subspecies level in another. Even if all the species in particular species groups were lumped, as the variation in ochlospecies is lumped, there would still be definable hierarchical elements amenable to formal classification. This is not the case in ochlospecies. Furthermore, in *Trichilia* the species within groups are largely allopatric whereas the component elements of ochlospecies are significantly sympatric and this appears to be a general phenomenon.

If the same sort of analysis is given to the species of *Streptocarpus* dealt with by Hilliard & Burtt (1971), remarkably similar patterns result if their three 'species aggregates' do duty for ochlospecies (Table 3). These aggregate species are like ochlospecies in that they contain a series of intergrading forms. For instance in the *S. rexii* aggregate, there is a north-south intergrading series of forms: *S. parviflorus* – *S. cyaneus* – *S. primulifolius* – *S. rexii*, in that order (there is even a well-marked satellite species, *S. gardenii*). But here the constituent species can be retained, as the chaos of non-hierarchical variation has not reached up so extensively from where it is natural: at the population level. Nevertheless, it would be perfectly possible to lump the component species of the *rexii* group and even, for a serious lumper, to deny the utility of subspecies.

TABLE 3. A classification of species types, following Table 1, for the genus *Streptocarpus* subgenus *Streptocarpus* in Africa. Data modified after Hilliard & Burtt (1971) with their 'aggregate species' doing duty for 'ochlospecies' for the sake of comparison.

Species relationship:	*Isolated*	*Group*	Total
Species type:			
Monotypic	49	8	57
Polytypic	4	3	7
Aggregate	1	1	2
Total	54	12	66

I have no doubt of the greater complexity of the *Diospyros mespiliformis* ochlospecies than of the *Streptocarpus rexii* aggregate, but we must nevertheless consider the possibility that what stands between the ochlospecies and the aggregate is merely a dash of personal preference and a pinch more intergradation. That would put the ochlospecies in the familiar realm of the age-old dialogue between splitters and lumpers. Against this is the perfectly reasonable contention that where so much complex polymorphism extends over such a wide geographical range and comprises so much variation, as in *D. mespiliformis* (Fig. 1), then some special and unknown process is at work, putting the ochlospecies outside the ordinary splitting/lumping continuum. The splitting/lumping debate is then confined to resolving the difference between polytypic species (a species with numerous subspecies) and the species group (several closely related species). In this we should bear in mind that polymorphic variation, being segregational, is fundamentally different from species differences, which are differences in particular gene combinations, often very complex combinations. The absence of discrete combinatorial variation distinguishes the polymorphic ochlospecies. Nevertheless, we should expect, and indeed do find, intergradation between these two types of variation.

Mention must be made here of Gentry's (1990) criticism of Pennington's taxonomic treatment of entities under the *Guarea glabra* ochlospecies. He noted that at the La Selva field station in Costa Rica six of the entities co-occur and are clearly distinguishable in the field. Here they are recognised as good species, passing locally what Gentry calls a "test of sympatry", which he suggested should take precedence over the complexity of variation patterns elsewhere. The implication of this is that when poorly known ochlospecies (such as little-studied tropical trees) become well known in the field, and characters that are cryptic in the herbarium are revealed, such as flowering and fruiting phenology, then the ochlospecies will resolve itself, like white light passing through a prism, into a spectrum of distinct forms. If there are then still problems of intergradation, it is incumbent on the taxonomist to try to solve them as best as possible, rather than to conceal important variation within the ochlospecies (although White intended ochlospecies variation to be well illustrated by means of pictorialized distribution maps). Further work is needed to clarify how many ochlospecies will be resolved in this way, but Gentry did concede that there appears to be a difference between the neotropics, where he contends that variation patterns are clear-cut, and Africa, where variation patterns appear to be more complex. Three further caveats need to be put on Gentry's critique.

