

Present-day distribution patterns of the holarctic Psylloidea (Homoptera: Insecta) with particular reference to the origin of the nearctic fauna

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ABSTRACT. The Psylloidea or jumping plant lice tend to be host-plant specific with related species usually occurring on closely related host plant species. The distribution of the eighty-two holarctic genera across eighteen floral realms was investigated. There is a marked faunal similarity between floral realms lying to the north of the deciduous forest regions. However, within the warmer Mediterranean/steppe/prairie/desert regions the faunas of the nearctic and palaearctic diverge with a large number of genera being endemic to their respective regions. Infiltration of tropical genera northwards occurs throughout holarctic but the genera involved tend to differ in different regions.

The probable origins of the nearctic fauna are discussed in detail. It is concluded that three distinct phases of development occurred. Firstly evolution of endemic genera from a stock existing prior to the separation of Europe and North America, secondly repeated waves of migration across a Beringia connection and finally a southern infiltration of neotropical genera and species.

Introduction

The Psylloidea or jumping plant lice are a group of usually narrowly polyphagous sap-sucking insects which feed almost exclusively on dicotyledenous plants (Eastop, 1972; Hodkinson, 1974). The psyllids as a group probably arose in the early Permian (Becker-Migdisova, 1973) and thus initially almost certainly were associated with the gymnosperms. This coniferous feeding habit has not survived and transfer on to the angiosperms probably occurred just prior to or coincident with the angiosperm explosion in the early Cretaceous, which probably heralded the evolution of the present-day forms. Certainly several of the extant psyllid genera had evolved by the Oligocene and by the Miocene these genera contained species very close to present-day forms (Becker-Migdisova, 1967). This situation is very similar to that pertaining to the flowering plants (Takhtajan, 1969). Thus psyllid evolution, making due allowance

for some possible disjunct host range extensions, appears to have closely paralleled that of the Angiosperms so that today closely related psyllid species tend to occur on closely related plant species. In general, but with the notable exception of the large genera *Cacopsylla* Ossiannilsson and *Trioza* Förster, which will be discussed later, the psyllids tend to form reasonably homogeneous groups and the analysis has been largely conducted at the generic level. However, more detailed information at the species level is presented, where appropriate, in the discussion of the origin of the nearctic fauna. The study is confined to the holarctic region as the fauna is reasonably well known: extension into other zoogeographical regions would require massive taxonomic revision. Eastop (1978), however, has discussed the broad geographical distribution of the major psyllid groups.

The psyllid data used in the study are drawn from a huge literature and from unpublished records in museums, especially the

British Museum (Natural History) and the U.S. National Museum. It is impractical to give a complete bibliography but the prime source references listed by geographical region are given below: Macaronesia (Loginova, 1976b), Morocco (Loginova, 1972b), Egypt (Samy, 1972), Spain (Ramirez-Gomez, 1956a, b, 1960), Britain (Hodkinson & White, 1979), Switzerland (Schaefer, 1949), Central Europe (Haupt, 1935), Poland (Klimaszewski, 1975), Rumania (Doboreanu & Manolache, 1962), Czechoslovakia (Vondracek, 1957), Scandinavia (Ossiannilsson, 1952; Lindberg & Ossiannilsson, 1960), European U.S.S.R. (Loginova, 1964), Turkey (Klimaszewski & Lodos, 1977, 1979), Asiatic U.S.S.R. and Mongolia (several references summarized by Klimaszewski, 1973), Northern India (Mathur, 1975), Japan (Miyatake, 1963, 1964, 1969, 1973, 1974, 1978; Kuwayama, 1908, 1910), China (Enderlein, 1937); Kuwayama & Miyatake, 1971), Greenland (Henriksen, 1939; Koponen, 1978), Alaska (Hodkinson, 1978), Canada (Strickland, 1938, 1939; Kitching, 1971; Hodkinson, 1976 and unpublished), U.S.A. (Crawford, 1914; Tuthill, 1943; Caldwell, 1937, 1938, Jensen, 1951a, b, 1957a, b; Russell, 1971, 1973), Mexico (Tuthill, 1944, 1945, 1950) and Central America (Caldwell, 1944a, b; Caldwell & Martorell, 1952). A complete list of the holarctic psyllid genera together with their world distribution and host plant associations is given in Appendix 1. This classification of the holarctic Psylloidea is in broad general agreement with those proposed by Becker-Migdisova (1973), Klimaszewski (1964) and Heslop-Harrison (1948, 1949a, b, c, 1951a, b, c, 1952a, b, 1958, 1959, 1961), but I have also made use of recent data on the classification of the Psylloidea presented by Loginova (1972a, 1974, 1975a, b, 1976a, c, 1977, 1978a, b).

A total of eighty-two psyllid genera occur in the holarctic and of these, twenty-one are monobasic. Fifty genera are endemic and of the remaining thirty-two a further fifteen exhibit maximum species diversity within the holarctic suggesting that their origin or their main centre of evolution was within the region. The residual seventeen genera exhibit maximum species diversity in other zoogeographical regions, usually the tropics,

and represent a southern infiltration into the holarctic fauna.

Information on continental drift is derived largely from Cox *et al.* (1973), Smith *et al.* (1973) and Schuster (1976); on the evolution of the flowering plants from Cronquist (1968), Takhtajan (1969), Hutchinson (1964, 1967, 1969, 1973) and Beck (1976), and on the present-day distribution of plants from Good (1974) and Willis (1973).

Present-day distribution patterns of the holarctic psyllid genera

Takhtajan (1969) classifies the holarctic region into nine distinct sub-kingdoms based on the dissimilarity of floras. This system has been used, with some further subdivision, to investigate psyllid distribution patterns. The subdivisions (Fig. 1) are:

1. Palaearctic tundra
2. West palaearctic coniferous forest
3. East palaearctic coniferous forest
4. West palaearctic deciduous forest
5. East palaearctic mixed forest
6. Mediterranean
7. Macaronesian
8. Palaearctic grassland/steppe/desert
9. Nearctic tundra
10. Greenland
11. Nearctic coniferous forest
12. Nearctic eastern deciduous forest
13. Rocky Mountains
14. Pacific northwest rain forest
15. Nearctic prairies
16. Nearctic southwest deserts
17. California
18. Nearctic subtropical

The basic presence (1) or absence (0) matrix for each psyllid genus in each floral realm (Appendix 2) forms the basis for interpretation. The psyllid communities associated with the different floral realms exhibit a general gradient of diversity from north to south which parallels the gradient in plant diversity. In the arctic tundra regions of both the nearctic and palaearctic regions just four psyllid genera *Aphalara*, *Psylla*, *Cacopsylla* and *Trioza* are present, usually associated with plants of the families Polygonaceae, Betulaceae and Salicaceae. Green-



FIG. 1. Subdivision of holarctic region into floral realms. For explanation see text.

land shows an impoverished fauna with just two genera, *Psylla* and *Cacopsylla*, represented.

As one moves south into the coniferous forest zones of both the nearctic and palae-arctic then the genus *Livia* on *Carex* and *Juncus* and the *Craspedolepta* species on Onagraceae appear. In addition a number of genera with a more southerly distribution reach their northern limit. These include *Strophingia* and *Psyllopsis* on *Calluna* and *Fraxinus* respectively in the palae-arctic and *Pachypsylla* on *Celtis* in the nearctic.

