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Chromosome numbers in the Aphididae and their taxonomic significance

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ABSTRACT. Diploid female chromosome numbers are listed for 180 aphid species not previously karyotyped. The list includes the first chromosome records for several aphid tribes (Tramini, Greenideini, Anomalaphidini, Nipponaphidini). Variation in chromosome number at different systematic levels is discussed. Usually the karyotype is particularly stable within a genus, but there are notable exceptions (e.g. *Amphorophora*) where considerable evolutionary increase in chromosome number has occurred by autosome dissociation with little accompanying morphological change. In several genera differences in gross chromosome morphology can be useful to the taxonomist. Within-species karyotype variation is relatively common in aphids, and instances of structural heterozygosity are particularly numerous in species and groups which have partially or completely abandoned the sexual phase of the life cycle in favour of permanent thelytoky.

Introduction

Chromosome numbers have been published for 328 species of Aphidoidea (Kuznetsova & Shaposhnikov, 1973; Gut, 1976), and in this paper an additional 180 are listed, bringing the total to 508, which is about 14% of the known species of aphid. Assessments of the evolutionary implications of aphid chromosome numbers have been based on information about far fewer species (Shinji, 1931; Steffan, 1968a). It therefore seems opportune to review the variations now known to occur in chromosome number at each systematic level within the Aphididae, and to discuss to what extent such information (a) contributes to an understanding of phylogenetic relationships within this family, and (b) is of use in practical taxonomy. Adelgidae and Phylloxeridae are not included here as the knowledge of these two families has not been significantly added to since Steffan (1968b).

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Methods

Chromosome squash preparations were made from young embryos removed from either fresh or pre-fixed material. Embryos were dissected from fresh material in hypotonic (0.75%) potassium chloride solution and fixed in a fresh mixture of 3 parts of absolute methanol to 1 part of glacial acetic acid. After 20 min and two changes of fixative the smallest embryos were transferred on the point of a pin to a small drop of 45% propionic acid on a clean microslide and squashed under a coverslip. Embryos dissected out of specimens pre-fixed in 3:1 methanol/acetic acid were transferred to 75% methanol (5 min), then to 1 N hydrochloric acid (5 min at 68°C), before squashing in 45% propionic acid. After examination under phase contrast, the best preparations were stained and made permanent. The coverslips were removed by flicking off with a sharp, pointed scalpel blade after the slides had stood, coverslips uppermost, on a flat block of solid carbon dioxide. The preparations were left to stand for 1 week at room temperature, then stained in 5% Giemsa

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solution (Gurr's R66) made up in M/15 phosphate buffer at pH 6.8 and mounted, after air-drying, in DePeX.

The parent aphids from which embryos had been removed were preserved and whole-mounted on slides for the BM(NH) collection. A cross-referencing system was used so that each chromosome preparation could be matched with the specimen from which it originated. This procedure if generally followed would remove any uncertainty about the assignation of a karyotype to a species in the light of any future taxonomic revision.

Results and Discussion

New records

Table 1 lists diploid chromosome numbers for female somatic cells of 180 species of Aphididae which have not been previously recorded. The systematic arrangement is that proposed by Eastop (1977), and the nomenclature mainly follows Eastop & Hille Ris Lambers (1976). The table also gives the number of samples of each species examined and their countries of origin. Various points arising from this table will be discussed in subsequent sections. However, here it should be noted that the diploid chromosome numbers reported, range from 6 to 72. Two species with 2n = 4 have previously been reported, but none with a diploid number higher than 40. It should be noted that there are examples of within-group variation in chromosome number at all taxonomic levels, and frequently within species where more than one sample of a species has been examined. The karyotypes of a remarkably high number of species (twenty-two, or over 12%) show some clear structural heterozygosity; i.e. the chromosomes cannot be matched into pairs on the basis of their relative lengths, as should be possible if they formed a normal, diploid set.

In addition, the karyotypes of about 100 other species, for which chromosome numbers have already been reported in the literature, were re-examined. In most cases the previous report was confirmed, but there were some cases where the karyotype did not agree with that cited in the literature. Some of these discrepancies are probably due to karyotype variation within species, and these will be discussed later. Others are less readily explained. Morgan (1909) in North America and Shinji (1927) in Japan examined spermatogenesis stages from aphids which they respectively named as *Lachnus dentatus* and *Pterochlorus viminalis*, both synonyms of *Tuberolachnus salignus* (Gmelin), and they both recorded n = 4 for spermatocytes. However, no males of *T.salignus* have ever been recorded, so it seems likely that the immature males used in their studies were of other species occurring in association with adult parthenogenetic females of *T.salignus*. There are species of *Pterocomma* with n = 4 on *Salix* in both North America and Japan. Two samples of parthenogenetic females of *T.salignus* from Britain had 2n = 20 in somatic cells.

Sun & Robinson (1966) and Robinson & Chen (1969) recorded 2n(♀) = 8 for *Euceraphis deducta* Baker. Having examined some of Robinson's slides the present writer believes that their samples were probably aphids of the *E.betulae* group. Three samples of *E.deducta* collected in North America on *Betula populifolia* had 2n(♀) = 16.

Kuznetsova & Shaposhnikov (1973) estimated the chromosome number of *Pterocomma salicis* (L.) as 2n(♀) = 30–34 in northern Russia. A sample from Britain had 2n(♀) = 58 in somatic cells. The discrepancy may merely be due to the difficulty of counting large numbers of dot-like chromosomes. On the other hand, Kuznetsova & Shaposhnikov list 2n = 10 for both *Glyphina betulae* (L.) and *G.schrankiana* Börner, but a sample of *Glyphina* from *Betula* in Britain was found to have embryos (presumably male because they had one long unpaired chromosome) with 2n = 55. Here the discrepancy seems to imply that a third, hitherto unrecognized, species is involved.

Gut (1976) recorded 2n(♀) = 14 for *Hyadaphis foeniculi* Pass. collected from *Conium* in Holland. A sample of *Hyadaphis* collected from *Lonicera* in Britain had 2n = 12. This supports the opinion of Börner (1952) that there are two species of *Hyadaphis* in western Europe with different host-plant associations.

In nettle aphids of the genus *Microlophium* the position is a little more complicated.

TABLE 1. Chromosome numbers for 180 species of Aphididae

Subfamily, tribe and species	2n (♀) (somatic cells)	No. of samples	Country of origin of sample(s)*
Lachninae			
Cinarini			
Cinara fresai Blanchard	13†	1	B
C.juniperi (de Geer)	12	1	B
C.kochiana (Börner)	10	2	B
C.ponderosae (Williams)	10	2	Am
C.tujafilina (del Guercio)	12	4	Am, Ir
Essigella californica (Essig)	8	2	Am
Eulachnus agilis (Kaltenbach)	8	4	B, Sw
E.brevipilosus Börner	30	2	B
E.rileyi (Williams)	8	4	Am. Ir
Lachnini			
Maculolachnus submacula (Walker)	10	4	B
Tramini			
Neotrama caudata (del Guercio)	9†, 11†	2	B
Protrama flavescens (Koch)	*c.* 42†	5	B
P.radicis (Kaltenbach)	*c.* 60†	6	B
P.ranunculi (del Guercio)	*c.* 36†	2	B
Trama rara Mordvilko	13†	1	B
T.troglodytes von Heyden	14†, 15†, 16† 17†, 18†, 19†, 20†, 21†, 22†.	23	B
Chaitophorinae			
Chaitophorini			
Chaitophorus capreae (Mosley)	30	2	B
C.salicti (Schrank)	28	1	Sw
C.leucomelas Koch	40	2	B
Chaitophorus sp. (from *Populus euphratica*)	22	3	Ir
Siphini			
Atheroides hirtellus Haliday	8	1	B
A.serrulatus Haliday	8	1	Sw
Drepanosiphinae			
Callaphidini			
Betulaphis quadrituberculata (Kaltenbach)	20	1	Sw
C.betulella Walsh	18	1	Am
C.coloradensis Granovsky	18	1	Am
C.viridipallida Palmer	18	1	C
Callipterinella callipterus (Hartig)	20	2	Am
C.tuberculata (von Heyden)	20	1	B
Eucallipterus tiliae (L.)	10	5	B
Euceraphis gillettei Davidson	15†, 16, 18†	18	Am, C
E.lineata Baker	16	1	Am
E.mucida (Fitch)	20	3	Am
E.punctipennis (Zetterstedt)	7†, 8†, 9†	49	B
Melanocallis fumipennellus (Fitch)	14	1	Am
Monellia caryella (Fitch)	18	2	Am
M.microsetosa Richards	18	3	Am
Monelliopsis caryae (Monell)	18	1	Am
M.nigropunctata (Granovsky)	10	3	Am, C
Oestlundiella flava (Davidson)	8	3	Am, C
Protopterocallis gigantea Bissell	10	1	Am
Pterocallis alni (de Geer)	20	3	Am
Sarucallis kahawaluokalani (Kirkaldy)	6	1	Am
Sensoriaphis nothofagi Cottier	10	2	NZ
Stegophylla essigi Hille Ris Lambers	12	1	Am
Symydobius intermedius Gillette & Palmer	16	1	Am
Takecallis arundinariae (Essig)	18	2	Am, B
Therioaphis trifolii (Monell)	16	1	Am

