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**Morphometric Variation within and between Populations of Rhopalosiphum maidis with a Discussion of the Taxonomic Treatment of Permanently Parthenogenetic Aphids (Homoptera: Aphididae)**

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Morphometric variation within and between karyotypic variants ( $2n = 8, 9$  or  $10$ ) of the permanently parthenogenetic aphid *Rhopalosiphum maidis* (Fitch 1856) was analysed, using multiple discriminant techniques (canonical variates analysis, linear discriminant analysis). Samples from populations localised in time and space clustered according to karyotype. The separation was much poorer when a broader range of localities, years of collection and host plants were included in the analysis. This was mainly because of greater within-karyotype morphological variation, due largely to an increased environmental component of variance. There was also evidence of genotypic heterogeneity within the  $2n = 8$  form, which did not however reflect any particular host plant associations. Guidelines for the taxonomic treatment of permanently parthenogenetic aphids are suggested and discussed.

**Key words:** *Rhopalosiphum maidis* (Fitch 1856) — aphids — multivariate morphometrics — taxonomy — parthenogenetic/unisexual species.

Blackman, R.L., & Brown, P.A. [Abtg. Entomol., Naturhist. Mus., London, UK]: **Morphometrische Variabilität in und zwischen Populationen von Rhopalosiphum maidis, mit Bemerkungen zur taxonomischen Behandlung permanent parthenogenetischer Blattläuse (Homoptera: Aphididae).** — Entomol. Gener. 16(2): 097–113; Stuttgart 1991. — [Abhandlung].

Die morphometrische Variabilität in und zwischen verschiedenen Karyotypen ( $2n = 8, 9$  oder  $10$ ) der permanent parthenogenetischen Blattlaus-Art *Rhopalosiphum maidis* (Fitch 1856) wird analysiert unter Verwendung von Diskriminanzanalysen (kanonische Vektoranalyse, lineare Diskriminanzanalyse). Proben von zeitlich und räumlich beschränkten Populationen gruppieren sich entsprechend dem Karyotyp. Die Trennung erweist sich als beträchtlich unschärfer, wenn eine größere Breite von Lokalitäten, Sammeljahren und Wirtspflanzen in die Analyse einbezogen wird. Der Hauptgrund hierfür liegt in der größeren inner-karyotypischen Variabilität als Resultat höherer Varianz der Umweltkomponenten. Es ergeben sich auch Anzeichen genotypischer Heterogenität innerhalb der  $2n = 8$ -Form, die sich jedoch als unabhängig von bestimmten Wirtspflanzenbeziehungen erweist. Es werden Richtlinien für die taxonomische Behandlung permanent parthenogenetischer Blattlaus-Formen vorgeschlagen und diskutiert.

**Schlüsselwörter:** *Rhopalosiphum maidis* (Fitch 1856) — Blattläuse — Multivariate Morphometrie — Taxonomie — Parthenogenetisch-monosexuelle Arten.

## 1 Introduction

One of the most fundamental questions in biology concerns the ubiquity of sexual reproduction; why do the great majority of organisms reproduce by bisexual means? [Bell 1982: examples]. Interest in this problem has been reawakened in recent years, particularly by the realisation that those parthenogenetic (= unisexual) organisms that do exist, appear to maintain considerable genetic variability and evolutionary potential, at least in the short term [e.g. Jackson et al 1985]. There is a need to understand the population genetics and mechanisms of evolutionary change in such organisms.

Aphids are one of the few groups that employ thelytokous (i.e. all female) parthenogenesis as an evolved adaptation, within a life cycle that also retains a phase of bisexual reproduction. The genetic and evolutionary consequences of such cyclical parthenogenesis are very different from those that follow the complete abandonment of sexual reproduction [Lynch & Gabriel 1983]. Most aphids retain the bisexual phase but, in comparison with most other groups of insects, a relatively large number of aphid species including many of economic importance have lost the ability to reproduce bisexually and become permanently parthenogenetic.

One of the consequences following from the complete abandonment of sex and its associated meiotic processes is an increase in the frequency of observable variation in the karyotype, sometimes including complex structural heterozygosity. This phenomenon is very clear in permanently thelytokous aphids [Blackman 1980], although the best studied example is the Australian parthenogenetic grasshopper *Warramaba virgo* [White 1979]. The question arises of whether the karyotypic differences between clones in thelytokous organisms are associated with consistent morphological differences. Atchley [1981] investigated this question in *W. virgo*, and found some significant discrepancies between morphometric and cytogenetic data. *W. virgo* is a wingless insect of low vagility and of hybrid origin, so that its population genetics may be expected to differ greatly from that of a highly vagile, crop-infesting aphid.

The Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch 1856) is a world-wide pest of cereal and grain crops, and one of the principal vectors of Barley Yellow Dwarf Virus. Populations are all believed to be permanently parthenogenetic, no functional bisexual phase ever having been observed. However, ♂♂ have occasionally been recorded both in the field [Eastop 1954] and in reared colonies [Wildermuth & Walter 1932], and a single ovipara has been described from wheat in India [Menon & Ghai 1969], so the possibility that occasional bisexual reproduction occurs somewhere in the world cannot be discounted. The parthenogenesis is thelytokous and apomictic, so that populations are clonally structured. Brown & Blackman [1988] showed that Corn Leaf Aphid populations on barley (*Hordeum vulgare*) in the N Hemisphere have a different karyotype ( $2n = 10$ ) from those on maize (*Zea mays*) and *Sorghum* spp. (sorghum, Johnson Grass), which usually have  $2n = 8$ . In the NW United States, the 10-chromosome form occurs on eupanicoid grasses such as *Echinochloa crus-galli* growing as weeds within fields of maize, without colonising the crop itself [Blackman et al 1990]. Wheat (*Triticum vulgare*), however, is not preferentially colonised by forms of any one karyotype. Other karyotypic variants also occur, for example a form with  $2n = 9$ , but no clear host associations have yet been demonstrated for other karyotypes. Preliminary morphological studies [Brown & Blackman 1988] revealed some significant differences between morphometric characters of  $2n = 8$  and  $2n = 10$  forms based on large samples, but with considerable overlap between individual values. Even multivariate techniques such as canonical variates analysis (CVA) failed to discriminate completely between the different karyotypes. This was partly because there were strong genotype-environment interactions, so that all canonical variates were strongly dependent on environmental factors. Another possible factor, contributing to partial failure of multivariate discriminant techniques, is the clonal structure of populations of *R. maidis*. The ancestral karyotype is probably  $2n = 8$ , like that of most sexually reproducing species of *Rhopalosiphum*, and could be represented by any number of clones on various host plants. A derived karyotype such as the 10-chromosome form, however, is more likely to be a widely distributed but nevertheless monoclonal lineage, with a single origin from the ancestral karyotype, recognisable by its particular features of karyotype and host association, but not morphologically discrete in any one character or suite of characters from all other extant clones recognised as *R. maidis*.

