Tracking the elusive: leafhoppers and planthoppers (Insecta: Hemiptera) in tree canopies of European deciduous forests

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Abstract

This paper provides a brief review of the taxonomic situation, guild composition, life cycles, biogeography (with special reference to alien species), potential ecosystem functions and some evolutionary aspects of arboreal leafhoppers and planthoppers of the European deciduous forest zone. At least 191 species, accounting for nearly one quarter of the central European fauna of leafhoppers and planthoppers, are permanently arboreal. Further, 68 species perform an obligatory vertical migration into tree tops, where maturation feeding takes place. Taxonomically, the central European canopy fauna of Auchenorrhyncha is very well known, in comparison with other regions of the world. Although some nomenclatural problems persist, the numbers of newly described species have been decreasing steadily since the mid 1950s. Generally, patterns of Auchenorrhyncha species richness on trees are congruent with patterns of overall diversity of herbivorous arthropods. Abundant, tall-growing and widespread species are more strongly preferred, whereas fruit trees, conifers, and, interestingly, *Fagus* and *Fraxinus*, two of the most common forest trees, are utilised by proportionately fewer species. Life histories are affected greatly by autumnal leaf fall and the lack of resources and shelter during the cold season. Significant strategies to cope with these adversities include overwintering as an egg in the host tissue, overwintering as a nymph in the soil, and overwintering as an adult on adjacent evergreen plants. Endemism is common among European canopy Auchenorrhyncha. In almost half of the species, geographic ranges are more or less congruent with those of typical deciduous trees. This pattern stresses the role of this region for the evolution and diversification of forest biota. Almost all alien Auchenorrhyncha species are arboreal, and it is probable that transport of eggs in host plants is an important factor for their spread. Currently, there are nine species known to be introduced six of them originating from eastern North America, two from eastern Asia, and one from central Asia. In this group, leafhoppers (Cicadomorpha) and, in particular, Typhlocybinae appear to be over-represented. Moreover, polyphagy and egg overwintering are more common than in native faunas. Conversely, alien ornamental plants are utilised only rarely by native leafhoppers and, among the few known cases, host generalists clearly dominate. Given the central position of Auchenorrhyncha in many food webs, their high densities and the variety of direct and indirect interactions, including honeydew production, faecal staining, transmission of pathogens and the consumption of large quantities of plant sap and biomass, they may have a significant impact on crucial ecosystem functions. Finally, evolutionary implications of Auchenorrhyncha biology, notably of vertical migration, shifts between vegetational layers and permanent arboreal life, are discussed briefly within the context of the Caenozoic rise of angiosperm plants.