In the deciduous forest zones throughout the holarctic, species of the genera *Livia*, *Aphalara*, *Craspedolepta*, *Psylla*, *Cacopsylla* and *Trioza* predominate but with an infiltration of genera which exhibit maximum diversification in more southerly floral realms. In the west palae-arctic these include *Camartoscena* on *Populus*, *Spanioneura* on *Buxus* and a number of Arytainine legume-feeding genera – *Arytaina* sensu stricto, *Alloeoneura*, *Arytainilla*, *Floria*, *Livilla* and *Amblyrhina*. There are no true endemics but *Psyllopsis* spp. on *Fraxinus* show maximum diversification in the region and the monotypic genus *Rhinocola* on *Acer* is typical of the warmer parts of the region.

In the eastern palae-arctic forest the picture is similar with several oriental genera including *Paurocephala* on *Ficus*, *Togepsylla* on *Litsea* and *Euphalerus* on *Gleditsia* and *Caesalpina* reaching their northern limit and supplementing the dominant ubiquitous genera previously listed.

In addition, seven endemic genera *Anomoneura* on *Morus*, *Epitrioza* on *Eleagnus*,

Metapsylla on *Gleditsia*, *Syntomoza* on *Myroxylon*, *Syringilla* on *Syringa*, *Ligustrinia* on *Ligustrum* and *Epheloscyta* (host unknown) are apparent. The presence of *Calophya* on Anacardiaceae and *Pachypsylla* on *Celtis* indicate links with the nearctic deciduous forest fauna.

In the nearctic deciduous forest the six ubiquitous genera are again dominant. Characteristic genera include *Pachypsylla*, but there appears to be only a single monotypic endemic, *Hemitrioza* on *Sonchus*. However, more southerly elements are present in *Neotrioza* (host unknown), *Amorphicola* on *Amorpha* and *Gyropsylla* on *Ilex*.

The faunas of the Pacific North West rain forest and the Rocky Mountains are again dominated by *Livia*, *Aphalara*, *Craspedolepta*, *Psylla*, *Cacopsylla* and *Trioza*. Endemics are absent but there is again an infusion of southern genera including the Arytainines *Euglyptoneura* and *Ceanothia* on *Ceanothus* and the Aphalaraoidine *Neophyllura* on *Arctostaphylos* and *Arbutus*.

Thus in general there are broad similarities throughout the holarctic region in the psyllid genera associated with floristic regions lying north of the more arid or warmer zones and it is not until these zones are reached that differences become marked.

Within the palae-arctic Mediterranean zone the fauna changes: *Aphalara*, *Craspedolepta*, *Psylla*, *Cacopsylla* and *Trioza*, while still present, cease to dominate and genera associated with xerophilous plant species become predominant. Endemism is rare as most genera have spread outwards from the Mediterranean:

the monotypic trioqid genus *Engytatoneura* (host unknown) from Morocco and the monotypic Arytainine genus *Pseudacanthopsylla* on *Retama* from Egypt appear to be exceptions. However, several genera have their centre of distribution in the region. These include a large number of closely related Arytainine genera associated with the fabaceous shrubs of the tribe Genisteae, namely *Arytaina* sensu stricto, *Alloeoneura*, *Amblyrhina*, *Arytainilla*, *Floria* and *Livilla*; a number of *Strophingia* species associated with Ericaceae, and *Euphyllura* on Oleaceae. The fauna also encompasses a large desert-steppe element which appears to have its origins further to the east. This includes the Aphalaroidine genera *Camartoscena*, *Acaerus* and *Pachypsyllodes*, the Aphalarine genera *Xanioptera*, *Caillardia*, *Rhodoclanis*, *Colposcena* and *Crastina*, the Arytainine genus *Cyamophila* and the Trioqid genera *Egeirotioza* and *Eutrioza*. In addition two genera *Acizzia* (*Psylla bicolorata* Samy) on *Acacia* and *Albizia* and *Pauropsylla* on *Ficus* appear to have entered the region via a southern route, either from India or Africa south of the Sahara where their centres of distribution lie. Also, for the genus *Diaphorina* it is possible to postulate a similar northward movement, although a westward movement from an Asian centre of origin must also be considered. *Homotoma*, a genus associated with *Ficus* spp., which exhibits maximum diversity in the eastern Oriental region completes the fauna (Miyatake, 1973).

The Macaronesian fauna can be derived by reduction from the Mediterranean fauna although two highly specialized endemic Aphalaroidine genera *Lisronia* on *Cistus* and *Megadicrania* (host unknown) are present and the Arytainine genus *Arytainilla* on Fabaceae has undergone explosive evolution.

The desert-steppe region of central Asia is especially interesting in that it contains a large endemic fauna associated with xerophilous plants. The genera involved are the Aphalaroidine *Eremopsylloides* on *Calligonum*, the Aphalarines *Brachystetha* on *Nitraria* and *Zygophyllum*, *Xenaphalara* on *Ceratocarpus*, *Eurotica* on *Eurotia*, *Eumetoecus* on *Kochia* and *Camphorosoma*, *Rhombaphalara* on *Halocnemum* and the Arytainine *Astragilita* on *Astragalus*. In addition the genus *Craspedolepta* has undergone explosive evolution on

Artemisia. A number of genera are also present which appear to have spread westwards into the Mediterranean and beyond yet exhibit maximum diversity in the steppe/desert, suggesting that this is the centre of their diversification. These include the Aphalaroidine genera *Pachypsyllodes* and *Acaerus* on *Calligonum*, the Aphalarine genera *Caillardia* on *Anabasis* and *Haloxylon*, *Rhodoclanis* on *Salsola*, *Suaeda* and *Salicornia*, *Crastina* on *Myricaria*, *Colposcena* on *Tamarix*, the Arytainine genus *Cyamophila* on *Caranga*, *Glycyrrhiza* and *Astragalus* and a mixture of Triozine forms including *Egeirotioza* on *Populus* and *Eutrioza* on *Pinus* (unconfirmed). The Aphalaroidine genus *Diaphorina* on *Lycium*, *Convolvulus*, *Zygophyllum*, *Clutia* and *Salvadora* is especially interesting. It has undergone wide diversification within this region but it also occurs abundantly throughout the Ethiopian and Oriental regions. Its origins are somewhat obscure. The ubiquitous *Cacopsylla*, *Aphalara* and *Trioza* are present but not dominant.

It is interesting to note that relic populations of certain arctic-temperate species such as *P. zaecevi* Sulc, *P. viburni* Löw, *Aphalara maculipennis* Löw and *Trioza urticae* (L.) are found south of the arid zone in the mountains of northern India.

The fauna of the North American prairies is derived from the ubiquitous northern element *Livia*, *Aphalara*, *Craspedolepta*, *Psylla*, *Cacopsylla* and *Trioza* with the addition of Californian/desert forms including *Aphalaroida*, *Euglyptoneura*, *Amorphicola* and *Leurolophus*. The genus *Craspedolepta* has undergone only moderate diversification in this region. The presence of *Rhinopsylla* and *Heteropsylla* indicates an infiltration of southern neotropical forms.

The faunas of the nearctic desert and California are similar with a number of typical genera exhibiting maximum species diversity. These include the Aphalaroidine genera *Aphalaroida* and *Heteropsylla* on the Mimosoidea, *Neophyllura* on *Arctostaphylos* and *Arbutus*, the Arytainine genera *Amorphicola* on *Amorpha*, *Purshivora* on *Purshia*, and *Ceanothia* on *Ceanothus*. True endemics are uncommon but the Aphalaroidine genus *Paraphalaroida* on *Fremontia*, the Arytainine genus *Pexopsylla* on *Cercocarpus* and the

Trioziid *Levidea* on *Parthenium* are unique to these regions. In addition a number of genera of clearly neotropical origin are present including *Leuronota*, *Metatrioza*, *Neotriozeila* and *Kuwayama*. Northern forms including *Aphalara*, *Craspedolepta*, *Cacopsylla*, *Pachypsylla* and *Calophya* on *Rhus* are present but no longer dominant.