Firstly, it is not clear to me why a morphotype should not behave as a good species in one place (e.g. La Selva) and not elsewhere. Indeed, it would seem an evolutionary axiom that this should occasionally be the case. A good example is that studied by Beeks (1962) in *Diplacus* (Scrophulariaceae). In Southern California, complete intergradation occurs between *D. longiflorus* and *D. puniceus,* and they behave therefore as intergrading races. However, in parts of the Santa Ana Mountains populations of the two entities occur together without intergradation, and behave as sympatric species.

Secondly, it is still disputed whether variation patterns in South America are uniformly clear-cut in comparison to Africa as Gentry suggested from his studies of the Bignoniaceae. Variation patterns do indeed appear to be clear-cut in the geologically old regions of the Guianan and Brazilian shields, but are not always so in the Andes or in Central America (T. Pennington, pers. comm.). This observation is based on repeated subjective inference from identification of large field collections from different parts of South America, and if confirmed would imply a process of 'variation sorting' in geological time.

Thirdly, it could be argued that if there are indeed serious problems with the recognition of taxa, at least over part of the range, then it is incumbent on the taxonomist to admit these problems frankly under the ochlospecies, and not to offer a false dawn of a workable taxonomic treatment where none exists. Thus we come back to our bottom line: whether ochlospecies is part of the age-old debate between splitters and lumpers, or represents variation that is genuinely outside that debate.

Examples of ochlospecies and their patterns

Tropical trees

The abundance of tropical trees among the recorded cases of ochlospecies (Table 4) begs the question of whether this pattern of variation is especially characteristic of tropical woody plants. I suspect, however, that the preponderance is a result of the research interests of those prepared to use the term ochlospecies (White worked almost exclusively on tropical woody plants). It may also reflect the discovery procedure for ochlospecies which involves thorough revision of a relatively large genus over a wide geographical area. Such studies, often associated with the *Flora Malesiana* or *Flora Neotropica* projects, have generally been tropical and, because of the economic, botanical and ecological importance of trees, have often involved woody plants.

TABLE 4. A table of some actual or putative ochlospecies.

Dicotyledons		
Impatiens hawkeri	Balsaminaceae	Grey-Wilson (1979)
Licania apetala	Chrysobalanaceae	Prance (1972)
Licania heteromorpha	Chrysobalanaceae	Prance (1972)
Diospyros ferrea	Ebenaceae	White (1962)
Diospyros mespiliformis	Ebenaceae	White (1962)
Diospyros natalensis	Ebenaceae	White (1962, 1998)
Diospyros parviflora	Ebenaceae	White (1993)
Chisocheton lasiocarpus	Meliaceae	Mabberley (1979)
Cedrela odorata	Meliaceae	Pennington (1981)
Guarea glabra	Meliaceae	Pennington (1981)
Trichilia pallida	Meliaceae	Pennington (1981)
Trichilia micrantha	Meliaceae	Pennington (1981)
Vavaea amicorum	Meliaceae	Pennington (1969)
Ficus thonningii	Moraceae	Berg & Wiebes (1992) Berg & Hijman (1989)
Cybianthus spicatus	Myrsinaceae	Pipoly (1983)
Triplaris americana	Polygonaceae	Brandbyge (1986)
Myrmecodia tuberosa	Rubiaceae	Huxley (1981) Huxley & Jebb (1993)
Drimys piperita	Winteraceae	Vink (1970)
Monocotyledons		
Alocasia nicolsonii	Araceae	Hay & Wise (1991)
Cyrtosperma macrotum	Araceae	Hay (1988)
Schizochilus zeyheri	Orchidaceae	Linder (1980)
Pentaschistis pallida	Poaceae	Linder & Ellis (1990)
Vellozia hirsuta	Velloziaceae	Mello-Silva (1990)

Recorded cases of ochlospecies exist from the Myrsinaceae, Chrysobalanaceae and Ebenaceae, but the studies of Pennington (1981) and Mabberley (1979) on the Meliaceae have been particularly fruitful in bringing forward cases of ochlospecies. Pennington prefers to use the term 'complex species' rather than ochlospecies, to avoid imposing a term coined for African ebonies onto other groups in other areas. However, using the criteria suggested here, Pennington's complex species are equivalent to ochlospecies.