In the present paper, the morphological variations within and between samples of known karyotype of the Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch 1856), are studied more intensively, examining populations that are localised in time and space and comparing these with populations from a broader range of localities, years of collection and host plants. By this method, a better understanding of variation is tried to obtain in apomictic aphid populations, and particularly aimed to see whether there is any reliable basis for a morphometric discrimination of forms with different karyotypes and/or host associations.

The biological species concept is inappropriate for aphids that have irretrievably lost the bisexual phase of the life cycle. Shaposhnikov [1981] formulated a "universal species concept" for aphids, which attempts to accommodate their varied breeding systems. However, this still leaves considerable practical problems for the taxonomist confronted with populations comprising an unknown or indefinite number of mutually isolated unisexual lineages. Here therefore, some guidelines for the taxonomic treatment of permanently parthenogenetic aphids are discussed and suggested. This topic was of particular interest to Professor F. P. Müller, and indeed the senior author's last communication with him was on this very subject, so it seems particularly appropriate in a paper dedicated to his memory.

## 2 Materials and Methods

The study material comprised 109 collections of *R. maidis* (Tab 1), most of which were from the NW USA in 1986 and 1987: in Idaho by S.E. Halbert (67 samples) and in Montana by T.W. Carroll (27 samples; Tab 1). Idaho samples originated from *Hordeum*, *Zea*, *Echinochloa* and *Triticum*, but were all from clonal cultures reared on *Hordeum*, irrespective of the host plant of collection. The Montana material included samples collected on *Zea* and *Hordeum* but maintained as laboratory cultures for 10–13 months on *Avena sativa*. These all originated from single colonies but were not necessarily clonal. Samples from other states of the USA, as well as collections from Europe and Asia, including some of the material listed in Brown & Blackman [1988: Tab 1], were subsequently included in the analysis. Additional host plants sampled included *Sorghum bicolor*, *S. halepense*, *Bromus catharticus*, *Panicum capillare* and *Setaria* spp.

Aphids for karyotyping were preserved in 3 : 1 methanol/acetic acid. Embryos were dissected from 2–3 usually immature aphids of each sample, hydrolysed in 1N hydrochloric acid and squashed in 45% propionic acid [Blackman 1980]. Aphids for morphometric study were macerated, cleared and mounted in Canada balsam using Martin's method [Martin 1983]. 10 specimens were measured from each of 99 samples of adult apterous virginoparae and 81 samples of adult alate virginoparae. In order to reduce the work load, and because a main aim of the work was to discriminate between  $2n = 8$  and  $2n = 10$  forms of *R. maidis*, 4 parameters were used that had contributed most to this discrimination in previous work. These were length of processus terminalis (PT); length of antennal segment 4 (AS 4); length of antennal segment 5 (AS 5); and length of second segment of hind tarsus (HT 2). Measurements were recorded using a Kontron Videoplan image analysis system. The morphometric data, totalling 7,440 measurements on 1,860 individual specimens, were analysed using programmes written in BASIC by I. M. White; the canonical variates analysis (CVA) is based on Blackith & Rayment [1971], and the linear discriminant analysis (LDA) is based on Davies [1971].

## 3 Results

### 3.1 Idaho 1986 samples

Canonical variate (CV) means of 27 samples from 5 sites in a small area of W Idaho, collected in IX–XI 1986, grouped according to karyotype (Fig 1: a, b). Scores on the first canonical

**Tab 1:** Collection data for samples of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae], karyotyped and/or measured for the present study (supplements Tab 1 in Brown & Blackman [1988]) (\* indicates that samples from the same population(s) reared on *Avena* in the laboratory were also included in the analysis.)