TABLE 1.–*Continued*

Subfamily, tribe and species	2n (♀) (somatic cells)	No. of samples	Country of origin of sample(s)*
Drepanosiphinae			
Callaphidini			
Therioaphis trifolii f.maculata (Buckton)	16	2	Am, A
Tuberculoides annulatus (Hartig)	14	3	Am, B
Drepanosiphini			
Drepanaphis utahensis Smith & Knowlton	30	2	Am
Drepanosiphum braggii Gillette	30	1	Am
Saltusaphidini			
Subsaltusaphis flava (Hill Ris Lambers)	8	1	Sw
S.picta (Hill Ris Lambers)	10	1	Sw
Israelaphidini			
Israelaphis tavaresi Ilharco	18	1	P
I.tavaresi alistana Durante	18	1	Sp
Aphidinae			
Aphidini			
Rhopalosiphina			
Melanaphis sacchari (Zehntner)	8	2	In
Aphidina			
Aphis amaranthi Holman	8	1	Am
A.armoraciae Cowen	8	1	Am
A.craccivora Koch	8	8	Am, Ir
A.craccivora (from *Lupinus*)	9†	1	Ir
A.cytisorum Hartig	8	1	Am
A.epilobiaria Theobald	8	1	B
A.eugeniae van der Goot	8	2	Ph, A
A.euonymi Fabricius	8	1	B
A.hederae f.pseudohederae Theobald	8	1	Am
A.idaei van der Goot	8	2	B
A.ilicis Kaltenbach	8	1	B
A.loti Kaltenbach	8	1	B
A.maidiradicis Forbes	8, 9†	3	Am
A.nerii Bpyer de Fonscolombe	8	2	K, A
A.newtoni Theobald	8	1	B
A.ruborum (Börner)	8	1	B
A.solanella Theobald	8	1	B
A.solanella (from *Solanum*)	7†	4	Ir
A.taraxicicola (Börner)	8	2	B
A.ulicis Walker	8	1	B
A.umbrella (Börner)	7†	1	Ir
A.(Absinthaphis) cinae (Nevsky)	8	1	Ir
A.(Protaphis) terricola Rondani	8	1	Sp
A.(Protaphis) sp. (from *Artemisia dracunculus*)	8, 9†	2	Ir
Toxopterina vandergooti (Börner)	8	1	B
Macrosiphini			
Acyrthosiphon gossypii Mordvilko	6	1	Ir
A.kondoi Shinji	10	1	Am
A.loti (Theobald)	10	1	B
A.pelargonii (Kaltenbach)	10	1	B
Amphorophora ampullata Buckton	12	3	B
A.gei (Börner)	12	1	B
Amphorophora idaei Börner	18	27	B, G
A.pacifica Hill	18	1	Am
A.parviflori Hill	12	3	Am, C
A.rubi (Kaltenbach)	20	50	B
A.rubi (Kaltenbach)	21	8	B
A.rubitoxica Knowlton	30	10	Am, C
A.sensoriata Mason	72	6	Am, C
A.stachyophila Hille Ris Lambers	12	1	Am
A.stolonis Robinson	48	1	C
Aphidura pannonica Szelegiewicz	12	1	Gr

TABLE 1.—*Continued*

Subfamily, tribe and species	2n (♀) (somatic cells)	No. of samples	Country of origin of sample(s)*
Aphidinae			
Macrosiphini			
Aulacorthum speyeri Börner	10	1	Ir
Capitophorus horni Börner	16	1	B
Cavariella aegopodii (Scopoli)	10	3	B, Ir
C.cicutae (Koch)	10	1	Ir
C.archangelicae (Scopoli)	6	1	B
C.intermedia Hille Ris Lambers	6	1	B
C.theobaldi (Gillette & Bragg)	8, 10†	3	B
Cryptomyzus alboapicalis (Theobald)	12	2	B
C.ballotae Hille Ris Lambers	12	5	B
C.galeopsidis (Kaltenbach)	12	1	B
Cryptosipum artemisiae Buckton	8	1	B
Diuraphis noxia (Mordwilko)	10	1	SA
Dysaphis apiifolia (Theobald)	12	2	Ir
D.crataegi (Kaltenbach)	12	1	B
D.radicola (Mordvilko)	12	1	B
D.tulipae (Boyer de Fonscolombe)	11†, 12	2	B
Elatobium abietinum (Walker)	18	5	B
Holcaphis agrostidis Muddathir	12	1	B
Hyadaphis coriandri (Das)	13†	1	Ir
Hyalopteroides humilis (Walker)	16	1	B
Hyperomyzus lampsanae (Börner)	12	1	B
H.(Neonasonovia) picridis (Börner & Blunck)	12	1	B
Idiopterus nephrelepidis Davis	13†	3	B
Illinoia alni (Mason)	10	1	C
Illinoia liriodendri (Monell)	10	1	Am
Illinoia richardsi (MacGillivray)	10	1	C
I.(Oestlundia) davidsoni (Mason)	12	1	Am
I.(Oestlundia) maxima (Mason)	12	1	C
Liosomaphis berberidis (Kaltenbach)	18	1	B
Macrosiphoniella sejuncta (Walker)	10	1	B
Macrosiphum albifrons Essig	10	1	Am
M.amygdaloides Theobald	10	2	B
M.californicum (Clarke)	10	1	Am
M.funestum (Macchiati)	10	1	B
M.stellariae Theobald	10	2	B
Metopeurum fuscoviride Stroyan	8	1	B
Metopolophium frisicum Hille Ris Lambers	16	1	B
Myzus dianthicola Hille Ris Lambers	14†	2	B, NZ
M.ligustri (Mosley)	12	2	B
M.ornatus Laing	12	2	B
M.varians Davidson	12	1	B
M.varians Davidson	13†	1	Am
M.(Sciamyzus) cymbalariae Stroyan	12	3	B
Nasonovia nigra (Hille Ris Lambers)	11†	1	B
N.ribisnigri (Mosley)	12	2	B
Nearctaphis bakeri (Cowen)	12	1	B
Neomyzus circumflexus (Buckton)	8	3	B
Paczoskia obtecta Börner	12	1	Sw
Pentatrichopus tetrarhodus (Walker)	14	2	B
Phorodon humuli (Schrank)	12	3	B
Pleotrichophorus duponti Hille Ris Lambers	14	1	B
P. glandulosus (Kaltenbach)	14	1	B
Sitobion nigronectarium (Theobald)	18	1	K
S.pterícolens (Patch)	16	2	B, Am
S.wikstroemiae (Mamet)	16	1	K
Uroleucon achilleae (Koch)	12	1	B
U.jaceae (L.)	12	1	B
Utamphorophora humboldti (Essig)	20	1	B
Wahlgreniella nervata (Gillette)	12	1	B