In contrast to the arid zones of the old world the nearctic arid zone fauna appear to contain fewer endemic genera and a lower species diversity. Whereas in the forest zone northwards the typical genera exhibit holarctic distributions, in the arid zones the nearctic–palaeartic links are at the tribe or subfamily level through the subfamilies Aphalaroidinae and Arytaininae: there are no common typical genera. Furthermore, within the subfamily Aphalarinae the massive radiation which occurred in the Old World has not occurred in the nearctic. The implications of this will be discussed later.

The subtropical south-east zone retains a small proportion of the ubiquitous *Livia*, *Aphalara*, *Cacopsylla* and *Trioza* within the fauna but also contains a large element of genera having their centre of distribution either in the neotropical zone or at least within the tropics. These genera are *Gyropsylla* on *Ilex*, *Rhinopsylla* (host unknown), *Leuronota* on *Celtis*, *Ceropsylla* on *Sideroxylon*, etc., and *Euphalerus* on *Piscidia*.

Analysis

To summarize the basic data matrix, to identify recurrent groupings of psyllid genera with common distributions and to measure the faunal similarity at the generic level between faunal kingdoms two similarity matrices were calculated. These were firstly a matrix expressing, on a scale from 0 → 1, the similarity between the faunas of the eighteen floral realms based on the psyllid genera which occur in them and secondly a matrix expressing the similarity between the distributions of the psyllid genera based on their occurrence in the different floral realms. In both instances Jaccard's coefficient of similarity $A/(A + B + C)$ was used, where, for example, to calculate the faunal similarity between two floral realms A is the number of

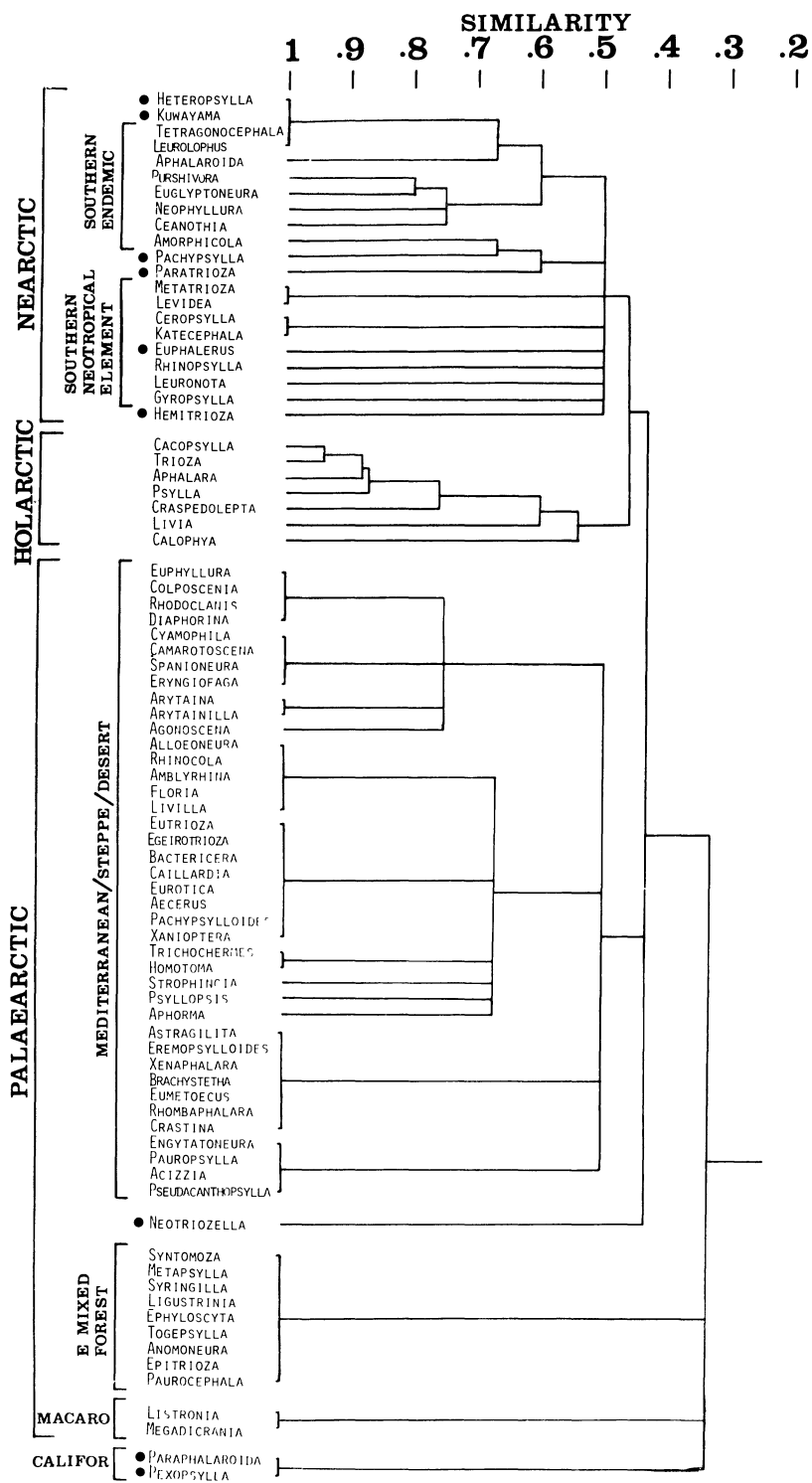
genera occurring in both realms, B is the number of genera found in the first realm only, and C is the number of genera found in the second realm only. Minimum spanning trees were calculated across each of the matrices which were then clustered by single linkage (Gower & Ross, 1969; Farris, 1970) to produce classifications in dendrogram form (Figs. 2 and 3).

Within the classification of psyllid genera (Fig. 2) a number of basic groups can be recognized above the 0.5 similarity level, i.e. the level at which genera occur together more often than they occur apart.

There are three tight clusters of endemic genera (1.0 similarity) associated with the eastern palaeartic forest (nine genera), Macaronesia (two genera) and the Californian region of the nearctic (two genera). A further four looser major clusters can be identified. These are firstly a typically Mediterranean/steppe/desert group of forty genera associated with the more arid southern zone of the palaeartic. This group contains generic elements such as the *Alloeoneura*/*Livilla* cluster which have spread northwards into the west palaeartic deciduous forest and the *Pauropsylla*/*Acizzia* which represents a southern infiltration into the palaeartic fauna. The second major grouping includes seven genera which exhibit a broad distribution throughout the holarctic and which, with the exception of *Calophya*, can be regarded as an ubiquitous northern element. A third very loose cluster encompasses a group of seven genera which appear to have entered the southern nearctic from the neotropical region. The apparent looseness of this cluster is partly a reflection of sporadic records across a few floral kingdoms. The final major cluster incorporates a group of seven genera which are endemic to the warmer southern regions of the nearctic.

One further cluster is worthy of note, namely, that including *Pachypsylla* and *Paratrioza*. These genera occur both in the east palaeartic and the nearctic but their more widespread occurrence in the latter gives them a high similarity with the endemic nearctic genus *Amorpha*.