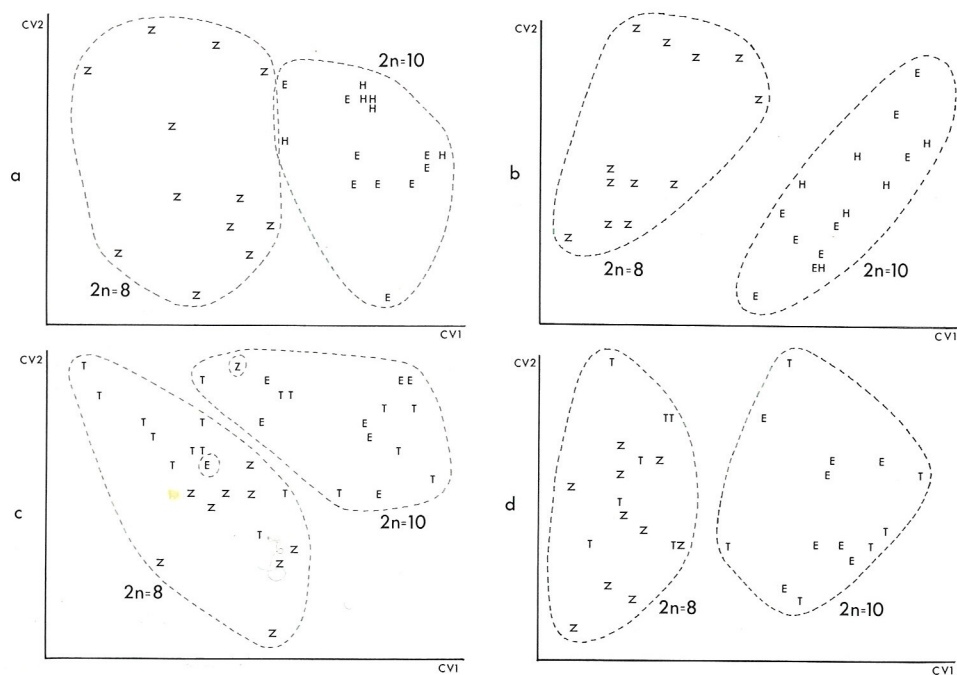
Sample No	No of chromo-somes	Host plant (No of samples in brackets)	Locality	Date	No of measured specimens	
					Alatae	Apterae
3542	8	?	Kansas	26.ix.85	—	10
3548	8	<i>S. halepense</i>	Mississippi	17.v.85	—	10
3553	8	<i>S. halepense</i>	Alabama	16.v.85	—	10
3558-9	8	<i>Zea</i> (62)	Montana	26.ix.85	20	20
3563	10	<i>Hordeum</i> *	Montana	18.vii.85	20	20
3565	10	<i>Hordeum</i> *	Montana	26.ix.85	10	10
3567-8	10	<i>Hordeum</i> * (2)	Montana	19.viii.85	30	40
3576	8	<i>S. halepense</i>	Alabama	16.v.85	10	10
3629	8	<i>S. halepense</i>	USA	20.vi.85	—	10
3755-7	8	<i>Zea</i> * (3)	Montana	9.xi.87	40	60
3758	8	?	New York	14.x.86	10	10
3759-60	10	<i>Hordeum</i> (2)	Montana	x.87	20	20
3761-5	10	<i>E. crus-galli</i> (5)	Idaho	25.ix.86	50	50
3766-71	10	<i>Hordeum</i> (6)	Idaho	12.xi.86	60	60
3780	9	<i>Hordeum</i>	Syria	13.i.87	—	10
3781	10	<i>Hordeum</i>	Syria	26.iii.87	—	10
3782-5	10	<i>E. crus-galli</i> (4)	Idaho	24.ix.86	40	40
3786-96	8	<i>Zea</i> (11)	Idaho	24.ix.86	110	110
3799	8	<i>Zea</i>	Idaho	25.ix.86	10	10
3800	8	<i>Triticum</i>	Egypt	2.iii.87	—	10
3801	8	<i>Hordeum</i>	Egypt	2.iii.87	—	10
3876	10	<i>Hordeum</i>	Montana	4.viii.87	—	10
3877	8	<i>Zea</i>	Montana	15.ix.87	—	10
3878	10	<i>Hordeum</i>	Montana	4.viii.87	—	10
3879-84	8	<i>Zea</i> (6)	Montana	27.viii.87	—	60
3888-9	10	<i>E. crus-galli</i> (2)	Idaho	27.viii.87	20	20
3890-91	8	<i>Zea</i> (2)	Idaho	26.ix.87	20	20
3892	10	<i>E. crus-galli</i>	Idaho	27.viii.87	10	10
3893	8	<i>Zea</i>	Idaho	13.x.87	10	10
3894-5	8	<i>Zea</i> (2)	Idaho	26.ix.87	20	20
3896	10	<i>E. crus-galli</i>	Idaho	27.viii.87	10	10
3897-9	8	<i>Zea</i> (3)	Idaho	13.x.87	30	30
3900-3	9	<i>Triticum</i> (4)	Idaho	5.xi.87	40	40
3904	10	<i>Triticum</i>	Idaho	5.xi.87	10	10
3905-6	8	<i>Zea</i> (2)	Idaho	27.viii.87	20	20
3907-10	10	<i>E. crus-galli</i> (4)	Idaho	20.viii.87	40	40
3911-2	8	<i>Triticum</i> (2)	Idaho	5.xi.87	20	20
3921-5	8	<i>Triticum</i> (5)	Idaho	13.x.87	50	50
3926-8	8	<i>Triticum</i> (3)	Idaho	5.xi.87	30	30
3929-35	10	<i>Triticum</i> (7)	Idaho	5.xi.87	70	70



variate (CV1) just managed to separate  $2n = 8$  and  $2n = 10$  samples (but not individual specimens) of apterae (Fig 1a). With alatae the separation on CV1 was almost complete, and in the plot of CV1 versus CV2 the samples were well-separated (Fig 1b). CV1 had negative coefficients for AS4 and AS5 and a high positive coefficient for PT in both apterae and alatae, but with a high negative coefficient for HT2 only in alatae (Tab 2). Alatae of the  $2n = 8$  samples from *Zea* formed 2 clusters according to CV2 scores, but this grouping was less clear in apterae. CV2 values within karyotypes were highly correlated with general body size (using AS4 + AS5 + PT + HT2 as a general size index; Pearson's correlation coefficient,  $r = 0.93$ ,  $P < 0.01$ ), so the grouping of  $2n = 8$  alatae may reflect some variation in the rearing conditions. There was no differentiation between samples of the same karyotype from different sites, nor between  $2n = 10$  samples from *Hordeum* and *Echinochloa*.

### 3.2 Idaho 1987 samples

In 1987 *R. maidis* was found to be actively colonising wheat, which is not a regular host for this species. Samples from wheat at Caldwell, Idaho, included a mixture of 8, 10 and 9-chromosome karyotypes, in some cases cohabiting the same tillers [S.E. Halbert: pers comm]. CV1 scores for alatae of 14  $2n = 10$  clones and 17  $2n = 8$  clones originating from



**Fig 1:** Plots of mean scores on the first and second canonical variates for clonal samples of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae]. — Specimens collected in Idaho in 1986 and 1987 (see Tab 1): (a) apterae 1986; (b) alatae 1986; (c) apterae 1987; (d) alatae 1987. E (sample from) *Echinochloa crus-galli*; H *Hordeum vulgare*; T *Triticum vulgare*; Z *Zea mays*. Limits of scores for each karyotype are indicated by broken lines.

*Echinochloa*, *Zea* and *Triticum* clearly grouped according to karyotype (Fig 1d). (Aphids with  $2n = 9$  were not included in this analysis.) In the case of apterae, separation of 8- and 10-chromosome samples was less distinct, with a large overlap of CV1 scores. One clone of each karyotype was in the wrong group of a plot of CV1 versus CV2 (Fig 1c), although the alatae of these particular clones grouped correctly according to karyotype, so it is possible that these samples were transposed due to a labelling error. Apart from these 2 samples the overlap was largely due to general size correlation of CV1 as well as CV2 scores, so that the CV1 scores of  $2n = 10$  samples containing the largest individuals were similar to the CV1 scores of those  $2n = 8$  samples that contained the smallest individuals. Coefficients of CV1 scores were comparable in apterae and alatae (Tab 2).