TABLE 1.–*Continued*

Subfamily, tribe and species	2n (♀) (somatic cells)	No. of samples	Country of origin of sample(s)*
Greenideinae			
Anomalaphidini			
Anomalosiphum indigoferae Ghosh, Ghosh & RayChaudhuri	18	1	Sa
Schoutedenia lutea (van der Goot)	14	1	A
Greenideini			
Greenidea ficicola Takahashi	22	1	A
G.(Trichosiphum) kuwanai (Pergande)	20	1	J
Anoeciinae			
Anoeciini			
Anoecia corni (Fabricius)	6†, 6, 7†, 8	37	B, Ir
A.furcata (Theobald)	12, 13†	12	B
A.nemoralis Börner	12	6	B
A.vagans (Koch)	12	7	B, Sw
Hormaphidinae			
Hormaphidini			
Hamamelistes spinosus Shimer	*c.* 50	1	C
Nipponaphidini			
Euthoracaphis umbellulariae (Essig)	14	1	Am
Thoracaphis sp.	12	1	J
Pemphiginae			
Pemphigini			
Asiphum sp. (from *Populus euphratica*)	10	2	Ir
Pemphigus sp. (from roots of *Euphorbia supina*)	20	1	Am
Prociphilus pini (Burmeister)	16	2	B
Thecabius affinis (Kaltenbach)	38	1	B
Eriosomatini			
Colopha compressa (Koch)	16	1	B
Eriosoma patchiae (Börner & Blunck)	10	1	B
Kaltenbachiella pallida (Halliday)	28	1	B
Fordini			
Aploneura lentisci (Passerini)	16	3	B
Baizongia pistaciae (L.)	24†	2	B
Forda dactylidis Börner	30	1	Ir
F.hirsuta Mordvilko	18	1	Ir
Geoica eragrostidis (Passerini)	16†, 17†, 18	8	B
G.eragrostidis (from *Pistacia*)	18	1	It
G.setulosa (Passerini)	20, 24†, 28, 31†	5	B
G.setulosa (Passerini)	20	1	Ir
Geoica sp. (from *Pistacia palaestina*)	18	2	Is
Paracletus cimiciformis von Heyden	16	1	Is
Rectinasus buxtoni Theobald	26	1	Ir
Smynthurodes betae Westwood	8	4	B, Ir

* A = Australia; Am = United States of America; B = Great Britain; C = Canada; G = Germany; Gr = Greece; In = India; Ir = Iran; Is = Israel; It = Italy; J = Japan; K = Kenya; NZ = New Zealand; P = Portugal; Ph = Philippines; SA = South Africa; Sa = Sarawak; Sp = Spain; Sw = Sweden.

† Chromosomes show evident structural heterozygosity.

Robinson & Chen (1969) recorded 2n(♀) = 18 for *Microlophium carnosum* (Buckton) in Canada, but Kuznetsova & Shaposhnikov (1973) listed 2n(♀) = 16 for *M.evansi* (Theobald), which has been synonymized with *M.carnosum*, in the Crimea. In aphids provisionally identified as *M.carnosum* by the present writer, samples with 2n = 16 and 2n = 20 occur in England, 2n = 20 being by far the commonest karyotype on *Urtica dioica*. Samples with 2n = 18 have, however, been obtained from North America and from Iran.

The North American species may be *tenuicauda* Hille Ris Lambers 1949, and the other karyotypes may correspond to three Old World species which have been difficult to recognize by morphology alone, although several names are available.

All these problems will probably be resolved by more detailed morphological studies. A similar situation occurred in the genus *Amphorophora*, with European samples having either 2n = 18 or 2n = 20. Morphometric studies showed that two species with different host-plant associations were definitely involved, *A.idaei* Börner on *Rubus idaeus* and *A.rubi* (Kalt.) on other *Rubus* species (Blackman *et al.*, 1977). A difference in chromosome number provides a useful starting point from which to look for other less discrete differences between very similar or 'sibling' species.

Variation at the levels of subfamily and tribe

Shinji (1931) based a discussion of chromosomal evolution in the Aphididae on thirty-seven species from twenty-seven genera. He proceeded entirely on the assumption that the smallest chromosome number was most primitive, and concluded that a gradual increase in number had occurred during the evolution of each subfamily, so that genera with highest numbers could be regarded as most recent. Steffan (1968a), with evidence from a lot more species and more recent ideas about systematic relationships, turned this hypothesis entirely on its head and suggested that the general tendency has been towards a decrease in chromosome number, rather than an increase. In the last 10 years there has been a four-fold increase in the number of aphid karyotypes recorded and it has become clear that neither of these two theories are tenable.

It is not possible even to suggest an ancestral chromosome number for the Aphididae as a whole, although in all probability it lay somewhere between n = 4 and n = 10. Some subfamilies and tribes have clear modal numbers (Fig. 1), the extreme case being the Aphidini where over 90% of the species have n = 4. As pointed out by White (1973), there is no reason to suppose that even such a striking modal number as this is necessarily primitive to the group. Modal numbers within sub-

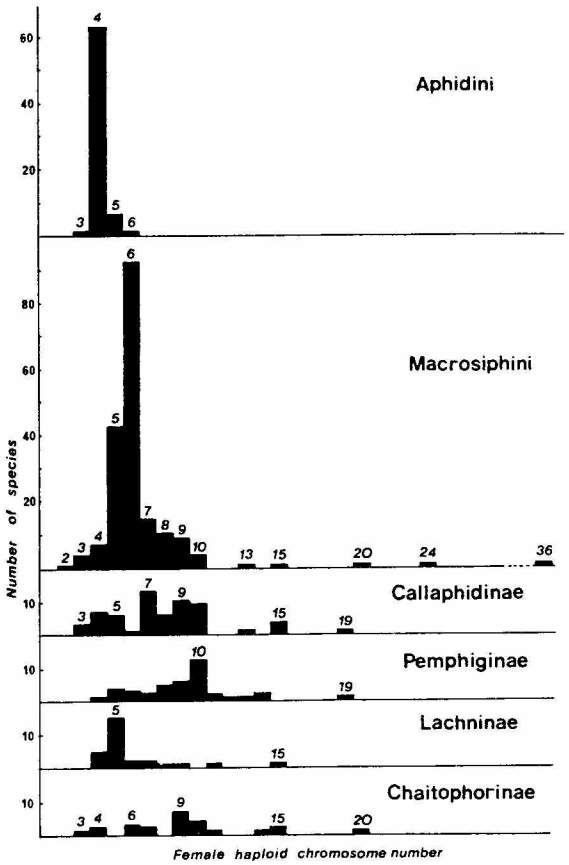


FIG. 1. Histograms showing the frequency distributions of female haploid chromosome numbers in some of the major groups of Aphididae.

families and tribes of aphids merely reflect the fact that there are certain dominant genera which contain a large proportion of the species in each group. There is a clear tendency for chromosome number to be stabilized at the generic level (see below), especially in the aphid genera which are dominant at the present time, and the modalities of the distribution of chromosome numbers within each of the most studied groups are adequately accounted for by the typical chromosome numbers of the largest genera: *Cinara* (n = 5) in the Lachninae; *Myzocallis* (n = 7) in the Callaphidinae; *Aphis* (n = 4) in the Aphidini; *Dysaphis* and *Myzus* (n = 6), and *Macrosiphum* (n = 5) in the Macrosiphini; and *Pemphigus* (n = 10) in the Pemphiginae. The largest genera are those which have undergone extensive speciation in recent times, and they are clearly not the place to look for primitive features.

It can be concluded that chromosome data do not provide a good basis for considering phylogenetic relationships among the higher

categories of the Aphidoidea. At the generic level it is usually impossible to decide which chromosome numbers are primitive and which derived, and certainly there are no detectable long-term trends of increase or decrease in chromosome number in the group as a whole.