Zusammenfassung

Diese Arbeit bietet einen kurzen Überblick über die taxonomische Erforschung, Gildenzusammensetzung, Lebenszyklen, Biogeographie (unter besonderer Berücksichtigung fremdländischer Arten), Ökosystem-Funktionen und Aspekte der Evolution baumbewohnender Zikaden der europäischen Laubwälder. Mindestens 191 Arten, die fast ein Viertel der Gesamtfauna mitteleuropäischer Zikaden ausmachen, leben permanent im Kronenraum. Weitere 68 Arten vollführen eine obligate Vertikalwanderung in den Kronenbereich, wo auch der Reifefraß stattfindet. Taxonomisch ist die mitteleuropäische Zikadenfauna der Kronenschicht im Vergleich mit anderen Regionen der Welt sehr gut bekannt. Obwohl noch eine Reihe von nomenklaturischen Problemen besteht, ist die Anzahl der Neubeschreibungen seit den 1950er Jahren kontinuierlich zurückgegangen. Insgesamt sind die Verteilungmuster der Zikadendiversität auf Baumarten mehr oder weniger deckungsgleich mit denjenigen der Gesamtdiversität phytophager Arthropoden. Häufige, weitverbreitete und großwüchsige Arten werden stärker bevorzugt, wohingegen Obstbäume, Koniferen und -interessanterweise- *Fagus* und *Fraxinus,* zwei der wichtigsten Waldbaumarten, nur von relativ wenigen Arten genutzt werden. Die Lebensgeschichte der einzelnen Arten wird stark geprägt durch den herbstlichen Laubfall und das Fehlen von Ressourcen und Unterschlupfmöglichkeiten während der kalten Jahreszeit. Die wichtigsten Strategien dagegen sind Überwinterung im Eistadium im Gewebe der Wirtspflanze, Überwinterung als Larve im Boden und Überwinterung im Adultstadium auf immergrünen Pflanzen in der Nähe des Sommerwirtes. Bei nahezu der Hälfte der baumbesiedelnden Zikadenarten sind die Verbreitungsgebiete mehr oder weniger deckungsgleich mit denjenigen der europäischen Hauptbaumarten, und viele Arten sind in diesem geographischen Raum endemisch. Diese Verteilungsmuster deuten darauf hin, dass Europa von großer Bedeutung für die Evolution und Diversifizierung der Waldflora und -fauna ist. Nahezu alle gebietsfremden Zikadenarten sind Baum- oder Strauchbesiedler, und die Verschleppung von Eiern mit den Wirtspflanzen spielt wahrscheinlich eine große Rolle. Derzeit sind neun eingeschleppte Arten bekannt, sechs davon stammen aus dem östlichen Nordamerika, zwei aus Ostasien und eine aus Mittelasien. In dieser Gruppe sind die Cicadomorpha und besonders die Typhlocybinae offenbar überrepräsentiert. Hinsichtlich ihrer Lebensstrategien sind Polyphage und Eiüberwinterer stärker vertreten als in der einheimischen Fauna. Umgekehrt werden eingeführte Pflanzen kaum von einheimischen Zikadenarten besiedelt, und unter den wenigen bekannten Fällen dominieren die Generalisten. Angesichts der zentralen Position in vielen Nahrungsnetzen, ihren oft hohen Siedlungsdichten und der Vielfalt von direkten und indirekten Interaktionen, u.a. der Produktion großer Mengen von Honigtau und Exkrementen, Übertragung von Pflanzenkrankheiten sowie durch die Konsumption großer Mengen von Pflanzensaft und Biomasse können die Zikaden wichtige Ökosystemfunktionen beeinflussen. Schließlich lässt ihre Biologie, insbesondere die Vertikalwanderungen, der Wechsel in der Nutzung verschiedener Vegetationsschichten innerhalb nahverwandter Arten sowie die vollständige Anpassung einiger Gruppen an das Leben im Kronenbereich, Rückschlüsse auf die Evolution von Insekt-Pflanze-Interaktionen zu, die vor dem Hintergrund des Aufstieges der Angiospermen im Laufe des Känozoikums diskutiert werden.

Introduction

Tree canopies play a crucial role for the global atmospheric environment and they support a considerable proportion of the world's biodiversity. Although ecological research is still constrained by physical adversities, it is moving from a purely descriptive to a more integrated approach (Lowman and Wittman 1996, Godfray et al. 1999, Basset 2003). Within arthropods, the stunning morphological and ecological diversity of beetles and ants has attracted many researchers, whereas most other groups have remained in their shadow (see Stork et al. 1997). The hemipteran subgroup of Auchenorrhyncha, the leafhoppers (Cicadomorpha) and planthoppers (Fulgoromorpha) in particular, has received little attention due to their complicated taxonomy. Only a minute proportion of the extensive material collected during most arboreal sampling programmes has been analysed in more detail. Therefore, even in temperate latitudes, community structure and functional relationships in this group are only inadequately known. However, Hemiptera are among the dominant groups in terms of both individual numbers and biomass on deciduous trees (Moran and Southwood 1982, Southwood et al. 1982) and along with some groups of Hymenoptera, e.g. some gall-forming Cynipidae or Symphyta, they are among the few arthropod taxa that have evolved permanently arboreal habits. The Auchenorrhyncha, in particular, occur in large numbers of species and individuals on many trees and shrubs (Claridge and Wilson 1976, 1981, Vidano and Arzone 1987a, 1987b, Kula 2002, Löcker 2003, Nickel et al. 2002, Nickel 2003). In contrast, most remaining insect groups are bound to water, the soil or herbaceous vegetation, at least during certain developmental stages, particularly in temperate forests, where leaf biomass is lacking for a considerable period of the year. Thus, shortage of food, water supply and shelter during the cold season may pose major constraints for a permanent life on trees.