**Tab 2:** Canonical coefficients of CV1 and CV2 for 4 variables in apterae and alatae of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae], and percentage of total variance accounted for by each vector. (For further explanation see text.)

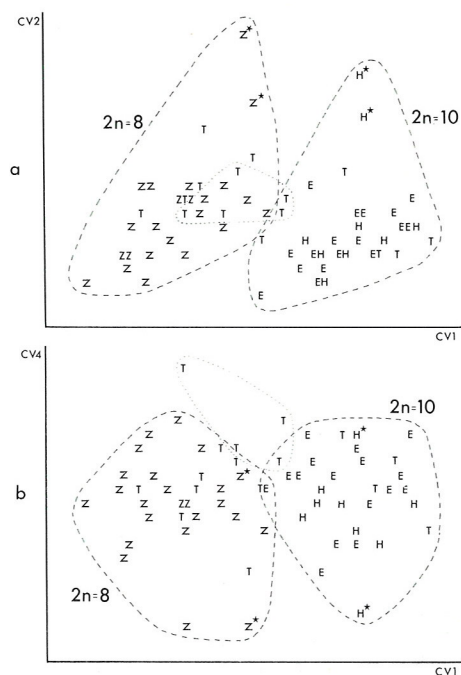
Apterae		Idaho 1986		Idaho 1987		Idaho/Montana 1986/87		All samples	
		CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2
AS4		-60.8	3.5	-28.4	-22.9	17.1	-4.1	5.8	-15.2
AS5		-46.1	13.8	-51.0	0.3	45.2	-46.5	7.8	-60.0
PT		71.8	21.4	44.6	61.3	-0.8	76.6	23.5	81.2
HT2		1.9	67.3	-68.8	20.7	34.0	-66.0	87.1	-72.5
% of total variance		49.7	31.1	55.7	27.4	55.3	29.7	58.5	27.5
Alatae		Idaho 1986		Idaho 1987		Idaho/Montana 1986/87		All samples	
		CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2
AS4		-15.2	5.2	-24.7	8.5	-15.7	20.7	-1.4	-28.3
AS5		-11.1	68.1	-28.0	30.6	-12.7	49.5	12.0	-40.9
PT		74.8	-26.2	78.9	12.5	76.6	-16.4	53.5	60.9
HT2		-83.4	30.5	-67.5	57.8	-78.4	24.4	-14.2	-83.2
% of total variance		72.4	17.5	65.5	22.0	49.4	39.2	59.8	25.1

### 3.3 Combined collections from Idaho and Montana 1986/87

The analysis was expanded to include 67 samples of alatae and 99 samples of apterae collected over a two-year period in Idaho and Montana. Clones with  $2n = 9$  were also included in this analysis.

For alatae (Fig 2a, b), there was a clear grouping of samples according to karyotype, although the clusters would have been far less evident without the chromosomal information. A plot of CV1 versus CV2 provided the best separation of  $2n = 8$  and  $2n = 10$  samples. The 4 samples from Montana (2 with  $2n = 10$  and 2 with  $2n = 8$ ) had high values on CV2, but this was due

to the relatively large size of the aphids in these samples, CV2 being strongly size-dependent. The four  $2n = 9$  samples (all from *Triticum*) had similar scores on all four CV's, with relatively high scores on CV4 drawing them away from the other karyotypes in a plot of CV1 versus CV4 (Fig 2b). CV1 accounted for 49.4%, CV2 for 39.2% and CV4 for 4.2% of total variance in the data. Coefficients of CV1 scores were consistent with the analyses for the 2 years separately, with negative values for AS4, AS5 and HT2, and a high positive coefficient for PT (Tab 2).



**Fig 2:** Canonical variates analysis of samples of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae]. — Alatae from collections in Idaho and Montana 1986/87, including  $2n = 8$ , 10 and 9 karyotypes. Montana samples are indicated by \*. The four  $2n = 9$  samples from *Triticum* are encircled by a dotted line. (a) plot of CVI versus CV2; (b) plot of CVI versus CV4. Letters denote host plants as in Fig 1.

In the case of apterae (Fig 3a), the picture was quite different. Apterae were extremely variable in size, and CV1, accounting for 55.5% of the variance, was highly size-correlated (Pearson's coefficient,  $r = 0.96$ ,  $P < 0.01$ ). This left CV2 (29.7%) as the main discriminant between karyotypes, as evidenced by the similarity of CV2 coefficients with those of CV1 in the analyses for Idaho 1986 and 1987 separately (Tab 2). A plot of CV2 versus CV3 therefore provided the best separation (Fig 3b). Again, CV2, CV3 and CV4 scores for  $2n = 9$  samples formed a consistent grouping, although not separate from the other karyotypes. The large and seemingly inconsistent effects of environment on morphology of the apterous morph are perhaps shown when CV scores of Montana samples from the original collections on *Zea* are compared with those from laboratory cultures of the same colonies reared on *Avena*. These colonies may not, however, have been clonal, so some of the difference could be due to genetic change.