Variation within the genus

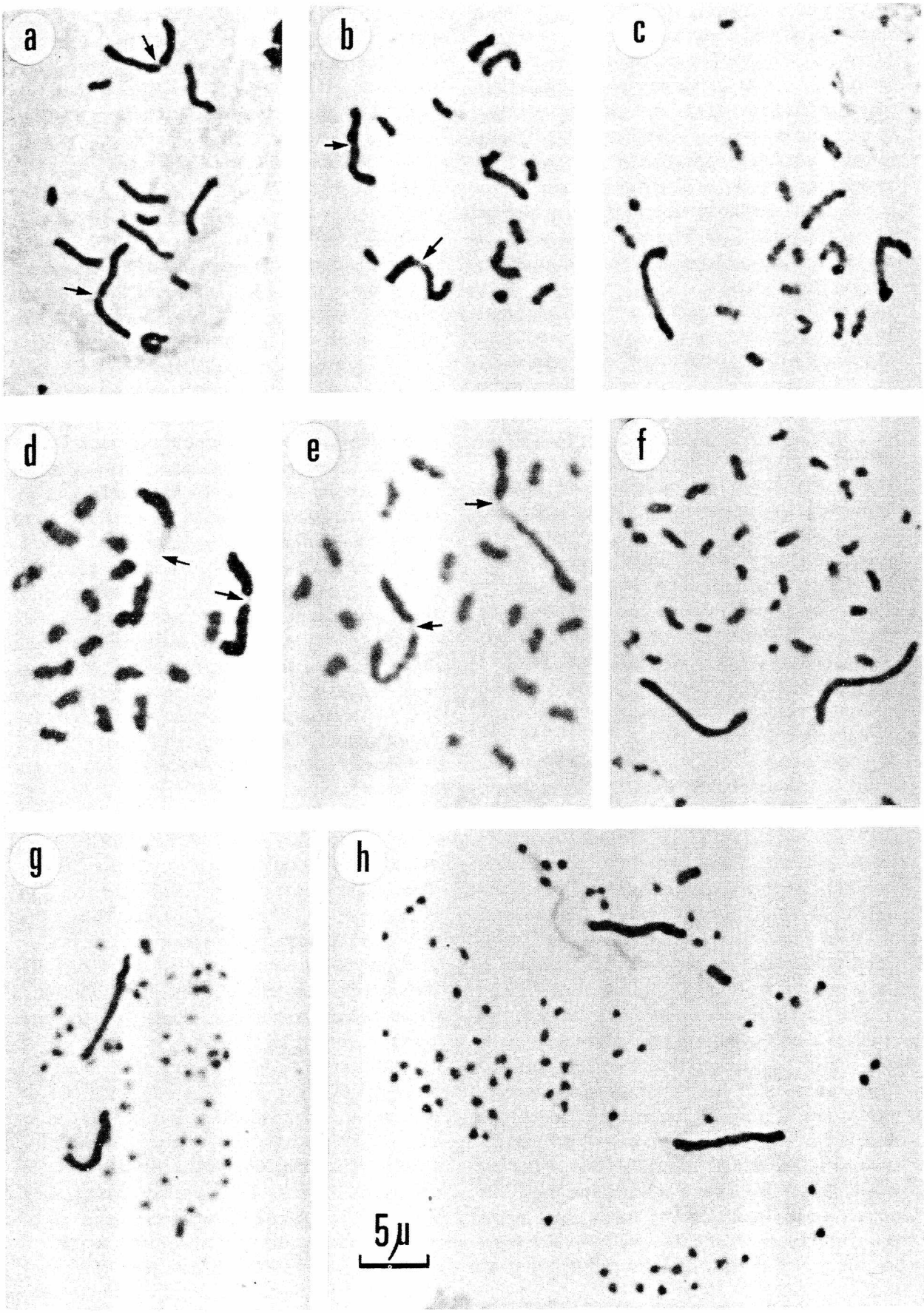
For evidence of the ways in which karyotype evolution has proceeded in aphids it is more important to look at the variations in chromosome number which occur below the generic level, within and between species. Only then can one find indications of the sort of chromosomal changes which are liable to occur within a species, and hence become involved in the speciation process. Most aphid genera in fact show a remarkable constancy of chromosome number. All of the twenty species of *Dysaphis* so far examined cytologically have n = 6, and all except one of forty-eight species of *Aphis*, representing about 10% of the species in this large genus, have n = 4, the single exception being *A.farinosa* with n = 3.

Differences in chromosome number sometimes agree with recognized sub-generic groupings; for example, *Cinara* subgenus *Cupressobium* Börner (which feed on Cupressaceae) have n = 6 as opposed to n = 5 for other *Cinara* (on Pinaceae), and the species in the *Illinoia* subgenus *Oestlundia* Hille Ris Lambers have n = 6, whereas species of *Illinoia s.str.* have n = 5. As noted by Kuznetsova & Shaposhnikov (1973), *Sitobion* (n = 9) has commonly been regarded as a subgenus of *Macrosiphum* (n = 5), but on the basis of karyotype and life-cycle it appears to have closer affinities to *Metopolophium*. On the whole, chromosome data provide very good confirmation for the generic concepts which are currently applied by aphid taxonomists.

However, variation in chromosome number within a genus does not always make taxonomic sense. In the large Macrosiphine genus *Uroleucon* (= *Dactynotus*), most species have n = 6 but a few have n = 4, 5 and 7. The exceptions do not relate in any way to subgeneric groupings which have been proposed on the basis of morphology supported by host-plant relationships. Richards (1965) separates *Monellia* and *Monelliopsis* (Callaphidini) on the basis of larval chaetotaxy. He argues strongly that the close morphological similarity between the adults of these two genera is due to convergence, and that *Monelliopsis* has closer affinities with *Therioaphis* than with *Monellia*. *Monelliopsis nigropunctata* has n = 5, but *Monelliopsis caryae* has n = 9 which is the same number as two *Monellia* species, whereas *Therioaphis* have n = 8. However, more species need to be looked at in these genera.

It appears that there are a few aphid genera in which chromosome number has been much more liable to change in the course of speciation. It is in such genera that cytotaxonomic studies seem most promising. A prime example is *Amphorophora* (Blackman *et al.*, 1977). The *Rubus*-feeding species of this genus in Britain and North America are all closely similar in morphology but they have a wide range of chromosome numbers (Fig. 2). Of these species looked at so far only *A.idaei* and *A.pacifica* share a common chromosome number (n = 9), but the karyotypes of these two species are distinguishable by differences in relative lengths of individual chromosomes. In *Amphorophora* the karyotype changes seem to have entirely involved the dissociation of autosomes, although in several species the X-chromosomes have a marked constriction and a tendency to appear dissociated in squash preparations. There seems little doubt that the primitive number for the genus is n = 6, as found in all non-*Rubus*-feeding species of *Amphorophora*. *A.stachyophila* on *Stachys*, with n = 6, is barely separable morphologically from *A.rubitoxica*, with n = 15 (V. F. Eastop, personal communication). To judge from the close morphological similarities between all the *Rubus*-feeding *Amphorophora*,

FIG. 2. Somatic prophase cells from female embryos of eight species of *Rubus*-feeding *Amphorophora*. (a) *A.parviflori* Hill, 2n(♀) = 12; (b) *A.agathonica* Hottes, 2n(♀) = 14; (c) *A.pacifica* Hill, 2n(♀) = 18; (d) *A.idaei* Börner, 2n(♀) = 18; (e) *A.rubi* (Kalt.), 2n(♀) = 20; (f) *A.rubitoxica* Knowlton, 2n(♀) = 30; (g) *A.stolonis* Robinson, 2n(♀) = 48; (h) *A.sensoriata* Mason, 2n(♀) = 72. Several species show similarly-placed constrictions on the X-chromosomes (arrowed).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the speciation of this group on *Rubus* has been relatively recent. Here is a difficult paradox; if, in very many aphid genera, the constraints upon any change in karyotype are such that the number and gross morphology of the chromosomes varies insignificantly between species, what has happened to remove these constraints in a genus like *Amphorophora*, so as to enable similar-looking species on similar host-plants with no obvious differences in ecology or life-cycle to have haploid numbers ranging from 6 to 36?