The classification of floral realms based on the distribution of psyllid genera (Fig. 3) shows that in the northerly vegetation zones, the tundra, the coniferous and the deciduous



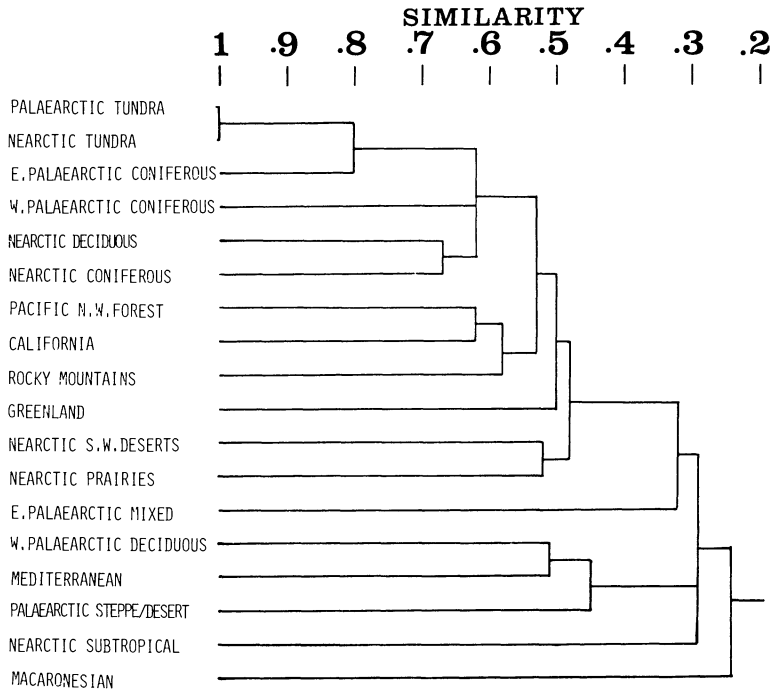


FIG. 3. Phenogram to illustrate the faunal similarity between the eighteen floral realms based on the presence of eighty-two psyllid genera.

forests, there is generally a high similarity (greater than 0.5) in the psyllid genera which occur. However, as one moves into the more southerly floral realms their level of similarity with the former zones decreases. Similarly the similarity between the nearctic and palaeartic regions also decreases. Again the east palaeartic forest, the nearctic subtropical and the Macaronesian zones appear as outliers showing low similarity with other floral realms.

The origins of the nearctic fauna

A number of species have been introduced into North America within recent times and should be excluded from the analysis. These species are *Arytaina genistae* (Latr.), *Arytainilla spartiophila* (Först.), *Acizzia unca-*

toides (Ferris & Klyver), *Psyllopsis fraxini* (L.), *P. fraxinicola* (Först.), *P. discrepans* (Flor), *Spanioneura fonscolombii* (Först.), *Cacopsylla mali* (Schmidt.), *C. sorbi* (L.), *C. pyricola* (Först.), *C. fatsiae* (Jensen), *C. buxi* (Först.), *Trioza alacris* Flor, and *Homotoma ficus* (L.).

The present-day nearctic psyllid fauna could possibly be derived in three separate ways: firstly by evolution *in situ* prior to and after the final separation of North America and Europe in the Late Cretaceous (70 million years BP, although island chains may have provided a migration corridor for a further 20 millions years); secondly by subsequent immigration from the palaeartic across a Beringia connection, and thirdly by immigration through the Isthmus of Panama, after the joining of North and South America in the Miocene (20 million years

FIG. 2. Phenogram to illustrate the similarity in range of distribution of the holarctic psyllid genera across the eighteen floral realms. ● indicates genera with unusual distributions which, as an artifact of the method used, cluster outside their expected groups. *Heteropsylla*, *Kuwayama* and *Neotriozeila* are southern nearctic in distribution, *Hemitrioza*, *Paraphalaroida* and *Pexopsylla* are endemics unique to one floral realm in the nearctic and *Pachypsylla* and *Paratrioza* are holarctic genera widespread in the nearctic but with restricted distribution in the palaeartic.

BP). Fossil evidence is rare and conclusions are drawn from zoogeographical and host plant data together with a consideration of adult and nymphal morphology.

In general the nearctic fauna is much poorer both in terms of number of genera and numbers of species when compared to the palaearctic. Sixty-one genera are recorded from the palaearctic whereas only thirty-one are recorded from the nearctic.

A number of nearctic genera, *Katecephala*, *Gyropsylla*, *Rhinopsylla*, *Kuwayama*, *Leuro-nota*, *Metatrioza*, *Neotrioza* and *Euphalerus* are largely associated with southern vegetation zones. Each of these genera exhibit maximum species diversity within the neotropical region and can undoubtedly be considered as having entered the nearctic via a southern route within the last 20 million years. In addition, within the heterogeneous genus *Trioxa*, a number of nearctic *Baccharis*-feeding forms, *T. proxima* Crawf., and *T. collaris* Crawf., have their nearest relatives in the *Baccharis*-feeding species of South America, again suggesting a neotropical origin for this segment of the genus. *Baccharis* itself is thought to have spread north up the mountain chains from a neotropical origin.

On the basis of adult morphology the Heteropsylline genus *Heteropsylla* has previously been placed in the Aphalaridae close to *Aphalaroida*. However, the structure of its nymph and the elongate eighth antennal segment in the adult suggests that it is a very highly evolved Ciriacreminae. *Heteropsylla* species feed on the Mimosidae section of the Fabales, the normal host plants of the neotropical Ciriacreminae. Furthermore *Heteropsylla* is distributed throughout Central and South America and shows certain morphological affinities with *Euceropsylla*, a neotropical genus. A neotropical origin for this genus appears most likely.

Since the final separation of the North American and European land masses and the final closure of the Atlantic corridor in the mid-Eocene (60 million years BP), faunal immigration into the nearctic must largely have been controlled by climatic conditions existing in the Beringia region. Recent evidence suggests that climatic conditions, as indicated by fossil floras, has undergone progressive deterioration from the Eocene onwards.

During the later Cretaceous the Alaskan flora was analogous to that found in North China and Korea today, while during the Palaeocene and Eocene a temperate deciduous flora became dominant (Cox *et al.*, 1973). At this time the northern limit of the subtropical vegetation lay about 15° N of its present position. From this time onwards the climate began to cool and a marked temporary severe deterioration occurred during the Oligocene, at which time forest persisted over much of Eurasia and this condition persisted through into the somewhat warmer Miocene. The final climatic deterioration began in the mid-Miocene and by the Pleistocene the simpler, cold-adapted arctic/sub-arctic vegetation types had developed and occupied the northern regions of the holarctic.

Hence, as climate has changed, vegetation type has changed and the potential for migration by different groups of psyllids has altered. Is there any evidence to support this hypothesis? A number of predominantly North temperate genera *Livia*, *Aphalara*, *Craspedolepta*, *Calophya*, *Pachypsylla*, *Psylla*, *Cacopsylla* and *Trioxa* are common to both the palaearctic and nearctic zoogeographical regions and do not, with the exception of *Calophya* and *Trioxa* *sensu lato*, occur in the neotropical region. An examination of the evidence from present-day species distribution patterns within these genera suggests that faunal exchange across Beringia must have occurred on many occasions. Working backwards through time it is possible to identify several distinct waves of migration.