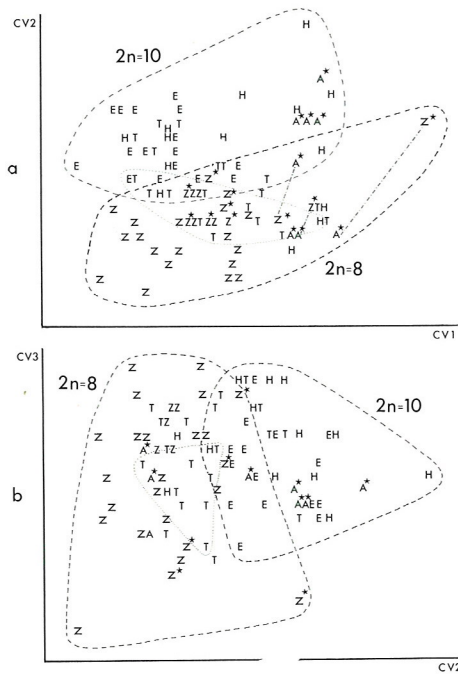


Fig 3

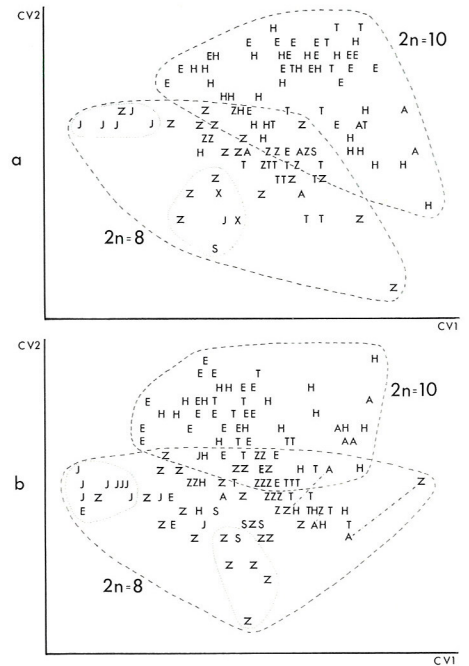


Fig 4

**Fig 3:** Canonical variates analysis of samples of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae]. — Apteræ from Idaho and Montana 1986/87, including  $2n = 8, 9$  and  $10$  karyotypes. The four  $2n = 9$  samples are encircled by a dotted line. (a) plot of CV1 versus CV2; (b) plot of CV2 versus CV3. Letters denote host plants as in Fig 1 and 2, plus A\* = sample from laboratory culture on *Avena sativa*; pairs of samples collected on *Zea* and reared on *Avena* are linked by interrupted lines.

**Fig 4:** Plots of mean scores on the first and second canonical variates for samples of *Rhopalosiphum maidis* (Fitch 1856) [Homoptera: Aphididae]. — Specimens collected in various parts of the world. (a) alatae; (b) apterae. Samples of each karyotype are encircled by broken lines, and postulated groupings of samples within  $2n = 8$  are indicated by dotted lines (see text). J field-collected sample from Johnson Grass, *Sorghum halepense*; S sample from sorghum, *S. bicolor*; X sample from unknown host plant; otherwise as in Fig 1, except that E includes other eupanicoid grasses as well as *Echinochloa* (e.g. *Setaria*, *Panicum*).

### 3.3 Variation among $2n = 8$ samples

To see whether any groupings could be detected among  $2n = 8$  samples from Idaho and Montana, analyses were carried out on the data for these samples alone. In both apterae and alatae scores on CV1, accounting for about 64% and 76% of total variance respectively, were strictly size-correlated (Pearson's "r" = 0.99), and comparison of scores on CV's 2-4 failed to reveal any consistent groupings. Samples from *Triticum* had CV scores scattered among those from *Zea*.



### 3.4 Addition of samples from further afield

When samples from other parts of the world and other host plants were included in the analysis, the separation of  $2n = 8$  and  $2n = 10$  forms was even poorer and chiefly due to CV2, which accounted for 25–27% of the total variance in both alatae and apterae (compare CV2 coefficients in Tab 2). Two new groupings emerged in the  $2n = 8$  data. These were particularly evident in alatae (Fig 4). One grouping, with lower scores on CV1 than any of the Idaho and Montana samples, comprised various samples collected by D.J. Voegtlin from *S. halepense* in the S' USA, plus a sample of apterae from *Echinochloa* in Iran, and samples from *Zea* of apterae from Peru and alatae from Tasmania. The aphids in these samples were smaller than any included in previous analyses, and CV1 is strongly dependent on size, so the grouping may be partly influenced by environmental effects on size. Nevertheless, this grouping agrees well with the findings of Steiner et al [1985], who found fixed enzyme differences between samples from these same S' US populations of *R. maidis*, when compared with Illinois populations. One sample of apterae from an Illinois population studied electrophoretically by Steiner et al was also included in the present analysis, and grouped with the Idaho and Montana samples.

The second grouping of  $2n = 8$  samples was differentiated by its scores on CV2, and included samples from *Zea* in the Middle East (Iran, Israel) and South Africa, plus samples from California (*S. bicolor*), Israel (*S. halepense*), and Ontario and Ivory Coast (unknown hosts). Some of these samples were also available as apterae and grouped together, along with 3 additional samples from *Zea* in Egypt for which alatae were not available; but in the apterae this grouping was not so distinct from the rest of the  $2n = 8$  samples (Fig 4b).

### 3.5 Linear discriminant analysis

Linear discriminant functions (LDF's) calculated from limited data sets with similar numbers of  $2n = 8$  and  $2n = 10$  individuals, from Idaho in 1986 for example, correctly classified 80–90% of individual aphids. LDF's based on only 2 characters (PT and AS4, or PT and HT2) performed almost as well as those based on 4 characters. However, as might be predicted from the results of CVA, functions computed for one set of data failed to discriminate when applied to samples collected in other years or other localities, misclassifying 30% or more of individuals. Thus, although samples of the 2 karyotypes may be morphologically distinguishable when reared under the same conditions, or collected at the same time and place, none of the computed LDF's was sufficiently reliable for general application.

## 4 Discussion

### 4.1 Significance of the observed variation in *R. maidis*

Canonical variates analysis has proved a powerful technique for separating morphologically similar aphid taxa [Blackman et al 1977; Blackman 1987, and in press]. Previously unrecognised "sibling" species can often be separated by their scores on CV1 alone, or by CV1 in conjunction with another vector, although with field-collected samples the environmental component of variation may be very large and reduce the separation to such an extent that the grouping of samples would not be readily discernible without additional information such as differences in karyotype or host plant.

In the case of a permanently parthenogenetic aphid such as *R. maidis*, the situation is rather different. There are an unknown number of genetically isolated lineages, which may have

diverged morphologically to an extent depending on how long they have been evolving independently, and on the particular selection pressures to which they have each been exposed. Analysis has indeed shown that forms distinguished by karyotype and host association may also differ significantly in several morphometric characters, but with a broad range of overlap of the ranges of individual measurements [Brown & Blackman 1988]. Such broad overlap is, of course, normal for single morphometric characters, but is usually well-correlated with general body size, so that it can often be eliminated by use of simple ratios or bivariate plots, or when general size is extracted as one of the principal vectors in a multivariate analysis. Complete separation of  $2n = 10$  and  $2n = 8$  forms of *R. maidis* could not, however, be achieved by these methods.