Seemingly, 'explosive' increases in chromosome number due to autosome dissociation have occurred in several other aphid genera, so that odd species have a very high chromosome number compared with the typical number for the genus. Presumably intermediate numbers once existed but have become extinct. Kuznetsova (1975) investigated the case of *Anuraphis subterranea* (n = 13) and compared the DNA content of this species with *A.farfarae* (n = 6). She found that although the ratios of the lengths of X-chromosomes to autosomes in each species were the same, the species with the larger chromosome number had a smaller DNA content. Dissociation was apparently accompanied by loss of genetic material, which is the reverse of what might be expected (White, 1973, p. 417). Instances of untypically high chromosome number occur in most aphid subfamilies; for example, *Eulachnus brevipilosus* (n = 15) in Lachninae, *Glyphina* sp. (n = 28) in Thelaxinae, *Pterocomma salicis* (n = 29) in Pterocommatinae, and *Vesiculaphis theobaldi* (n = 20) in Macrosiphini. It would be interesting to know if loss of DNA had also accompanied the evolutionary increase in chromosome number in these cases.

The Callaphidine genus *Euceraphis* shows much evidence of karyotype instability, but in this genus the changes have not been confined to the autosomes. In the *betulae/punctipennis* group the X-chromosomes have undergone dissociation, and there are additional heterochromatic elements which behave in many ways like accessory or B-chromosomes, but appear to be more-or-less stable features of the karyotype (Blackman, 1976). Variation in this group is further discussed in the next section.

There are several other aphid genera which appear to be exceptions to the general rule karyotype stability at the generic level, i in which few species have so far been kar typed. Examination of the chromosomes additional members of such genera as *Chai phorus*, *Subsaltusaphis*, *Cavariella*, *Anoe* and *Forda* may well reveal differences of tax nomic significance.

Variation within the species

Chromosomal determinations have usuall been based on a single sample of the partheno genetic morphs of each aphid species, and i many cases this is probably taken from a colony consisting of a single clone. As Table 1 shows, examination of more than one sample often reveals differences in chromosome number within what is commonly regarded as a single species. In those cases where five or more samples of a species have been looked at, 47% of the species showed some variation in karyotype. Where ten or more samples were examined, 75% showed karyotype variation. These figures must overestimate the amount of chromosomal variability in aphid species as a whole because when differences between samples were found within a species, there was a tendency to follow these up by collecting and examining more samples. They nevertheless indicate that natural populations of aphids show an unusual degree of variability in gross chromosome morphology.

Aphids might be expected to show more variation of karyotype within species than many other organisms for two reasons. Firstly, they have holocentric chromosomes. As remarked by White (1973, p. 200), the principles of chromosome rearrangement may be somewhat different in organisms with holocentric chromosomes. The centromeric activity of a holocentric chromosome is dispersed along its entire length, so that if a chromosome (or chromatid) breaks into two or more parts the fragments can all still move independently into the daughter cells, and thus be propagated at mitosis (Ris, 1942). This contrasts with the situation in organisms which have chromosomes with localized centromeres, where fragments of broken chromosomes left without a centromere will tend to be eliminated at mitosis. However, although fragments of holocentric chromosomes may survive mitosis, it is not

known for certain whether the freshly broken ends have any long-term stability, or whether two breaks and an exchange of parts between chromosomes are necessary to produce a stable change of karyotype, as seems to be the case in most organisms.

The second factor which seems likely to promote karyotype variation within populations of an aphid species is their thelytokous reproduction. Most aphids have a succession of thelytokous generations alternating with a single, annual sexual generation. Therefore any chromosomal dissociation, fusion or other rearrangement which could survive mitosis might increase in frequency in apomictic populations prior to being selected against or eliminated in the meiotic process. There are, in addition, many aphid species which have partially or completely abandoned sexual reproduction, and in these it is possible that an unlimited number of alterations to the ancestral karyotype could accumulate in independently evolving parthenogenetic lines.

Chromosomal changes arising in anholocyclic populations, following the virtual abandonment of sexual reproduction, seem to account for the major part of the karyotype variation found within species in the present work. These will be considered in a separate section below. Very few cases have been found of karyotype variation within species which are obligatorily holocyclic, and some of these may be due to the existence of two or more morphologically similar species under a single name, as discussed above.

In the Callaphidine genus *Euceraphis*, aphids developing on *Betula pubescens* in Europe have only one pair of autosomes, whereas those on *B.pendula* have two autosome pairs. Corresponding morphological differences were discovered which confirm that two species are definitely present (Blackman, 1977). These two species, *E.betulae* (Koch) on *B.pendula* and *E.punctipennis* (Zett.) on *B.pubescens*, also differ in their mode of spermatogenesis (Blackman, 1976).

Recently, the writer examined the karyotypes of the North American species of *Euceraphis*, and found a considerable amount of variation in the number and gross morphology of their chromosomes, the differences corresponding to some extent with the species of *Betula* or *Alnus* colonized (Table 2). The taxonomic significance of differences between populations of the *E.betulae* group is difficult to ascertain because the chromosomes most

TABLE 2. Chromosome numbers of North American *Euceraphis*

Host plant	Region	No. of samples	2n (♀)	2n (♂)	Provisional species designation
Alnus rubra, *A.rhombifolia*	Western U.S.A.	12	16	?	*Euceraphis gillettei* Davidson
A.rubra	British Columbia	3	18	?	*E.gillettei* group
A.rugosa	Ontario, New Brunswick	3	15, 16	?	*E.gillettei* group
Betula papyrifera, *B.populifolia*, *B.cordifolia*	Widespread in U.S.A. and Canada	15	9 (rarely 10)	8	*E.betulae* group
B.papyrifera	N.W. Territories	1	7	6	*E.betulae* group
B.glandulosa	Manitoba, N. W. Territories	2	8	7	*E.betulae* group
B.occidentalis	Utah	4	11	?	*E.betulae* group
B.pendula	Western N. America	9	10 (rarely 9)	8	*E.betulae* (Koch) s.str.
B.lenta	New York, Pennsylvania	3	20	?	*E.mucida* (Fitch)
B.populifolia	New York	1	16	?	*E.lineata* Baker
B.populifolia	New York, New Brunswick	3	16	?	*E.deducta* Baker

commonly involved are heterochromatic elements and resemble accessory or B-chromosomes, which might be expected to vary in number within a species. In *E.betulae* and *E.punctipennis* in Britain, these heterochromatic elements have been regarded as B-chromosomes on the basis of their behaviour at meiosis (Blackman, 1976), although unlike most B-chromosomes they are never entirely absent from the karyotype. In *E.punctipennis*, individuals have been found with one, two or three heterochromatic elements, which may vary in size as well as in number. In *E.betulae*, all British populations seen so far have consistently had two rather large heterochromatic chromosomes. Aphids with a similar or identical karyotype occur on varieties of *B.pendula* planted as ornamentals in North America, except that some individuals from southern California were found to have only one large heterochromatic element.

The components of the karyotype in other populations of *E.betulae* group in Nor America are difficult to identify as the meio stages of most of them have not yet be studied, and without information about m osis it is not possible to distinguish satisfa torily between X- and B-chromosomes. O *B.papyrifera* by far the commonest form h 2n(♀) = 9, and aphids of similar or identica karyotype occur also on *B.populifolia*, wher 2n(♀) = 10 individuals have also been found These populations on native Nort American birches all have a karyotype unlike that of *E.betulae* on introduced *B.pendula*, and male embryos in one sample had only one chromosome less than females, indicating that there is a single pair of functional X-chromosomes. (Both the European *Euceraphis* species have two functional pairs of X-chromosomes.) *Euceraphis* collected on *B.occidentalis* in Utah, however, consistently had 2n(♀) = 11, and samples from *B.glandulosa* in Manitoba and North West Territories both

TABLE 3. Karyotype variation in the *Myzus persicae* group

Karyotype of female	No. of samples	Life cycle	Known distribution	Other information
2n = 12 (normal)	93	Holocyclic or partially anholocyclic	World-wide	Polyphagous, susceptible or resistant to OP insecticides
2n = 12 (autosomal 1, 3 translocation)	81	Holocyclic or partially anholocyclic	World-wide	Polyphagous, normally resistant to OP insecticides
2n = 13 (autosome 3 dissociation)	2	Holocyclic or partially anholocyclic	Japan	Normally resistant to OP insecticides?
2n = 13 or 14 (dissociation of autosome 3, or autosomes 2 and 3)	19	Anholocyclic	Europe	Especially in glasshouses (= *dianthi* Schrank?)
2n = 13 (autosome 3 dissociation)	10	Anholocyclic	California	Especially on Pittosporaceae
2n = 13 (autosome 2 dissociation?)	1	?	Japan	Variants obtained in laboratory breeding experiments
2n = 13 (rearrangement)	1	?	Japan	
3n = 18 (triploid)	1	No males	Japan	
2n = 11 (rearrangement)	1	?	California	On *Chaenomeles sinensis*
2n = 11 (rearrangement)	1	?	Chile	On *Brassica*
2n = 14 (complex rearrangement)	2	Anholocyclic	Europe, New Zealand, California	On *Dianthus* in glasshouses (*M.dianthicola* Hille Ris Lambers)

had identical karyotypes with 2n(♀) = 8, again with apparently only one pair of functional X's. The question of how many of these different forms should be given specific status must await further cytological study, coupled with a more thorough investigation of ecological and morphological differences.