A number of holarctic species occur within the genera *Craspedolepta*, *Psylla*, *Cacopsylla* and *Trioxa* (Table 1). Nearly all these species exhibit a far northern distribution on circumpolar plant species within the genera *Salix*, *Alnus*, *Betula*, *Vaccinium*, *Ledum* and *Epilobium*. The circumpolar continuity of these psyllid species reflects the known Pleistocene history of the vegetation. The opening of the Bering land bridge during glacial maxima provided a corridor for faunal/floral exchange of arctic species. There is an excellent correlation between the psyllids which have retained their circumpolar integrity and the presence of their host plant, as indicated by pollen spectra, in the Wisconsin and Illinoian glaciation zones of sediment cores

TABLE 1. The holarctic psyllid species

Species	Host plant
<i>Craspedolepta subpunctata</i> (Först)	<i>Epilobium angustifolium</i>
<i>C. nebulosa</i> (Zett)	<i>Epilobium angustifolium</i>
<i>C. sonchi</i>	<i>Sonchus</i> , <i>Leontodon</i>
<i>Psylla alni</i> (L.)	<i>Alnus</i> spp.
<i>P. betulae</i> (L.)	<i>Betula</i> spp.
<i>P. hartigi</i> Flor	<i>Betula</i> spp.
<i>P. carpinicola</i> (Crawf.)	<i>Carpinus</i> spp.
<i>P. betulaenanae</i> Oss.	<i>Betula nana</i>
<i>Cacopsylla palmeni</i> (Löw)	<i>Salix</i> spp.
<i>C. zaecevi</i> (Sulc)	<i>Salix</i> spp.
<i>C. myrtilli</i> (Wag.)	<i>Vaccinium</i> sp.
<i>C. ledi</i> (Flor)	<i>Ledum palustre</i>
<i>C. phlebophyllae</i> (Hod.)	<i>Salix</i> spp.
<i>C. tenuata</i> (Jensen)	<i>Salix</i> spp.
<i>Trioza salicivora</i> Reut.	<i>Salix</i> spp.
<i>T. atkasookensis</i> Hod.	<i>Salix</i> spp.
<i>T. arctica</i> Hod.	<i>Salix</i> spp.

taken from the Beringia region (Hopkins, 1967). *Craspedolepta sonchi* is somewhat exceptional as it has only been found in sub-montane nearctic habitats further to the south and this possibly indicates extinction in the northern parts of its range. The position of *Cacopsylla tenuata* and *Psylla carpinicola* is discussed later.

In summary, these species represent the most recent groups which have been geographically isolated for about 13 000 years since the last closure of the Bering land connection and which have not yet diverged.

However, the effects on speciation of repeated glaciation are manifest *within* the nearctic region. Some holarctic species such as *C. palmeni*, *P. alni* and *C. subpunctata* which are broadly distributed within the palaearctic appear to have diverged within the nearctic. For instance, in North America *C. palmeni*

is confined to the old glacial refugium north of the Brooks Range in Alaska; further south it is replaced by the closely related but morphologically distinct *C. alaskensis* (Ashmead). Similarly *C. subpunctata* appears to have given rise to the arctic/alpine *C. alaskensis* (Ash.), and *P. galeaformis* (Patch) and *P. caudata* (Crawf.) appear to have separated from *P. alni*. In these cases the exact isolating mechanisms leading to speciation are obscure.

A slightly earlier, but still recent, wave of migration is indicated by the presence of pair species within the genera *Psylla*, *Cacopsylla* and *Trioza* (Table 2). These pair species are morphologically similar and of undoubted common origin yet exist as distinct palaearctic and nearctic forms. In general these species tend to occur in a latitudinal zone lying just to the south of that occupied by the circum-polar species. They are again largely associated

TABLE 2. Palaearctic–nearctic psyllid pair species

Palaearctic species	Nearctic species	
<i>Craspedolepta malachitica</i> (Dahl.)	<i>C. vancouverensis</i> (Klyv.)	<i>Artemisia</i>
<i>Psylla fusca</i> (Zett.)	<i>P. floccosa</i> Patch.	<i>Alnus</i>
<i>Cacopsylla zinovjevi</i> (Log.)	<i>C. sinuata</i> (Crawf.)	<i>Salix</i>
<i>C. elegantula</i> (Zett.)	<i>C. fibulata</i> (Crawf.)	<i>Salix</i>
<i>C. propinqua</i> (Schaeff.)	<i>C. macleani</i> (Hod.)	<i>Salix</i>
<i>C. arcuata</i> (Log.)	<i>C. kananaskensis</i> (Hod.)	<i>Salix</i>
<i>C. sibirica</i> (Log.)	<i>C. rufipennis</i> (Hod.)	<i>Salix</i>
<i>Trioza acutipennis</i> (Zett.)	<i>T. singularis</i> Tut.	<i>Alchemilla</i> , <i>Comarum</i>
<i>T. urticae</i> (L.)	<i>T. albifrons</i> Crawf.	<i>Urtica</i>
<i>T. apicalis</i> Först.	<i>T. stygma</i> Tut.	<i>Umbelliferae</i>
<i>T. curvatinnervis</i> Först.	<i>T. incerta</i> Tut.	<i>Salix</i>

with the plants of the genera *Salix* and *Alnus*, although species pairs on *Alchemilla/Comarum*, *Urtica*, Umbelliferae and temperate species of *Artemisia* also occur. The sequence of events leading to their separation appears to be that the parent species crossed through Beringia when climatic conditions were slightly more favourable, prior to the Pleistocene. Subsequent climatic deterioration pushed the species southwards and geographical isolation leading to speciation resulted.

Craspedolepta vancoverensis is especially interesting. It occurs on *Artemisia*, the same host as *C. malachitica*, but it also occurs on *Achillea millefolium*, the normal host of *C. nervosa* (Först.) in the palaeartic. The latter occurs across the palaeartic from Europe to Eastern Siberia and Japan but has not crossed into the nearctic. This suggests that disjunct host-range extension can occur in the absence of competition from closely related species.

A much earlier wave of migration of species within the genera *Aphalara*, *Craspedolepta* (temperate species), *Livia*, *Cacopsylla* and *Trioza* appears to be associated with the somewhat warmer conditions extant in the Oligocene or Miocene, at which time the Beringia flora was cool temperate. Most of these genera are well documented in palaeartic Miocene fossil records. The species groups involved are today generally associated with deciduous forest vegetation types and are widely distributed throughout the holarctic yet still remain coherent groups. This suggests an older common ancestry followed by diversification throughout each region. For instance, the palaeartic *Aphalara polygoni* Först./*borealis* H-H/*calthae* (L.)/*longicaudata* Sch./*sibirica* Log. group has its North American counterpart in the *A. loca* Cald./*A. nubifera* Patch./*nigra* Cald./*curta* Cald./*persicaria* Cald. complex. Similarly the palaeartic *A. exilis* W & M/*hedeni* End. and *A. maculipennis* Low/*itadori* (Shinji) groups are close to the nearctic *A. rumicus* Mally/*monticola* Hod. and *A. manitobaensis* Cald./*dentata* Cald. groups respectively. The family Liviidae (one genus *Livia*) and the genus *Craspedolepta* both contain equivalent species groups with apparent common ancestry. Fossil evidence suggests that by the Miocene the genera *Cacopsylla* and *Trioza* had undergone wide divergence onto a variety of host plants within the

palaeartic and it is reasonable to assume multiple migration by different groups of these genera, with subsequent proliferation in each region. This phenomenon is best illustrated by the *Salix*-feeding species in each genus which have undergone wide diversification in each region to form large distinct species groups which nevertheless retain a certain common morphological identity. Similarly certain *Cacopsylla* which feed on Eleagnaceae show similar divergence. The nearctic *C. magnicauda* (Crawf.)/*tuthilli* (Cald.)/*stricklandi* (Cald.) complex is very close to the palaeartic *C. hippophaes* (Zett.)/*zetterstedti* (Thoms.) group.