Herbaceous and suffruticose ochlospecies

Although there appear to be fewer herbaceous ochlospecies than woody ones, these species are of particular interest as they may provide more tractable experimental material with which to investigate the phenomenon. This is particularly true of the *Impatiens hawkeri* ochlospecies described by Grey-Wilson (1979) in New Guinea. Many of the forms of this ochlospecies are already in cultivation in Europe and North America under a variety of species names.

Another Papuasian species which might form a typical or strong ochlospecies is *Alocasia nicolsonii* as treated by Hay & Wise (1993). However, the local segregation of distinct entities tends to be allopatric rather than sympatric. Another Papuasian species, *Cyrtosperma macrotum*, described by Hay (1988) may also be an ochlospecies (A. Hay pers. comm.).

A case of a strong ochlospecies confirmed by White himself is the widespread ant-inhabited epiphyte of the Rubiaceae, *Myrmecodia tuberosa* (Huxley, 1981; Huxley & Jebb, 1993). In this case 23 names became one, and all the definitional criteria are met. The whole entity forms a continuum of variation from Indochina to Australia and the Philippines to the Solomon Islands (Figs 2 and 3).

Several of the ochlospecies already mentioned come from Papua New Guinea, and there are other examples such as *Chisocheton lasiocarpus* (Mabberley, 1979). Mabberley (1992) implicates the possible exacerbating effect of the geological instability of New Guinea on variation patterns, if those patterns are archaic.

Animal ochlospecies

The only case in which White's term has found its way into zoology is in the case of the polymorphic South American scorpion *Tityus silvestris* (Lourenço, 1988). Lourenço (1994) described a number of variation types to accommodate the major patterns of distribution and differentiation of tropical South American scorpions, defining monomorphic, polytypic, mosaic polymorphic, clinal polymorphic and ochlospecies polymorphic species. His ochlospecies polymorphic type corresponds to the ochlospecies of White. His mosaic polymorphic and clinal polymorphic types have intergradation of forms, but greater ecogeographic patterning to the forms than in the most complex ochlospecies. These two forms may constitute weak ochlospecies of other authors. For instance, *Alocasia nicolsonii,* discussed above, may perhaps be more exactly characterised as a mosaic polymorphic species.