Interactions of Auchenorrhyncha with other ecosystem components include competition, transmission of plant pathogens, and faecal staining which feeds other insects, pollutes plant surfaces for other arthropods, and promotes microbial and fungal growth. However, the quantification of feeding is a difficult task, since food intake of phloem and xylem feeders must exceed their own body weight by two or three orders of magnitude in order to compensate the dramatic nutritional imbalance of this food type and, hence, the removal of resources may be considerable.

Whereas Nickel (2003) described and discussed the utilisation of plant resources in the German Auchenorrhyncha fauna, emphasising host specificity, life cycles, and dispersal, the present paper focuses on arboreal species and discusses further aspects of stratification and guild composition, with consideration of the taxonomic situation, comparison of guilds on tree genus and species level, as well as life cycles and biogeography. Further, the potential impact of these insects on ecosystem functioning shall be discussed, as well as some evolutionary aspects of arboreal life.

Data base and methods

This study is mainly based on substantial material collected during the past 15 years in more than 1000 localities of central Europe (Germany, Austria, Switzerland, Czech Republic, Luxembourg) with more than 5000 records on identified host plant species. Available literature records were analysed and checked, since many published host records include the plant genus alone, for example in *Ulmus* (Ulmaceae) and *Quercus* (Fagaceae), or may refer to single vagrant individuals (tourists), or may be based on misidentifications of plants or insects (see Ward 1988). Therefore, almost all published host associations which could not be verified through the present author’s data sets were eliminated from the data matrix. Unlike most other canopy studies, this paper is based, almost exclusively, on sweep-net samples taken from low branches near the ground. A few trees have been sampled by tree trunk eclectors [only *Quercus robur*, *Fagus sylvatica* (Fagaceae), *Betula pendula* (Betulaceae), *Populus tremula* (Salicaceae)] and canopy flight interception traps [*Abies alba*, *Picea abies* (both Pinaceae), *Q. robur*]. The taxonomy of Auchenorrhyncha follows Holzinger et al. (2003) and Nickel and Remane (2002), plant systematics follow The Angiosperm Phylogeny Group (2003) and Stevens (2001) and plant taxonomy follows Wisskirchen and Haeupler (1998). Ecological data on plants were taken from Haeupler and Muer (2000) and Oberdorfer (2001).

Results and discussion

State of taxonomic research

In comparison with tropical faunas, the arboreal Auchenorrhyncha of central Europe can be considered as taxonomically very well known. Fig. 1 shows a cumulative curve of valid descriptions of species known from Germany. Despite sonographic techniques that have been applied during recent decades (e.g. Claridge and Reynolds 1973, Tishechkin 2002a, 2002b, Gogala and Trilar 2004), the curve shows a roughly sigmoid shape, indicating an asymptotic approach to a total number of no more than 230. However, molecular techniques may provide further potential, particularly in the genera *Edwardsiana* and *Kybos* (both Cicadellidae: Typhlocybinae).

Altogether, these techniques may produce powerful explanations concerning the mechanisms of isolation and speciation, and may resolve some critical species groups, but they are unlikely to promote description of many, hitherto unknown, species. In fact, it appears that there remain only very few undescribed species in Europe, except Mediterranean countries. During the past 20 years of the last century, only six arboreal species were described from north of the Alps, and all of these were present in older collections, although unrecognised or misidentified. Surprisingly, many of these species were distinguished not by their genital morphology, but by characters of coloration, i.e. by characters commonly used by taxonomists of the 18th and 19th century. Since the turn of the millennium, the only new species name is *Acericerus ribauti* Nickel and Remane, 2002, and even this was recognised many years earlier by Ribaut (1952), although assigned to an invalid original description of Kirschbaum (1868). At present, the number of unrecognised and undescribed arboreal species in central Europe can be estimated to no more than ten or 20. Finally, it should be stressed that taxonomists' knowledge of species or forms is not always in accord with nomenclatural clarity. After all, such uncertainties concerning the correctness of names remain in more than 10% of the species (see Nickel and Remane 2002, Nickel 2003). To conclude, the ample taxonomic information from this insect group in temperate latitudes stands in sharp contrast with the poor knowledge of their position and significance in terrestrial food webs and the role they play in ecosystem processes.