Cacopsylla tenuata Jensen on *Salix* and *P. carpinicola* Crawf. on *Carpinus* are two species which occur only in Japan and the lower U.S.A. and do not appear to be introduced. These may well be Miocene relict species which have retained their morphological integrity.

Evolutionary links between several groups of temperate *Cacopsylla* and *Trioza* species within the nearctic and palaeartic faunas remain obscure but it is reasonable to assume that their divergence and proliferation probably occurred during Oligocene–Miocene times when climatic conditions were favourable for their development.

A slightly earlier migration during a warmer climatic period, perhaps the late Eocene, is suggested by the distribution of two genera, the Pauropsylline *Calophya* on *Rhus* (see earlier) and the Pachypsylline *Pachypsylla* on *Celtis*. These two genera are largely concentrated in the warmer temperate forest zones of the eastern palaeartic and the nearctic regions south of Canada. The endemic North American genus *Tetragonocephala* appears to be an offshoot of *Pachypsylla*. Although the majority of Pachypsylline genera and species occur in North America, suggesting a nearctic origin, the most primitive lerp-forming species *Pachypsylla japonica* Miyatake occurs in the east palaeartic. This suggests a palaeartic origin.

The endemic nearctic Euphyllurine genera *Neophyllura* and *Leurolophus* are possible Eocene derivatives, via a Bering connection, from the Euphyllurine stem which proliferated in the east palaeartic. However, for reasons stated later a trans-Atlantic origin from a *Euphyllura* line appears most likely.

Thus migration of species associated with Arcto-Tertiary vegetation types through Beringia appears to have played a significant role in the development of the nearctic psyllid fauna. However, it does not explain the origin of many endemic nearctic genera and an alternate origin must be sought.

The residual endemic genera belong to just three groups; firstly the Aphalaroidines *Aphalaroida* on *Prosopis*, *Pithecellobium*, *Acacia* and *Mimosa* and *Paraphalaroida* on *Fremontia*, secondly the Euphyllurines *Neophyllura* on *Arctostaphylos* and *Arbutus*, and *Leurolophus* on *Rhus*, and thirdly the Arytainines, *Purshivora* on *Purshia*, *Pexopsylla* on *Cercocarpus*, *Euglyptoneura* and *Ceanothia* on *Ceanothus* and *Amorphicola* on *Amorpha*. All these genera have their centres of distribution within the warmer more southerly vegetation zones of the nearctic, suggesting that their evolution occurred within such a region. It is significant to note that these three psyllid stocks also form the dominant elements in the faunas of the drier Mediterranean areas of the Western palaearctic. Two possible origins can be postulated for these genera, evolution from a neotropical element and/or evolution from an early Laurasian stock. The evidence suggests the latter.

The Aphalaroidini, with the exception of the primitive *Paurocephala* and *Tainarys Brethes*, do not occur in the neotropical region and *Aphalaroida* and *Paraphalaroida* have their closest relative in *Strophingia*, a west palaearctic Mediterranean/Macaronesian genus feeding on Ericaceae. This strongly suggests that these genera can be derived from a common Laurasian stock which existed prior to the separation of the land masses in the mid-Eocene. Certainly *Strophingia* itself had differentiated by the Oligocene (Enderlein, 1915). Within the Euphyllurines, *Neophyllura* is morphologically closer to the European *Euphyllura* than to the east palaearctic genera centred around *Syntomoza* or the neotropical *Katecephala*. This again suggests a trans-Atlantic connection.

The origin of the nearctic Arytainine genera is again open to speculation: as possible candidate stock is available in both South America and the palaearctic. The evidence, however, again suggests that the North

American genera are derived from an old Laurasian Arytainine type stock which proliferated within the region rather than from a neotropical Euphalerid type ancestor. In its North American usage the genus *Euphalerus* is very broad, containing several only distantly related species. The true 'nest making' *Euphalerus* centred around *E. nidifex* Schwarz are found only in the extreme south of the nearctic (Russell, 1971). The remaining species, on both host plant and nymphal morphology data, are referable to other groups within the Arytainini and possibly the Euphyllurini. The Arytainine genera *Euglyptoneura*, *Pexopsylla*, *Ceanothia*, *Amorphicola* and *Purshivora* form a relatively close group, most probably derived from a common stock. These genera are closer to the old world genera than to extant South American forms yet have retained more primitive Arytainine characters (e.g. open frons, two basal-metatarsal spines) than some of their more highly derived palaearctic counterparts. The genus *Amorphicola* on *Amorpha* (Fabaceae) retains a link with the legume-feeding habit of the postulated ancestor, whereas the other genera have moved onto other closely related host plant families, *Pexopsylla* and *Purshivora* onto Rosaceae, and *Euglyptoneura* and *Ceanothia* onto Rhamnaceae. Wide proliferation of the latter two genera on a large endemic plant genus like *Ceanothus* (forty known species) suggests a long parallel evolutionary association between the psyllid and its host. Certainly on the evidence of rates of psyllid evolution from elsewhere, the 20 million year time scale obligated by the neotropical origin hypothesis appears far too short. All other nearctic genera of neotropical origin have not proliferated and are usually confined to an extreme southern distribution.

Further evidence for the Laurasian origin of the endemic genera is provided by the known history of the Madro-tertiary flora of the southwestern U.S.A. which began its development possibly as early as the late Cretaceous (Raven, 1973). Plant communities of a Mediterranean type containing the host plants *Acacia*, *Amorpha*, *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Fremontia*, *Pithecellobium*, *Prosopis* and *Rhus* had already differentiated by the Miocene (Axelrod,

1973). In discussing the origin of the California Mediterranean type vegetation Axelrod concluded that 'the close similarities between the mid-Cretaceous floras of southern Europe and the central U.S.A. must have been due to east-west connections which have since been removed by sea floor spreading'.

It is interesting to speculate that, in the absence of competition from *Cacopsylla* species during the initial stages of their evolution, the nearctic Amaryllidaceae were able to transfer onto the Rosaceae and Rhamnaceae, the normal *Cacopsylla* host plants.

In conclusion, the development of the nearctic psyllid fauna can be traced through several phases. First, the development of a common fauna with the western palaearctic followed by the final separation of the two regions in the mid-Eocene with the residual faunas continuing their development *in situ*. Secondly, successive waves of immigration through the Beringian region in response to climatic changes which continued up until about 13 000 years BP. Finally, small-scale immigration into the southern regions from the neotropical kingdom subsequent to their joining in the Miocene (20 million years BP).

Discussion

Within the holarctic region the main centres of psyllid diversification, each with their own highly characteristic fauna, are the Mediterranean basin, the steppe/deserts of Central Asia, the east palaearctic forests and the desert/Californian region of south-western North America. In contrast, the characteristic faunas of the deciduous forest zones of the Old and New World are simpler and share the same major elements in common. The faunas of the arctic and boreal forest zones appear to be derived by reduction from the deciduous forest fauna and several species exhibit an holarctic distribution. There is evidence to indicate penetration of the southern nearctic by neotropical genera and the southern palaearctic by Ethiopian and Oriental genera.