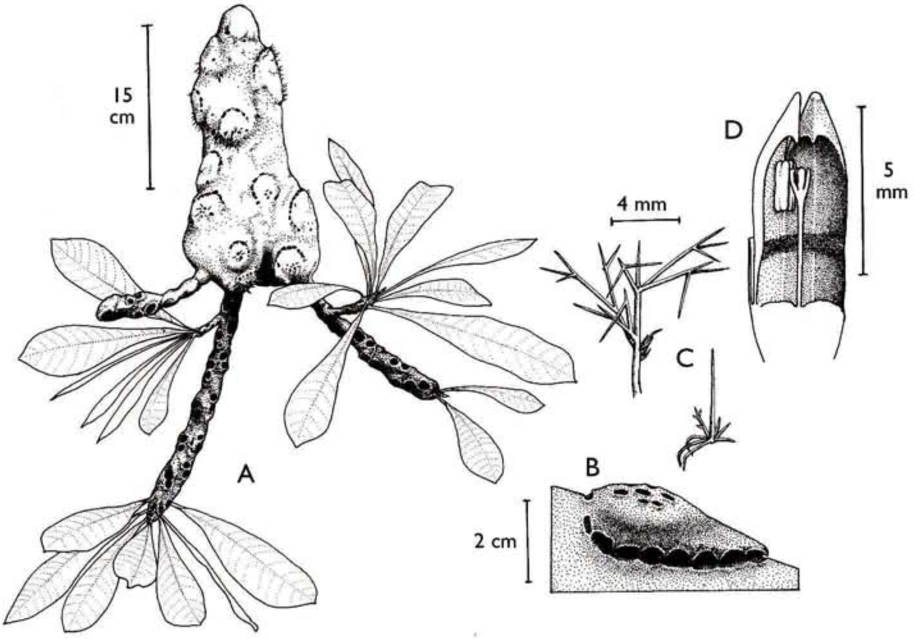

FIG. 2. Example of an ochlospecies from New Guinea, the ant-inhabited epiphyte *Myrmecodia tuberosa* 'versteegii'. **A** habit; **B** tuber surface showing raised area surrounded by entrance holes; **C** spines; **D** section of flower. Note the bract filled alveoli along the stem. Drawn by Eleanor Catherine. Reproduced with permission from Blumea (Huxley & Jebb, 1993).

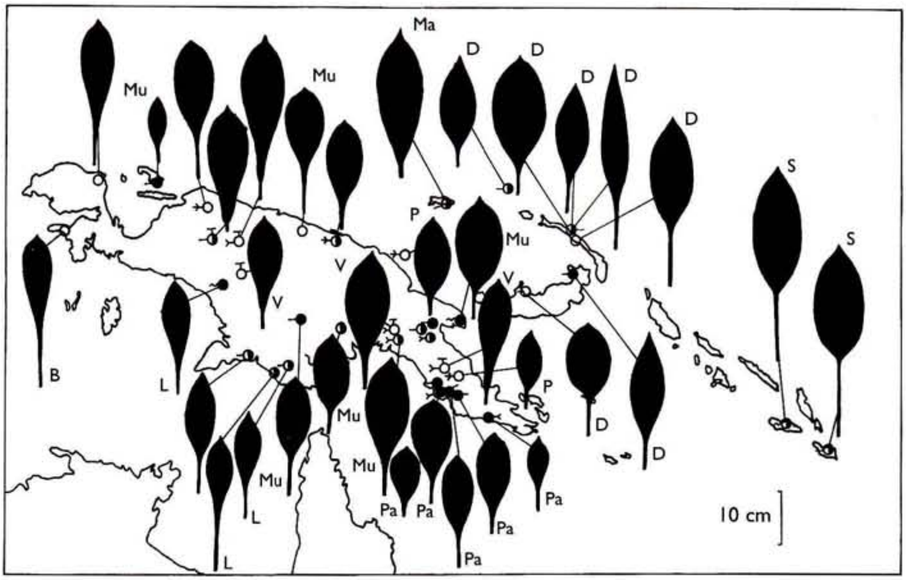

FIG. 3. A pictorialised distribution map of the ant-plant ochlospecies *Myrmecodia tuberosa* in New Guinea and the Solomon Islands. Leaf silhouettes and ideographs depicting spine and bract characters are shown for representative specimens of the eight informally recognized variants. **B** = *M. tuberosa* 'bullosa'; **D** = *M. tuberosa* 'dahlii'; **L** = *M. tuberosa* 'lanceolata'; **Ma** = *M. tuberosa* 'manusensis'; **Mu** = *M. tuberosa* 'muelleri'; **Pa** = *M. tuberosa* 'papuana'; **Pu** = *M. tuberosa* 'pulvinata'; **S** = *M. tuberosa* 'salomonensis'; **V** = *M. tuberosa* 'versteegii'. The ideographs show variation in the following characters: ○ = bracts not conspicuous; ◑ = bracts filling alveoli in stem; ● = bracts forming cushions protruding from the alveoli; ♁ = raised areas on tuber surrounded by arcs of entrance holes; ○ = spines absent or sparse; –○ = spines mostly simple; ≻○ = spines mostly branched; +○ = spines mostly club-like; ~○ = spines mostly sinuate. (The spine symbols are shown at different angles where the ideographs are too close for them to be in the usual position). (From Huxley, 1981).