Species inventory and stratification

In deciduous forests, permanently arboreal Auchenorrhyncha are found exclusively

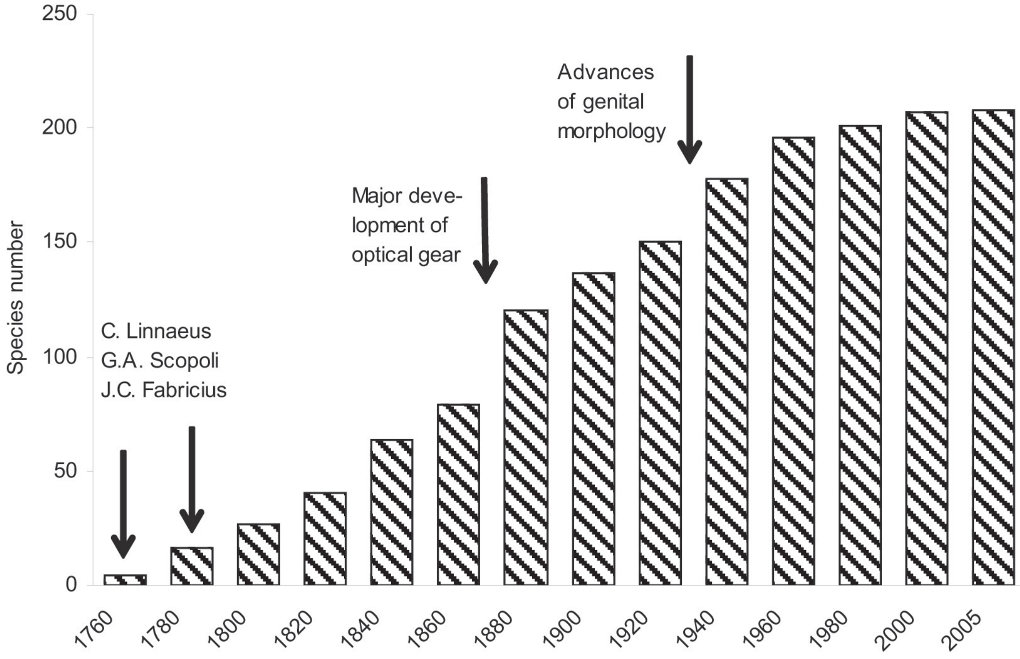

Fig. 1: Cumulated numbers of currently valid species descriptions of arboreal Auchenorrhyncha in the German fauna since Linnaeus (1758) and other early workers.

in cicadomorphans, particularly in Macropsinae, Idiocerinae, Typhlocybinae, Ledrinae, as well as in some subgroups of Aphrophoridae, Agalliinae, Iassinae and Deltocephalinae. Some species of Cercopidae and Deltocephalinae perform a vertical migration, and ascend to the canopy layer only in the adult stage after emergence or for hibernation. Such movements are also found in some fulgoromorphan groups, notably in most Cixiidae, Issidae and Achilidae. At least some species of Tettigometridae frequently migrate up to trees and shrubs, but this movement is probably not obligatory. Thus, the overall tendency towards arboreal habits is clearly more pronounced in Cicadomorpha.

Although forests are the dominant type of vegetation in central Europe, the proportion of arboreal Auchenorrhyncha is relatively small (Fig. 2). There are only 310 out of 801 species (accounting for almost 39% of the total species number), which live at least temporarily or locally on trees or shrubs. Among these, eight species are introduced, 14 species are either taxonomically uncertain or their European records are dubious. A further 29 species are not obligatorily arboreal, but ascend only occasionally or locally onto woody plants. These are defined here as multi-layer species that include, for example, the highly polyphagous *Philaenus spumarius* (Linnaeus, 1758), *Lepyronia coleoptrata* (Linnaeus, 1758), *Empoasca decipiens* Paoli, 1939, *Cercopis* spp., some oligophagous feeders of Fabaceae that feed both on the shrub *Cytisus scoparius* and creeping dwarf shrubs, such as *Genista* spp. or *Ononis* spp., as well as some largely epigaeic species seeking moisture and cooler temperatures on lower branches during hot summer days, e.g. *Neophilaenus campestris* (Fallén, 1805) and probably most tettigometrids (Nickel 2003, and unpublished data, see Appendix).