At the generic level there is close correlation between the holarctic floral kingdoms recognized by Takhtajan (1969) and Good (1974) and the main centres of psyllid diversi-

fication. This is not surprising in view of the close association between psyllids and their host plants. Nevertheless, the insect and plant data are complementary and thus mutually supportive.

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APPENDIX 1. The classification, worldwide distribution and host-plants of the holarctic psyllid genera. Key: P – Palearctic, E – Ethiopian, N – Nearctic, NO – Neotropical, O – Oriental, A – Austro-Oriental, PN – Polynesian. * Indicates monobasic genera.

SUPER-FAMILY PSYLLOIDEA Burm.

Family	Subfamily	Tribe	Genus	Distribution	Host plants
APHALARIDAE	Aphalaroidinae Vond.	Rhinocolini Vond.	* <i>Rhinocola</i> Först.	P	<i>Acer</i> (Aceraceae)
		Euphyllurini B.M.	<i>Euphyllura</i> Först.	P, E, O	<i>Olea</i> , <i>Phillyrea</i> (Oleaceae)
			* <i>Syntomoza</i> Enderl.	P	<i>Myroxylon</i> (Fabaceae)
			* <i>Megadicrania</i> Log.	P	?
			* <i>Syringilla</i> Log.	P	<i>Syringa</i> (Oleaceae)
			* <i>Ligustrinia</i> Log.	P	<i>Ligustrum</i> (Oleaceae)
			<i>Neophyllura</i> Log.	N	<i>Arctostaphylos</i> , <i>Arbutus</i> (Ericaceae)
			* <i>Leurolophus</i> Tut.	N	<i>Rhus</i> (Anacardiaceae)
			<i>Katecephala</i> Crawf.	N, NO	?
		Aphalaroidini B.M.	<i>Agonosцена</i> Enderl.	P, E, O	<i>Peganum</i> , <i>Ruta</i> , <i>Pistacia</i> (Zygophyllaceae, Rutaceae, Anacardiaceae)
			<i>Aphorma</i> Hod.	P	?
			<i>Strophingia</i> Enderl.	P	<i>Calluna</i> , <i>Erica</i> (Ericaceae)
			<i>Camarotoscena</i> Enderl.	P, E	<i>Populus</i> (Salicaceae)
			* <i>Lisronia</i>	P	<i>Cistus</i> (Cistaceae)
			<i>Aphalaroida</i> Crawf.	N	<i>Prosopis</i> , <i>Pithecellobium</i> , <i>Acacia</i> , <i>Mimosa</i> (Mimosaceae)
			<i>Heteropsylla</i> Crawf.	N, NO	<i>Mimosa</i> , <i>Pithecellobium</i> , <i>Prosopis</i> , <i>Acacia</i> , <i>Quassia</i> (Mimosaceae)
			* <i>Paraphalaroida</i> Log.	N	<i>Fremontia</i> (Bombaceae)
			<i>Paurocephala</i> Crawf.	P, E, O, NO, A, PN	<i>Ficus</i> (Moraceae)
		Pachypsylloidi Log.	<i>Pachypsylloides</i> Bergev.	P	<i>Calligonum</i> (Polygonaceae)
			<i>Acaerus</i> Log.	P	<i>Calligonum</i> (Polygonaceae)
			<i>Eremopsylloides</i> Log.	P	<i>Calligonum</i> (Polygonaceae)
		Diaphorinini Vond.	<i>Diaphorina</i> Löw	P, O, E, A	<i>Lycium</i> , <i>Convolvulus</i> , <i>Zygophyllum</i> , <i>Clutia</i> , <i>Salvadora</i> (Solanaceae, Convolvulaceae, Zygophyllaceae, Euphorbiaceae, Salvadoraceae)

LIVIIDAE	PSYLLIDAE	Aphalarinae Löw	Aphalarini Vond.	<i>Aphalara</i> Först.	P, N, O	<i>Polygonum</i> , <i>Rumex</i> , <i>Caltha</i> (Polygonaceae, Helleboraceae)
				<i>Craspedolepta</i> Enderl.	P, N	Asteraceae and Onagraceae, several genera
				<i>Brachystetha</i> Log.	P	<i>Nitraria</i> (Zygophyllaceae)
				* <i>Xanioptera</i> Enderl.	P	<i>Artemisia</i> (Asteraceae)
				<i>Gyropsylla</i> Breth.?	N, NO, A	<i>Ilex</i> (Aquifoleaceae)
				<i>Epheloscyta</i> Log.	P	?
			Xenaphalarini Log.	* <i>Xenaphalara</i> Log.	P	<i>Ceratocarpus</i> (Chenopodiaceae)
				<i>Eurotica</i> Log.	P	<i>Eurotia</i> (Chenopodiaceae)
			Caillardiini Log.	<i>Caillardia</i> Bergev.	P	<i>Anabasis</i> , <i>Haloxylon</i> (Chenopodiaceae)
				* <i>Eumetoecus</i> Log.	P	<i>Kochia</i> , <i>Camphorosoma</i> (Chenopodiaceae)
				<i>Rhodoclanis</i> Log.	P	<i>Suaeda</i> , <i>Salsola</i> , <i>Pterosimonia</i> , <i>Salicornia</i> (Chenopodiaceae)
				<i>Rhombaphalara</i> Log.	P	<i>Halocnemum</i> (Chenopodiaceae)
			Colposceniini Log.	<i>Colposcencia</i> Enderl.	P, E, O	<i>Tamarix</i> (Tamaricaceae)
				<i>Crastina</i> Log.	P, E	<i>Myricaria</i> , <i>Tamarix</i> (Tamaricaceae)
				<i>Livia</i> Ltr.	P, N, O	<i>Carex</i> , <i>Juncus</i> (Cyperaceae, Juncaceae)
			Ciriacreminae End.	Anomoneurini B.M.	P	<i>Morus</i> (Moraceae)
			Arytaininae Crawf.	Arytainini Vond.		
				<i>Alloeoneura</i> Löw	P	<i>Cytisus</i> (Fabaceae)
				<i>Amblyrhina</i> Löw	P	<i>Genista</i> (Fabaceae)
				<i>Arytaina</i> Först. sensu stricto	P	<i>Cytisus</i> , <i>Adenocarpus</i> , <i>Genista</i> (Fabaceae)
				* <i>Astragilita</i> Log.	P	<i>Astragalus</i> (Fabaceae)
				<i>Floria</i> Löw	P	<i>Genista</i> , <i>Retama</i> , <i>Cytisus</i> , <i>Ulex</i> , <i>Laburnum</i> (Fabaceae)
				<i>Livilla</i> Curt.	P	<i>Ulex</i> , <i>Genista</i> (Fabaceae)
				<i>Arytainilla</i> Log.	P	<i>Cytisus</i> , <i>Genista</i> (Fabaceae)
				<i>Cyamophila</i> Log.	P	<i>Caranga</i> , <i>Glycyrrhiza</i> , <i>Astragalus</i> (Fabaceae)
				<i>Acizzia</i> H.H.	P, E, O, A	<i>Acacia</i> , <i>Albizia</i> (Mimosaceae)
				* <i>Pseudacanthopsylla</i> Samy	P	<i>Retama</i> (Fabaceae)
				<i>Euglyptoneura</i> H-H	N	<i>Ceanothus</i> (Rhamnaceae)
				<i>Purshivora</i> H-H	N	<i>Purshia</i> (Rosaceae)
				<i>Amorpha</i> H-H	N	<i>Amorpha</i> (Fabaceae)
				<i>Ceanothia</i> H-H	N	<i>Ceanothus</i> (Rhamnaceae)
				* <i>Pexopsylla</i> Jensen	N	<i>Cercocarpus</i> (Rosaceae)

SUPER-FAMILY PSYLLOIDEA Burm. (cont.)