It is likely that there may be more animal ochlospecies than is immediately suggested by the useful, but simple, prevailing model of species in zoology: the biological species concept. Recent suggestions to replace the zoological concept of the biological species with a phylogenetic species concept, now that the significance of hybridization among differentiated taxa is more adequately acknowledged (Zink & McKitrick, 1995), may lead to increasing reappraisal of complex variation patterns in zoology.

Temperate ochlospecies

All the examples of ochlospecies given here are tropical, which raises the question of whether they are exclusively so. I will argue here that the apparent tropical bias is a historical artefact of the way floristics has developed this century. To explain this idea, an anecdote may be allowable. Several years ago, I put White's ideas of ochlospecies to Max Walters, who had argued cogently that much apparent general taxonomic pattern was eurocentric artefact (Walters, 1963; 1986). I was interested to learn whether Walters considered that ochlospecies could be just such an artefact.

The causes of such artefact can broadly be termed 'psychohistorical' (Cronk, 1990) and stem from two main processes. The first of these is *chaining* whereby new species tend to accrete in higher taxa described a long time ago, usually in Europe by early European botanists. As such entities grow they become more amorphous and easier to place new species inside (Cronk, 1989). This eventually results in colossal, ill-defined and unmanageable higher taxa, such as the genus *Senecio*. The second process is the excessive *splitting* of genera with a long history of eurocentric interest, relative to tropical or less familiar groups. Classic examples are the Umbelliferae (many small genera) versus the Araliaceae (fewer, larger genera) (Walters, 1963) and the papilionoid legumes versus the mimosoid legumes (Cronk, 1990).

Walters did indeed consider that the ochlospecies might be psychohistorical in origin, with the relative undercollection of tropical plants making complex but tractable patterns of variation appear chaotic. This circumstance then might lead to the understandable psychohistorical response of chaining the variation into ochlospecies. Some time afterwards I put this idea to White. He declined to give a detailed response immediately, but I nevertheless gained the impression that he disagreed with this interpretation of the ochlospecies. Later, he gave me an offprint of an unrelated paper, at the top of which he had written: "Max is partly right about the ochlospecies, but for the wrong reasons". Shortly afterwards he became critically ill and I never was able to discuss this cryptic statement with him. Nevertheless, I think I know what he meant: that there are ochlospecies in temperate regions, but that the strong regionalisation of floristic work in these areas for largely eurocentric and political reasons, has prevented the necessary large scale monographic and floristic work that is now common in tropical plant systematics (for instance, that carried out by White and his colleagues, and under the auspices of *Flora Neotropica* and *Flora Malesiana*). The idea that ochlospecies may live unrecognised in temperate regions because of a psychohistorical artefact comes closer to Walters' central thesis that eurocentric bias is the problem, not the solution. For instance, a possible temperate ochlospecies is *Bupleurum falcatum* (Tutin, 1968) which occurs from central Asia to Western Europe exhibiting a complex variation pattern, but has not been the subject of recent critical study over the whole of its range. In this context it is also interesting to consider *Heracleum sphondylium*, although the constituent variation has been treated (with caveats) as a series of ill-defined subspecies (Brummitt, 1968; 1971). Another candidate is the *Anthyllis vulneraria* complex (Cullen, 1968), although again subspecific treatments have been attempted with varying degrees of success.

Explanations of ochlospecies

The Prance hypothesis

Prance (1982) proposed that the Pleistocene refuge theory could act as an explanation of ochlospecies polymorphism. The refuge theory suggests that drier conditions at times of glacial maxima caused wet forest plants to become discontinuous. Some minor differentiation would then occur in these allopatric populations. On the resumption of humid conditions, ecologically adaptable species with good dispersal would then recolonise and different populations could meet. Thus the variation would no longer be geographically correlated. The variation would be further complicated by infraspecific hybridisation between the formerly geographically isolated populations. This kind of ochlospecies bears a strong relation to the 'syngameon of semispecies' concept of Grant (1971), i.e. the sum of a series of incompletely diverged 'species' linked by natural hybridization'. *Iris* species of the series *Californicae* (Lenz, 1959) are an example, in which 11 'species' are linked in a web of hybridization. Only one species, *I. munzii*, stands apart as a reproductively isolated satellite. This process of isolation and refusion can obviously be driven by climatic change, and there is palaeobotanical evidence for this. For instance, Mason (1949) showed that Pleistocene climatic change was linked to patterns of population isolation and refusion in *Pinus remorata* and *P. muricata* in California. In particular, Prance suggested that the divergence-refusion mechanism might be an appropriate explanation for the variation shown by two ochlospecies, *Licania apetala* and *L. heteromorpha* (Chrysobalanaceae) (Prance, 1972).