The 'B-chromosomes' of *Euceraphis* are anomalous and it seems probable that they represent a non-functional part of the X-chromosome system in this genus. Accessory or B-chromosomes of a more conventional kind, small heterochromatic elements which occur in some individuals and are additional to the normal complement of the species, are a principle source of variation in chromosome number within species in many groups of animals and plants. That such additional small elements have only been found in a few species of aphids, is probably a reflection of the lack of work on this group. The present writer has found individuals with a single B-chromosome in two Callaphidine species, *Calaphis flava* and *Myzocallis coryli*. Gut (1976) recorded a karyotype for *Rhopalosiphoninus latysiphon* as 2n = 6+1, the additional element apparently being a B-chromosome. Gut also listed the karyotype of *Lipaphis erisymi* as 2n = 10. His illustration of a somatic metaphase of this species shows two very short chromosomes. A sample of *L.erysimi* from California was found to have 2n = 9 in female somatic cells, with one very short, unpaired element. It thus seems probable that the basic karyotype of *L.erysimi* has 2n(♀) = 8, and that the additional components found in these two samples are B-chromosomes. Both *R.latysiphon* and *L.erysimi* are anholocyclic over much of their geographical range, and it is likely that the absence of meiosis may enable B-chromosomes to become established more widely in a species. This has perhaps reached an extreme in the Tramini, which are discussed in the next section.

Karyotypes of aphids with partial or complete anholocycly

The most studied example of the effects on the karyotype of partial or complete abandonment of the sexual process in aphids is the peach-potato aphid, *Myzus persicae* (Sulz.)

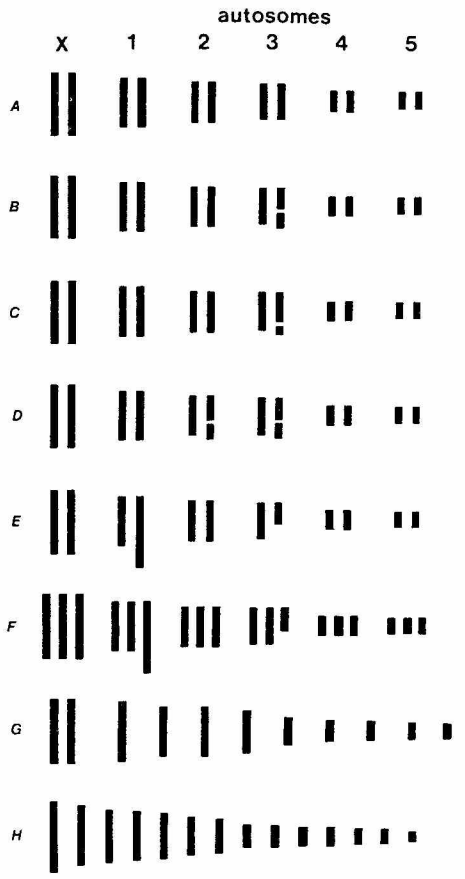

FIG. 3. Karyotype variation in the *Myzus persicae* group. Idiograms are based on relative length measurements, where possible pairing presumed homologues. (A) *Myzus persicae* (Sulzer), normal karyotype 2n(♀) = 12; (B) and (C) karyotypes with autosome 3 dissociation, 2n(♀) = 13; (D) autosomes 3 and 4 dissociated, 2n(♀) = 14; (E) karyotype heterozygous for an autosome 1,3 translocation, 2n(♀) = 12; (F) triploid form with autosome 1,3 translocation, 3n(♀) = 18; (G) karyotype with 2n(♀) = 11 from California, X-chromosomes identifiable but autosome relationships unknown; (H) *M.dianthicola* Hille Ris Lambers with complex structural heterozygosity, '2n(♀)' = 14.

(Table 3, Fig. 3). The normal diploid complement of *M.persicae* is 2n = 12, and this karyotype is indistinguishable in its gross morphology from that of closely related species such as *M.certus* (Walker). *M.persicae* has a world-wide distribution, and in all except the coldest parts of the world it has the ability to pass the winter without going through a sexual phase (Blackman, 1974). It is common for clones of this aphid to fail to respond to sexual morph-inducing stimuli except by producing a few males ('androcycly'). This enables *M.persicae* to have widespread partial

anholocycly whilst still maintaining some gene flow (via the males) between androcyclic and holocyclic forms, and thus preserving the integrity of the species.

There is one chromosomal variant in *M.persicae* which is very common throughout the world (Blackman *et al.*, 1978). This is a translocation between the first and third autosome pairs, giving females with a 2n = 12 karyotype with marked structural heterozygosity (Fig. 3E). Such translocations are normally very rare in natural populations of sexually-reproducing animals, because they give rise to a high proportion of gametes with duplications of deficiencies of genetic material. Translocation heterozygotes are presumably no problem to *M.persicae* in those parts of the world where it is anholocyclic. In Japan and Australia, however, the translocation has been found to occur in holocyclic populations on the primary host, *Prunus persica*.

There is now clear evidence that the success of translocated *M.persicae* is due to linkage between the translocation and genes conferring a high level of resistance to organophosphate insecticides (Blackman *et al.*, 1978). The translocation was first discovered in highly resistant, androcyclic clones of *M.persicae* from glasshouses, and it seems likely that it first established itself in such clones. The spread of this translocated, resistant form throughout the world may then have occurred by predominantly thelytokous reproduction, but with some recombination introduced by the occasional holocycle. The translocation might even survive regular holocycly because of the compensating advantage of the associated organophosphate resistance, but then the linkage between translocation and resistance might disappear in the course of regular recombination, in which case the translocation would presumably soon be eliminated. Such a course of events may now be happening in Japan, where recent results suggest that the translocation is no longer invariably associated with resistance (H. Takada, personal communication).

It is also possible that the translocation is not a unique event, but has occurred more than once in different parts of the world. Supporting evidence for this hypothesis is the frequent occurrence of *M.persicae* with 2n = 13, resulting apparently from a dissociation of one of the third pair of autosomes (A3, Fig. 3B). This could be the first step in the translocation. In Japan, aphids with 2n = 13 are indistinguishable morphologically from those of normal or translocated karyotype and can produce sexuales and breed with them, the dissociation being inherited according to Mendelian expectations (Blackman & Takada 1977). In Europe, however, aphids with an apparently similar A3 dissociation are dark green in colour, have certain distinguishing morphological features, and are entirely anholocyclic (Blackman, 1971). Some *M.persicae* of similar appearance have a second dissociation, apparently of autosome A2, to give a 2n = 14 karyotype. In Europe, both the 2n = 13 and 2n = 14 forms are commonly found in glasshouses. In California, another anholocyclic form of the *M.persicae* group also has 2n = 13 with an apparent autosome A3 dissociation, but this Californian form shows slight morphological differences from the European 2n = 13 form and appears to be associated mainly with Pittosporaceae.