There are 2 possible reasons for this. Firstly, there appears to be a particularly strong interaction between genetic and environmental components of variation, so that all CV's depend considerably on the environmental conditions experienced during development. Such phenotypic plasticity was also encountered in *Myzus antirrhinii* (Macchiati 1883) [Blackman 1987], and may be a feature of the genome of permanently parthenogenetic aphids. It could be associated with the high level of heterozygosity found in old parthenogenetic lineages, perhaps coupled with the selection of epistatic mechanisms that may help to maintain adaptability in the absence of genetic recombination [Atchley 1977, Parker 1979].

A second possible reason for failure to discriminate between forms of known karyotype was mentioned in the introduction to this paper, and concerns the unknown number of separate lineages present in the data base. There is evidence that the  $2n = 10$  form is a single parthenogenetic lineage, but no a priori reason to suppose that forms with the presumed ancestral karyotype of  $2n = 8$  comprise a single, monophyletic group. Populations with  $2n = 8$  from *Zea* and *Sorghum* might, for example, comprise separate lineages, or there might be other  $2n = 8$  lineages with different host associations or restricted geographical distribution. What evidence do the present results provide towards a resolution of this question?

When samples from a single year or collection locality were analysed, there was generally no problem in discriminating between  $2n = 10$  and  $2n = 8$  forms with CVA, either on the basis of CV1 scores alone or using CV1 and CV2 when both these vectors were size-correlated (Fig 1). Even in the case of the 1987 Idaho apterae, CV1 contributed much more than CV2 to the separation of the 2 karyotypes, CV2 being always very size dependent. Within the  $2n = 8$  samples, there was no evidence of any grouping that could be attributed to genotypic differences. The 1986  $2n = 8$  alatae cluster distinctly on CV2, but these clusters seem to reflect differences in general body size, possibly caused by different rearing conditions. Samples from *Triticum* in the 1987 material with  $2n = 8$  were scattered among samples from *Zea*, and in the same way,  $2n = 10$  samples from *Triticum* were scattered among those from *Echinochloa*. When all  $2n = 8$  samples from Idaho and Montana were analysed alone, the correlation of CV1 with general body size was remarkably high, indicating that CV1 was effectively removing general size from the data, yet CV's 2-4 still failed to show any grouping of samples that might indicate the presence of separate lineages.

Extending the data base to a two-year period reduced the ability of CVA to discriminate between  $2n = 8$  and  $2n = 10$  samples, but only in the case of apterae. The environment appears to have a greater effect on the morphology of apterae than of alatae, and presumably the addition of another year's data increased the environmental component of variation relative to the genetic component, so that CV1 ceased to contribute anything to the separation of karyotypes.

The  $2n = 9$  samples presumably represent a single parthenogenetic lineage like the  $2n = 10$  form, but without any known specific host association. The consistent grouping of the CV

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scores of the  $2n = 9$  samples suggests that the analysis can discriminate smaller monophyletic groups within the data, even with the character set reduced to 4 variables. The absence of any such consistency of grouping of CV scores within the  $2n = 8$  samples from Idaho and Montana, other than those on CV1 that are clearly size-correlated, suggests that the  $2n = 8$  samples in this restricted time and area may be genetically rather homogeneous.

When a much wider range of samples of *R. maidis* was included in the analysis, 2 additional groupings of  $2n = 8$  samples were evident. One of these included all samples collected on *S. halepense* in S' USA, and therefore agreed with the results of an electrophoretic study by Steiner et al 1985 which showed genetic differences between N' and S' US populations of *R. maidis*. The other apparent grouping was of samples predominantly from Middle Eastern and North African countries. In neither case was there any consistent association with particular host plants.

Thus, CVA can group samples of *R. maidis* in a consistent fashion according to known genetic differences, eg in karyotype or electromorph, reflecting the clonal structure of populations of a permanently parthenogenetic aphid. The data suggest that on a world scale, and in addition to lineages already recognisable by their karyotypic differences, there may be a limited number of other separate lineages sharing a similar or identical  $2n = 8$  karyotype. However, these are not responsible for the failure to discriminate between  $2n = 8$  and  $2n = 10$  forms. It seems rather that the environment has a substantial influence on all canonical variates, and obscures the genotypic differences, to the extent that reliable discrimination between any genotypes on morphometric evidence alone is impossible.

#### 4.2 Taxonomic treatment of permanently parthenogenetic aphids

Shaposhnikov [1981] discussed the particular problems of applying the biological species concept to aphids, which may have obligate annual bisexual reproduction, mixed populations with bisexual and unisexual reproduction, or obligate unisexual reproduction. He discussed the development of a universal species concept that could accommodate these features. The difficulty lies mainly with permanently unisexual populations, for which the biological species concept, with its restriction to interbreeding populations, is clearly inappropriate. In aphids, there are many such permanently unisexual lineages, often closely related to bisexual species and derived from a common ancestor by loss of the bisexual phase of the life cycle. Aphid taxonomists have traditionally described and named species in unisexual aphids without establishing a conceptual framework for their use of the species category in this way. It is possible to do this because permanently parthenogenetic aphids do seem to exist as characterizable entities that are comparable to the species of those aphids that retain sexuality. They have, at least superficially, a similar range of phenotypic variation and a similar pattern of ecological relationships. Yet some conceptual basis for this equivalence between bisexual and unisexual species is clearly necessary, as a basis for standardizing the methods of delimiting species in a group where the structure of populations may vary greatly according to differences in the breeding system. It is also important that due consideration is given to current ideas about phylogeny.

Steffan [1961a, 1961b, 1962, 1963a, 1963c, 1964a] has discussed the origin and taxonomic status of unisexual lineages in the conifer woolly aphids (Adelgidae). He distinguishes between bisexual "biospecies" and unisexual "agamospecies", treating a bisexual ancestor and its unisexual derivatives as members of a "superspecies" [Steffan 1961a, 1961b, 1963a, 1963b, 1964a, 1972]. He also has evaluated the ecological and genetical background for the evolution



of agamospecies in Adelgidae [Steffan 1968a, 1968b, 1969a, 1969b, 1970, 1971]. These results and reflections should also be considered for the explanation of the origins of unisexual lineages in other aphid families.