The rapid expansion hypothesis

As an alternative to the refuge theory, I suggest that comparatively rapid spread of a taxon could lead to a complex variation pattern such as that seen in ochlospecies, without involving a fragmented, allopatric phase. The expansion of a colonising species with wide ecological tolerance will unleash a number of evolutionary forces within it: genetic drift in founding populations, rapid selection as the species colonises new habitats and climatic zones, and the conservation of mutations in an expanding population. Such recent dispersal will give rise to geographically unstructured variation, which will eventually become ecogeographically sorted with time. Zink & Dittman (1993) showed that despite marked geographic variation in size and plumage colour, mitochondrial DNA variation in the song sparrow (*Melospiza melodia*) was unstructured geographically. They suggested that rapid postglaciation dispersal scattered most DNA haplotypes across the range of the species. Morphological variation appears to have evolved faster and has been ecogeographically sorted, unlike the chaotic distribution of mitochondrial types.

Ecological and chorological transgressors, as many ochlospecies are, will have a tendency to occupy diverse niches at a particular site. Thus they are likely to come under strong disruptive selection. If polymorphism is promoted by niche width (Mather, 1955), then disruptive selection will accentuate the polymorphic divergence (Mather, 1955; Thoday & Boam, 1959). Although sympatric speciation may develop out of the polymorphic divergence (Mather, 1955; Thoday & Gibson, 1962), this will take more time and may not happen in all cases. In the case of a rapidly expanding population, variation will be rapidly exposed to a wide array of selectional forces, over a wide geographical range, and a highly complex polymorphic pattern can arise. However, the rapid expansion hypothesis may not be as plausible for more inert, tropical woody species, as for more vagile herbaceous species (and many animal species). In the contrasting case of a very slow spread of a taxon, this would allow equilibration between the variation and the selectional forces, resulting in sympatric speciation and niche specialization. Evolutionary change would therefore be inevitably incremental and not parallel, leading to highly structured patterns of variation.

A taxon cycle (Wilson, 1959; 1961), if it exists (Liebherr & Hajek, 1990), may be a repeated source of such events. The taxon cycle proposes a primitive and general ecological preference for a group and predicts habitat changes and specialization during diversification with a progression from a few invasive, colonising habitat generalists to many, non-invasive, endemic habitat specialists. The process is cyclical: new colonising generalists can be formed. This 'rapid expansion' or 'colonising generalist' hypothesis, like the Prance hypothesis, is amenable to testing.

Tests of hypotheses

First of all there is the possibility of testing the ochlospecies concept itself: that a particular and characteristic non-hierarchical variation pattern does exist, i.e. is not a sampling artefact, and is caused by processes as yet unknown — not the usual complicating factors of hybridisation between good species or apomixis. Once tested, many putative ochlospecies will perhaps be dismissed. *Schismatoglottis longispatha* (Araceae) appears to be an ochlospecies but nothing is known of its breeding system, and it is possible that it is a clonally-reproducing apomictic complex (A. Hay, pers. comm.)