Other apparently more complex chromosomal rearrangements with 2n = 11 in female somatic cells have been found in *M.persicae* from Chile and California. In Japan, three new chromosomal variants have appeared in the course of breeding experiments done by H. Takada. Two of these were new 2n = 13 karyotypes, one of which could have resulted from a new dissociation of autosome A3, the other involving a more complex rearrangement. The third variant was a laboratory-reared triploid with the autosomal 1, 3 translocation (Fig. 3F), obtained in a cross between oviparae from a clone heterozygous for this translocation and males of normal karyotype (Blackman & Takada, 1977). No triploid aphids have yet been found in nature. The laboratory-reared triploid is unable to produce any males, reproduction stopping short at the time when males would normally be produced in a short photoperiod regime Takada *et al.*, 1978). Presumably the triploid condition interferes with sex determination, and therefore cannot survive for long in the field when male production is an essential part of the life-system. It is less easy to understand, however, why permanently anholocyclic aphids seem never to have evolved a triploid or polyploid condition.

The story of karyotype variation in *M.persicae* can be concluded with an aphid

which has been described as a distinct species by Hille Ris Lambers (1966). *Myzus dianthicola* is a very sporadic pest of carnations (*Dianthus*) in glasshouses and has been recorded from Britain, California, Denmark and New Zealand. It is dark yellow-green in colour, anholocyclic, and causes chlorotic spotting of the leaves of its host. *M.dianthicola* possibly arose as an asexual offshoot of *M.certus* rather than *M.persicae*, but all three species are closely related. Samples of *M.dianthicola* from Britain and New Zealand were examined cytologically; both had the same distinctive karyotype consisting of seven long and seven short chromosomes (Figs. 3 and 4b).

The *M.persicae* group provides an illustration of how chromosome rearrangements can be associated with partial or complete anholocycly. In partially anholocyclic populations a chromosomal rearrangement can only persist in the short term or if by chance it is linked with some considerable selective advantage, such as resistance to an insecticide. Once complete anholocycly is acquired, however, such a rearrangement will become established in association with a particular genotype, and this will subsequently evolve in isolation from the parent species to produce a new form with its own characteristics which can logically be given specific status, as in the case of *M.dianthicola*.

Other examples of chromosomal rearrangements observed by the present author in partially or completely anholocyclic aphids are listed in Table 4. The suggestions about the possible nature of the rearrangements involved are very tentative and based solely on visual inspection of the karyotypes, some of which are illustrated in Fig. 4. In the majority of cases anholocycly is inferred from the lack of records of sexual morphs from the collection locality of the sample, or from the date of collection. For example, the sample of *Cavariella theobaldi* with a heterozygous 2n = 10 karyotype is presumed to be anholocyclic because it was collected from the secondary host-plant in March in Cornwall, England. In a few cases (*Amphorophora rubi, Aulacorthum solani, Cryptomyzus ballotae, Myzus dianthicola*), anholocycly was confirmed by laboratory experiments.

Many well-known, anholocyclic aphids do not appear in this list, notably such species as *Macrosiphoniella sanborni, Melanaphis sacchari, Myzus ascalonicus, M.cymbalariae, Neomyzus circumflexus, Toxoptera aurantii* and *Tuberolachnus salignus*. However, the list is confined to rearrangements which are readily observable, and changes of karyotype which involve inversions, or translocations of roughly equal lengths of chromosome, would not be apparent on visual inspection of conventionally stained preparations. The great preponderance of chromosomal rearrangements in aphids with partial or complete anholocycly is shown by the fact that over half (52.4%) of those examined had readily observable rearrangements of some kind, as opposed to only 0.3% of the species with obligate holocycly.

As might be expected, most of the changes involve increase or decrease in chromosome number of one chromosome compared with the normal karyotype of the species or group concerned, indicating a single dissociation or fusion event. In some cases there is a clear possibility that the rearrangement is associated with a distinct host-plant 'race' or 'biotype' of the aphid; for example, *Aphis craccivora* on *Lupinus* with 2n = 9, and *A.solanella* on *Solanum nigrum* in Iran with 2n = 7. In the case of *Aulacorthum solani*, anholocyclic clones collected in England with 2n = 9 and 2n = 11 respectively did not conform to any of the known subspecies within this species complex (Müller, 1970). Both these clones appear to belong to the common yellow-green anholocyclic form of *A.solani*, which also includes clones of normal (2n = 10) karyotype. F. P. Müller kindly supplied samples from his stock cultures of the typical holocyclic and anholocyclic polyphagous forms of *A.solani*, and of three subspecies; *A.s.prasinum* (dark green, anholocyclic), *A.s.langei* (holocyclic on *Pulmonaria*) and *A.s.aegopodii* (holocyclic on *Aegopodium*). All of these had similar 2n = 10 karyotypes.

Aphids of the genus *Anoecia* typically migrate from the primary host *Cornus* to produce thelytokous generations on the roots of grasses, but some populations of *A.furcata* and of the *A.corni* group are anholocyclic in Britain on grass roots. Paul (1977, and unpublished observations) studied the chromosomes of numerous samples from different localities. Some samples of *A.furcata* collected in winter on grass roots had a 13-

TABLE 4. Chromosomal abnormalities associated with partial or complete anholocycly in aphids

Aphid	No. of samples with abnormality (total no. of samples seen in parentheses)	Chromosome number (normal number if different, in parentheses)	Possible origin of abnormality	Other remarks
Cinara fresai	1 (1)	13†	Dissociation	Sexuales unknown
Neotrama caudata	2 (2)	9†, 11†	Complex rearrangement	Sexuales unknown
Protrama flavescens	5 (5)	*c.* 42†	Dissociation and rearrangement	Sexuales unknown
P.radicis	6 (6)	*c.* 60†	Dissociation and rearrangement	Sexuales very rare
P.ranunculi	2 (2)	*c.* 36†	Dissociation and rearrangement	Sexuales unknown
Trama rara	1 (1)	13†	Complex rearrangement	Sexuales unknown
T.troglodytes	23 (23)	14–22† inclusive	Complex rearrangements	Sexuales unknown
Rhopalosiphum maidis	1 (5)	9† (8)	Autosome dissociation	Presumed anholocyclic population in Australia
Aphis craccivora	1 (9)	9† (8)	Autosome dissociation	Presumed anholocyclic population in Iran
A.fabae	3 (11)	8†	Translocation?	Presumed anholocyclic population in California
A.solanella	4 (5)	7† (8)	Autosome fusion?	Presumed anholocyclic populations in Iran
Amphorophora rubi	8 (58)	21† (20)	Autosome dissociation	Anholocyclic forms in Britain
Aulacorthum solani	2 (13)	9†, 10†, 11† (10)	Fusion, dissociation and translocation	Anholocyclic forms in Britain and California
Cavariella theobaldi	1 (3)	10† (8)	Dissociations?	Anholocyclic population in Britain
Cryptomyzus ballotae	1 (5)	12†	Translocation?	Anholocyclic population in Britain
Dysaphis tulipae	1 (2)	11† (12)	Autosome fusion?	Sexuales unknown
Hyadaphis coriandri	1 (1)	13†	Dissociation?	Presumed anholocyclic population in Iran
Idiopterus nephrelepidis	3 (3)	13†	Dissociation?	Sexuales unknown
Myzus dianthicola	2 (2)	14†	Complex rearrangement	Sexuales unknown
M.persicae	See separate table			
M.varians	1 (2)	13† (12)	Autosome dissociation	Presumed anholocyclic population in California
Anoecia corni	8 (36)	6†, 7†, (6, 8)	Rearrangement, hybridization?	Anholocyclic populations in Britain
A.furcata	3 (11)	13† (12)	Dissociation	Anholocyclic populations in Britain
Baizongia pistaceae	4 (4)	24†	Complex rearrangement	Anholocyclic populations in Britain
Forda formicaria	7 (17)	21†, 22†, 23† (20?)	Dissociations	Anholocyclic populations in Britain and North America
F.marginata	12 (15)	24†, 25†, 26†, 27†, 32† (28?)	Fusions and dissociations?	Anholocyclic populations Britain and North America
Geoica eragrostidis	3 (9)	16†, 17† (18?)	Fusions?	Anholocyclic populations in Britain
Geoica setulosa	3 (7)	24†, 28†, 31† (20?)	Dissociations?	Anholocyclic populations in Britain

† Denotes structural heterozygosity.