Family	Subfamily	Tribe	Genus	Distribution	Host plants	
CARSIDARIDAE	Psyllinae Löw	Euphalerini B.M.	<i>Euphalerus</i> Schwarz	P, N, O, A, E NO, PN	In nearctic <i>Piscidia</i> (Fabaceae) In palaearctic <i>Gleditsia</i> & <i>Caesalpina</i> (Caesalpinaceae) <i>Gleditsia</i> (Caesalpinaceae)	
			<i>Metapsylla</i> Kuw.	P		
		Psyllopsiini B.M.	<i>Psyllopsis</i> Löw	P	<i>Fraxinus</i> (Oleaceae)	
		Pachypsyllini B.M.	<i>Pachypsylla</i> Riley	N, P, O	<i>Celtis</i> (Ulmaceae)	
			* <i>Tetragonocephala</i> Crawf.	N	?	
		Psyllini B.M.	<i>Psylla</i> Geoff.	P, N, O	<i>Alnus</i> , <i>Betula</i> (Betulaceae)	
			<i>Cacopsylla</i> Oss. (sensu Klimaszewski, 1975)	P, N, O	Many families incl. Rosaceae, Rhamnaceae, Salicaceae, etc.	
			* <i>Spanioneura</i> Först.	P, O	<i>Buxus</i> (Buxaceae)	
		Homotomini B.M.	Homotomini H.H.	<i>Homotoma</i> Guerin	P, O, A	<i>Ficus</i> (Moraceae)
		Pauropsyllinae Crawf.	Pauropsyllini Vond.	<i>Pauropsylla</i> Rubs.	P, E, O, E	<i>Ficus</i> (Moraceae)
				* <i>Togepsylla</i> Kuw.	P, O	<i>Litsea</i> (Lauraceae)
			Calophyini Log.	<i>Calophya</i> Löw	P, A, O, N, NO	<i>Rhus</i> (Anacardiaceae)
TRIOZIDAE	Triozinae Löw	Triozini B.M.	<i>Egeitrioza</i> Bos.	P, O	<i>Populus</i> (Salicaceae)	
			<i>Trioza</i> Först. sensu lato	P, N, etc.	Several plant families, esp. Asteraceae, Salicaceae, etc.	
			<i>Paratrioza</i> Crawf.	P, N	<i>Lycium</i> , <i>Lavatera</i> , <i>Solanum</i> (Solanaceae, Malvaceae)	
			<i>Eryngiofaga</i> Klim.	P	<i>Eryngium</i> (Apiaceae)	
			<i>Epitrioza</i> Kuw.	P	<i>Eleagnus</i> (Eleagnaceae)	
			<i>Kuwayama</i> Crawf.	N, NO, O, PN	<i>Lavatera</i> (Malvaceae) & Asteraceae	
			<i>Ceropsylla</i> Riley	N, NO, A, O	<i>Sideroxylon</i> , <i>Olmediella</i> , <i>Ocotea</i> , <i>Persea</i> (Sapotaceae, Lauraceae)	
				* <i>Hemitrioza</i> Crawf.	N	<i>Sonchus</i> (Asteraceae)
		Eutriozi B.M.	<i>Eutrioza</i> Log.	P	<i>Pinus</i> ?	
			<i>Trichohermes</i> Kirk.	P, O, E	<i>Rhamnus</i> , <i>Frangula</i> (Rhamnaceae)	
			Bactericerini H.H.	<i>Bactericera</i> Put.	P	<i>Artemisia</i> (Asteraceae)
Trioziid/Carsidarid genera not placed in tribes						
		* <i>Engytatoneura</i> Log.	P	?		
		<i>Rhinopsylla</i> Riley	N, NO, O	<i>Persicaria</i> (Polygonaceae)		
		<i>Leuronota</i> Crawf.	N, NO, O, PN	<i>Celtis</i> (Ulmaceae)		
		* <i>Levidea</i> Tut.	N	<i>Parthenium</i> (Asteraceae)		
		* <i>Metatrioza</i> Tut.	N, NO	?		
		<i>Neotriozella</i> Crawf.	N, A	?		

APPENDIX 2. Basic distribution matrix of the holarctic psyllid genera across the eighteen recognized floral kingdoms

	Palaearctic tundra	W. palaearctic confif. forest	E. palaearctic confif. forest	W. palaearctic decid. forest	E. palaearctic mixed forest	Mediterranean	Macronesian	Palaearctic steppe/desert	Nearctic tundra	Greenland	Nearctic confif. forest	Nearctic E. decid. forest	Nearctic mountains	Nearctic Pacific rainforest	Nearctic prairies	Nearctic desert	Nearctic California	Nearctic S.E. subtropical
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Acaerus	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Acizzia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Alloeoneura	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Alloeneura	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amblyrhina	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amorpicola	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0
Anomoneura	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphalara	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1
Aphalaroida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Aphorma	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Arytaina	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Arytainilla	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Astragilita	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bactericera	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Brachystetha	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cacopsylla	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Caillardia	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Calophya	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0
Camarotoscena	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Ceanothia	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Ceropsylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Colposcenia	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Craspedolepta	0	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0
Crastina	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cyamophila	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Diaphorina	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Egeirotriaza	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Engytatoneura	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Epheloscyta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Epitrioza	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Eremopsylloides	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eryingiofaga	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Euglyptoneura	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
Eumetoecus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Euphalerus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1
Euphyllura	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Eutroica	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eutrioza	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Floria	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Gyropsylla	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Hemitrioza	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Heteropsylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Homotoma	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Katecephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Kuwayama	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Leurolophus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Leuronota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1

APPENDIX 2.

	Palaeartic tundra	W. palaeartic conif. forest	E. palaeartic conif. forest	W. palaeartic decid. forest	E. palaeartic mixed forest	Mediterranean	Macronesian	Palaeartic steppe/desert	Nearctic tundra	Greenland	Nearctic conif. forest	Nearctic E. decid. forest	Nearctic mountains	Nearctic Pacific rainforest	Nearctic prairies	Nearctic desert	Nearctic California	Nearctic S.E. subtropical
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Levidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ligustrinia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Lisronia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Livia	0	1	0	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1
Livilla	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Megadicrania	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Metapsylla	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Metatrioza	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Neophyllura	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Neotriozaella	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0
Pachypsylla	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	0	0
Pachypsylloides	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Paraphalaroida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Paratrioza	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0
Paurocephala	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pauropsylla	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pexopsylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pseudacanthopsylla	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Psylla	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0
Psyllopsis	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Purshivora	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0
Rhinocola	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhinopsylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Rhodoclanis	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Rhombaphalara	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Spanioneura	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Strophingia	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Syntomoza	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Syringilla	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetragonocephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Togepssylla	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichohermes	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Triozia	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Xanioptera	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Xenaphalara	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Total	4	8	5	24	20	36	12	32	4	2	8	12	14	10	17	18	16	10

Corrigendum

Hodkinson, I.D. (1980) Present-day distribution patterns of the holarctic Psylloidea (Homoptera: Insecta) with particular reference to the origin of the nearctic fauna. *J. Biogeogr.* 7, 127–146.

The printers and publishers regret that a correction line was misplaced: in Appendix 2 (page 145) the third and fourth entries should read 'Agonoscena' and 'Alloeoneura'.