Next must come, assuming the reality of an ochlospecies, the generation and testing of hypotheses to explain the phenomenon. Two such exemplar hypotheses have been given above, but it is not difficult to imagine others. One of the most powerful ways to test and distinguish between the hypotheses given here would be to examine the mitochondrial genome (mtDNA) or microsatellite regions in the chloroplast genome (cpDNA-SSR). The comparison of haplotype distribution with morphotype distribution would be revealing. If the morphotype mosaic was due to ancient historical processes, such as past allopatry, then deep haplotype clades would be predicted, with probably more geographical structuring of the haplotypes than the morphotypes, since polytopic origin of haplotypes would be less likely. The idea that significant genetic admixture occurred between modern humans and the populations they replaced has been tested by just such methods (Manderscheid & Rogers, 1996).

If on the other hand, the patterns were due to rapid population expansion then a shallow haplotype tree would be expected with haplotypes scattered over the distributional range of the species. Sophisticated models have been developed for predicting population history from haplotype distribution using 'mismatch analysis', which is the frequency distribution of degree of haplotype mismatch in pairwise comparisons of all individuals sampled. Such studies have been used to show that there was a Pleistocene population explosion of *Homo sapiens* (Rogers, 1995).

It is highly probable that a concerted study of an ochlospecies, analysing reproductive biology, morphotype and haplotype across the whole distributional range, would unveil important aspects of plant evolution, as the quotation at the top of this article suggests.

Conclusions and prospects

Taxonomic treatment

While ochlospecies polymorphism may give the impression of nature outwitting the taxonomist, this is only the case if an attempt is made to force the variation into a formal taxonomic hierarchy in the first place. It has been truly said: "Never argue with Nature, her first word is a blow" (Lucretius), and taxonomic treatment should be in agreement with nature. A wide species concept with the main nodes of variation distinguished as *informally named morphotypes,* accommodates the need to acknowledge the existence of locally recognizable "entities" (Vink, 1970). It is difficult to produce workable dichotomous keys to such entities because of the existence of a continuum of intermediates, but multi-access, fuzzy-logic computer keys may be a workable alternative. In *Myrmecodia tuberosa,* Huxley & Jebb (1993) recognise 16 informal taxa, 'bullosa', 'dahlii', 'versteegii' etc. (Figs 2 and 3). Mabberley (1979) similarly recognises ten such informal entities in *Chisocheton.*

However, we must frankly recognise that in a situation of very rapid anthropogenic vegetation change, particularly in the tropics, and the consequent conservation concern, a species carries more political weight than an informal variant. Gentry (1990) went as far as to write: 'variation that is swept under the rug is lost from view, whereas that which is grappled with openly, albeit at great cost of taxonomic time and effort, makes information available to the general public... there is a political imperative as well as a scientific one to accord recognition to taxa that can clearly be demonstrated to behave, either genetically or ecologically, as species'. It is up to the individual taxonomist to find the balance between the political species concept (PoSC) and what is justified from the available evidence. Even if that evidence is scanty because of ignorance, it ill behoves us to invent taxa just because they might, probably do, or should, exist.

The hierarchy of nature

The ochlospecies is at the centre of concerns about the limits to hierarchy in nature: the boundary between reticulating population processes (tokogenesis) and dichotomous lineage formation (cladogenesis). In deer mice (Lansman *et al.*, 1983) a remarkable amount of hierarchical structure has been detected at the population level. In contrast, the ochlospecies appears from morphological evidence alone to be an example where a lack of hierarchical structure has crept up the taxonomic scale to the species and superspecies. A hierarchy of taxa is, of course, more properly a hierarchy of characters, and extending the characters under investigation by including genetic information may reveal an otherwise hidden hierarchy, or not. There is no necessary correlation between DNA variation in specific regions and overall morphology, and thus although the amount of DNA variation cannot be expected to be a guide to the species, the study of genomic regions which are evolving at an appropriate rate may be a valuable help in revealing underlying hierarchy. This can also show up parallel evolution (homoplasy) or phenotypic plasticity, features to which morphological characters are especially prone, if these are the root of observed chaotic variation. If there is to be a synthesis between microevolution and speciation, and between taxonomy and population genetics, then the complex patterns presented by ochlospecies would be an interesting place to start.

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