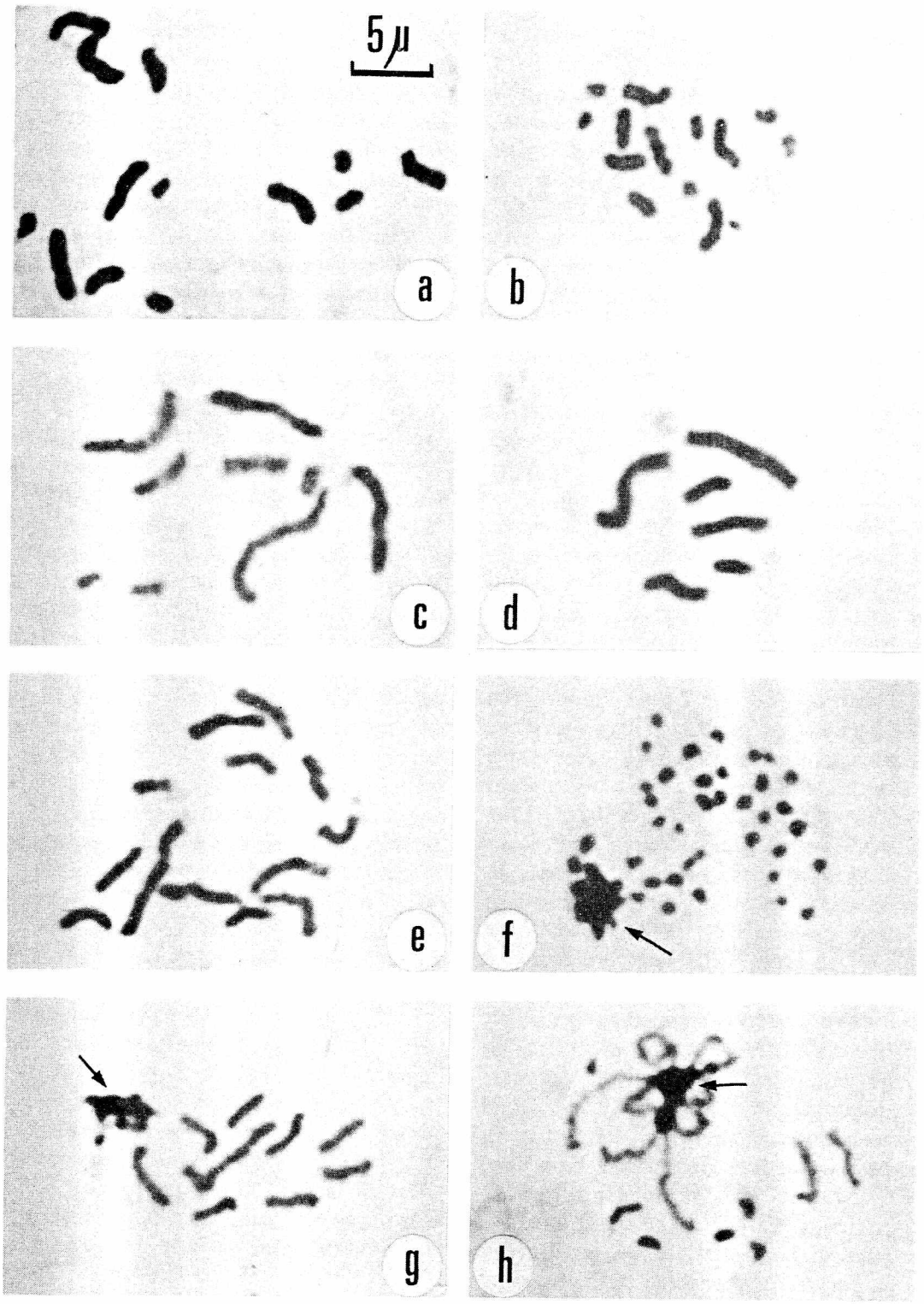

FIG. 4. Somatic prophase cells from female embryos of some anholocyclic aphids. (a) *Idiopterus nephrelepidis* Davis with 13 chromosomes; (b) *Myzus dianthicola* Hille Ris Lambers with 14 chromosomes; (c) an anholocyclic clone of *Aulacorthum solani* (Kalt.) with 9 chromosomes; (d) an anholocyclic clone of *Anoecia corni* (F.) with 6 chromosomes; (e) *Cinara fresai* Blanchard with 13 chromosomes; (f) *Protrama radicis* (Kalt.) with about 60 chromosomes; (g) *Trama rara* Mordvilko with 13 chromosomes; (h) *Trama troglodytes* von Heyden with 16 chromosomes. Associations of heterochromatin in the Tramini are arrowed.

chromosome complement, presumably due to a single autosomal dissociation. Samples of *A.corni* with both 2n(♀) = 6 and 2n(♀) = 8 were obtained from *Cornus*, along with a single sample containing females with 2n = 7. On grass roots, besides *A.corni* with structurally homozygous karyotypes, a structural heterozygote with 2n = 6 (Fig. 4d) was also common, especially in winter, and 2n = 7 aphids were also found which could be interpreted as natural hybrids between 2n = 6 and 2n = 8 forms. Attempts to find morphological differences between the 2n = 6 and 2n = 8 forms were unsuccessful, although it is possible that one of these is *A.major* Börner. Further work on the relationships of karyotype and taxonomy in this genus are necessary.

The two groups which show most chromosomal abnormalities and within-species variation in karyotype are the Fordini (Pemphiginae) and the Tramini (Lachninae). Both these groups have well-established anholocycly, but in different ways. Many species of Fordini have a complete 2 year holocycle in the Mediterranean region where they produce sexual morphs on the primary hosts, *Pistacia* spp., the thelytokous generations being spent on the roots of grasses. In other parts of the world without indigenous *Pistacia* many of these same species are permanently anholocyclic on grass roots. Cytological study of *Forda* is complicated by the fact that in the species of this genus, cells with two different chromosome numbers can be found within single embryos. A possible explanation is that different numbers of chromosomes occur in germ-line and somatic cells as, for example, in Cecidomyiidae, but this cannot be verified until the meiotic stages which take place in holocyclic populations on *Pistacia* have been studied. In Table 4, only the higher of the two numbers, perhaps that of the germ line, has been included. The variation between samples of *Forda* and *Geoica* collected in England and North America is such that the original karyotype can only be guessed at until more information is available from holocyclic populations.

The Tramini live mainly on the roots of Compositae, and seem as a group to have a long history of permanent thelytoky. There are only two records in the literature of sexual morphs in this group, both for species of *Protrama*. The cytogenetics of the whole group is anomalous. Species of *Protrama* have karyotypes with a large number of very small chromosomes, some of which are mainly heterochromatic and form conspicuous chromocentres in interphase nuclei of somatic cells. The heterochromatic elements remain clumped together until late prophase (Fig. 4f). Possibly they are part of a dissociated X-chromosome system. Chromatin bridges are common in late prophase and metaphase cells making it difficult to get a precise count of the number of chromosomes, so only an approximate number can be given. It is clear, however, that this differs between the three species examined.

The karyotypes of *Trama* and *Neotrama* are quite different from those of *Protrama*. The chromosomes are fewer and larger, there is considerable structural heterozygosity, and a large amount of constitutive heterochromatin. This heterochromatin is mainly located in large terminal blocks on otherwise euchromatic chromosomes and also in smaller, wholly heterochromatic elements which vary greatly in size and number both within and between populations. As in *Protrama* there is a tendency for certain of the heterochromatic segments to remain clumped together during prophase in conventional squash preparations (Figs. 4g and 4h). Aphids under the name *Trama troglodytes* von Heyden probably comprise a great many independent parthenogenetic lines (Eastop, 1953), and although one might expect some of these to have developed specific associations with the roots of particular species of Compositae, this has not so far been demonstrated. Almost every population of *Trama troglodytes* so far examined has had a different karyotype, the differences being not only in chromosome number but in the relative proportions of the chromosomes and in the distribution of heterochromatin.

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