Shaposhnikov's "universal species concept" in its shorter form, defines a species as "a safely isolated system of related populations capable of interactions and fusion (which) plays a particular role in the biosphere". This is a version of the evolutionary species concept developed by Meglitsch [1954] and Simpson [1961], and also by Wiley [1978] who defined it concisely as "species are the largest monophyletic groups whose components are not irretrievably on different phylogenetic trajectories". The applicability of the evolutionary species concept to unisexual as well as bisexual organisms has been argued by all its proponents. Meglitsch's original expression of this concept is worth quoting: "The species, in the case of uniparental and biparental organisms, may be visualised as a natural population, evolving as a unit in actuality, or retaining the capacity to evolve as a unit... if barriers are removed... The species population is the visible manifestation of a pool of genes which retains its character as a unified pool because, in theory, any allele present may eventually come to replace all the allelomorphs in the pool, either as a result of interbreeding or as a consequence of simple differential survival in the case of uniparental organisms... A species is thus an independent and distinctive region of gene spread, regardless of the mechanisms involved in the distribution of these genes, and is applicable to organisms which reproduce sexually and asexually". Such a definition gives some insight into the species as a functional entity, existing not because of reproductive barriers, but because it forms a historical group, with a unitary evolutionary role setting it apart from other species. Such a role can be played by both unisexual and bisexual species.

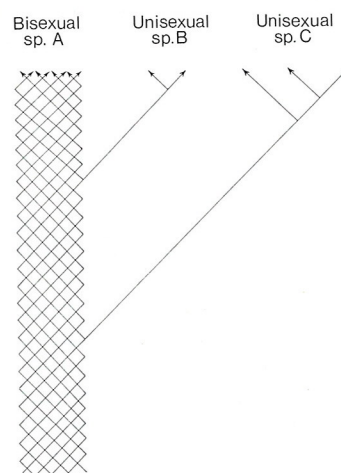
These ideas may provide a conceptual basis for an equivalence between unisexual and bisexual species of aphids. Nevertheless, the problems of practical aphid taxonomy still remain; the difficulty of recognizing and delimiting unisexual species which may consist of an unknown or indefinite number of clonal lineages. Questions to attempt to answer in individual cases are: (1) Is the loss of the bisexual phase complete and irreversible? (2) Does the complete assemblage of clonal lineages constituting the unisexual species appear to be monophyletic, i.e. share a common unisexual ancestor? (3) Is there a closely-related bisexual species with which the unisexual species is likely to share a common bisexual ancestor? (4) Could the unisexual species be of hybrid origin? (5) Even if the assemblage of clonal lineages appears to be monophyletic and constitute a true historical group, has the original role of the common ancestor of these lineages been significantly subdivided or extended, with the result that certain lineages have diverged "irretrievably on different phylogenetic trajectories"? Should this then be a basis for separate species designations for these lineages?

DeBach [1969], Enghoff [1976] and Saura [1980] all discussed the naming of parthenogenetic animals (without referring to aphids) and came to different conclusions. DeBach and Saura both adopted a purely phenetic approach, suggesting respectively that ethological/ecological and morphological criteria were adequate to define unisexual species. Enghoff considered that a unisexual taxon should only be given species status if it has no known bisexual relative; and even then, it should not be regarded as a "biological" species. It is difficult to see how species status can be made dependent on the extinction of closest relatives.

None of these authors proposed solutions incorporating phylogenetic criteria, based on inferred ancestry. Frost & Wright [1988] discuss the taxonomic treatment of unisexual species, with particular reference to parthenogenetic lizards of the genus *Cnemidophorus*, several of which are of known or presumed hybrid origin. Their recommendations are consistent both with existing taxonomic practice and with phylogenetic considerations, and we propose that per

manently unisexual aphids should be treated similarly (Fig 5). We suggest the following guidelines, which are modified from those of Frost & Wright to accommodate the origin of permanently unisexual species in aphids by loss of the bisexual phase:

- (1) Every origin of an obligately unisexual lineage from a bisexual ancestor, whether by loss of the bisexual phase, or hybridisation, or other means, constitutes the origin of a new evolutionary entity or historical group, and therefore a species (e.g. B and C in Fig 5).
- (2) Any unisexual historical group so derived, that can be characterized by any means, and that persists in nature, should be recognized as a species and formally named, regardless of whether its origin and phylogenetic relationships are fully understood.
- (3) Clonal lineages that diverge by mutational change and differential selection, but share a common unisexual ancestor (e.g. lineages 1, 2 and 3 of species C in Fig 5), should not be formally named as separate species, even if they can be characterized by their morphological or other differences. Those displaying particular properties may be recognised by some informal system of numbering or nomenclature associated with such properties (e.g. biotypes).



**Fig 5:** Diagrammatic representation of the phylogenetic relationships of bisexual and unisexual aphid species. The evolutionary nexus represented at present time by bisexual species A, has given rise by loss of the bisexual phase at various times in the past, to unisexual lineages, two of which have survived as unisexual species B and C. Divergent unisexual lineages are not regarded as separate species when they share a common unisexual ancestor.

(4) Clonal lineages that show resemblance because they have arisen from similar bisexual stock, but nevertheless originated independently and thus do not share a common unisexual ancestor, are not conspecific.

(5) In cases of uncertainty, arising either (a) because it is suspected that the bisexual phase may not have been irretrievably lost, or (b) when it is unclear whether an assemblage of clonal lineages shares a common unisexual ancestor, then one has to agree with Frost & Wright [1988] that it is best to indicate that the name being applied may not represent a single evolutionary entity in nature, by using a standard convention, the species complex. This simply denotes inadequate knowledge of the phylogenetic relationships involved and provides a temporary means of allowing communication while progress is made.

(6) If the uncertainty includes the relationship of one or more unisexual lineages with one (or more) bisexual species thought to be the closest relative(s) then the bisexual species should be included within the species complex, which should then take its name from the bisexual species.



These guidelines are primarily intended to apply to new work on aphid species complexes, as phylogenetic relationships within such complexes become clearer with the use of enzyme electrophoresis or DNA hybridization in conjunction with other techniques of experimental aphid taxonomy. Only minor changes seem necessary to the existing nomenclature and species status of unisexual populations. These include:

— *Lipaphis pseudobrassicae* (Davis 1914) is the correct name for the unisexual species colonising many Cruciferae throughout the world, with closest bisexual relative *L. erysimi* (Kaltenbach 1843), from which it differs in karyotype and morphology.

— *Anuraphis diana* Shaposhnikov 1974 should have the status of a full species, its closest relative being *A. farfarae* (Koch 1854).

— In the genus *Dysaphis*, *D. apifolia* (Theobald 1923) and *D. foeniculus* (Theobald 1923) are unisexual species, with closest bisexual relatives *D. petroselini* (Börner 1950) and *D. malidauci* Shaposhnikov 1986 respectively. (The latter 2 species were described as subspecies of the former, but the subspecies category is inappropriate for taxa which are completely isolated genetically.)

— *Brachycaudus persicaecola* (Boisduval 1867), and *B. semisubterraneus* Börner 1951, at present treated as synonyms of *B. persicae* (Passerini 1860), are probably good unisexual species, but perhaps more safely regarded as part of the *B. persicae* species complex pending further work.

— *Aulacorthum prasinum* Börner 1950 should have species rank instead of being variously regarded as a subspecies [Müller 1970] or synonym [Eastop & Hille Ris Lambers 1976] of *A. solani* (Kaltenbach 1843) — which is itself a complex of bisexual and unisexual species still to be resolved.

Other unisexual species with identifiable closest relatives include *Myzus antirrhinii* (Macchiati 1883), with closest relative *M. persicae* (Sulzer 1776); *Chaetosiphon jacobi* Hille Ris Lambers 1953, with a bisexual relative in the *C. fragaefolii* (Cockerell 1901) species complex; and in the Adelgidae, *Pineus pini* (Macquart 1819) related to the bisexual *P. orientalis* (Dreyfus 1889), and *Sacchiphantes abietis* (Linnaeus 1758) and *S. segregis* (Steffan 1961), both related to the bisexual *S. viridis* (Ratzeburg 1843). Some other well-known asexual species have no clearly identifiable bisexual closest relative; for example, *Tuberculolachnus salignus* (Gmelin 1790), *Myzus ascalonicus* Doncaster 1946, *M. cymbalariae* Stroyan 1954, *M. ornatus* Laing 1932, *Aulacorthum circumflexum* (Buckton 1876) and *Aphis nerii* Boyer de Fonscolombe 1841.

Unisexual populations which must in the present state of knowledge be regarded as members of species complexes are numerous, and include many important pest aphids. *Acyrtosiphon pisum* (Harris 1776), *Aphis craccivora* Koch 1854, *Brachycaudus helichrysi* (Kaltenbach 1843), *Schizaphis graminum* (Rondani 1852), and many other species complexes await further study to elucidate within-group reproductive and phylogenetic relationships.

Following the guidelines above, how should karyotypic variants of *R. maidis* be treated taxonomically? The  $2n = 10$  form is clearly characterizable, by host plant association and karyotype if not by morphology. However, it should not be formally named as a species unless it can be shown (for example, by DNA sequence analysis) that its origin from a bisexual ancestor occurred independently from that of the other karyotypic variants of *maidis* currently in existence. Conclusive proof of such independent ancestry is probably impossible so long as no bisexual populations are available for comparison, but it may be possible, as knowledge of the genetic structure of unisexual populations increases, to draw valid inferences from analogous situations in species complexes where bisexual and unisexual aphid populations do coexist.

At present, there is uncertainty about whether mutational changes can result in divergence within unisexual species to the extent that lineages evolve with different unitary roles, on “irretrievably different trajectories”, fulfilling the criteria for evolutionary species of Meglitsch, Wiley and Shaposhnikov. Our guidelines are based on the assumption, which may not be valid, that unisexual lineages are not able to evolve to such an extent. With greater knowledge it may be possible to infer, from the extent and nature of the genetic differences between two unisexual populations, whether they share a common unisexual ancestor or whether they are more likely to have arisen independently from a bisexual species. At present, however, we suggest that no attempt should be made to provide formal names for the various unisexual lineages that comprise the *R. maidis* species complex, and that they should continue to be referred to according to their karyotype, as  $2n = 8$  form,  $2n = 10$  form, and so on.

## 5 Acknowledgements

We wish to thank Dr Susan E. Halbert, Professor Thomas W. Carroll and Dr David J. Voegtlin for collecting, rearing and sending samples of *R. maidis* from the USA, and Dr A. Attia and Dr K. Makkouk for providing samples from Egypt and Syria respectively. We also thank Dr Ian M. White for use of his computer programmes.

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Diamond, J., & Case, T.J. (edit): **Community Ecology.** — [665 pp, num fig & tab, 190×240 mm, balacrharcovers]. — Publ: Harper & Row, New York-Cambridge-Philadelphia-San Francisco-London-Mexico-São Paulo-Singapore-Sydney; ISBN: 0-06-041202-X. — [EGR-Nr 1160].

This book aims to present a new approach to the ecology of biocoenoses and ecosystems, i.e. to synecology. Because of this field's complexity, researchers and authors usually are tempted to retreat into either of 2 extremes positions: descriptive particularism, which stresses that every system is unique and complex and that no generalizations other than superficial ones exist; or an oversimplifying search for universal statements and for The Best Method. Thus, the goal of this book is to steer between these extremes, and to seek conditional statements that are faithful to the diversity of life; specifically, the following questions are put to the readers: (a) For what species and what problems can each methodology be most profitably applied? (b) Given that observations can be carried out on various spatial and temporal scales, how does the choice of most appropriate scale depend on the species studied and the question asked? (c) How do effects of different organizing forces vary among communities? (d) Given that it is surely impossible to devise one model applicable to all ecological communities, can one at least partition communities among a modest number of types and devise a model for each type? — The 35 authors who have shared in writing the particular chapters of this book did not provide tidy solutions to these questions, but have offered extensive guidelines to the first 2, tentative partial answers to the third, a rudimentary start toward answering the fourth, and a status report on all 4 to guide future research.