Therefore, only 259 native species, accounting for one third of the total species number, can be classified as truly arboreal, i.e. living obligatorily and at least temporarily on trees or shrubs. The following analysis will be based on this group only, which comprises 191 permanently arboreal species and 68 vertical migrants.

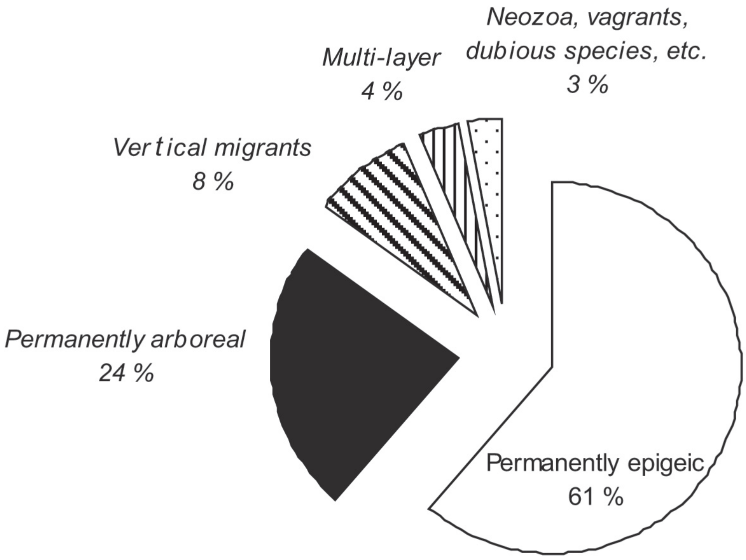

Fig. 2: Stratification of leafhopper and planthopper species in Central Europe, based on the faunas of Austria, the Baltic and Benelux countries, Belarus, Britain, the Czech Republic, Denmark, Germany, Ireland, Poland, Switzerland. Distribution data taken from Nast (1987), and literature thereafter. All names of groups utilising trees or shrubs at least temporarily are written in italics. S = 801.

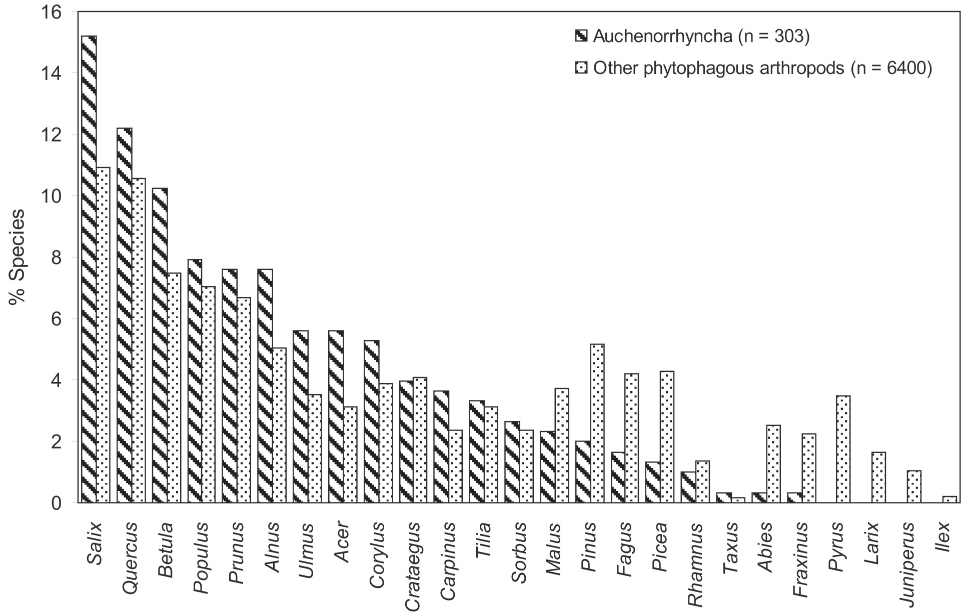

Fig. 3: Species richness of Auchenorrhyncha in comparison with other phytophagous arthropods on German trees and shrubs. Data of other phytophages taken from Brändle and Brandl (2001). Note that n ≠ S, since polyphages are counted in several bars.

Diversity and composition of guilds on main trees and shrubs

Generally, on German trees at generic level, patterns of species richness of Auchenorrhyncha are roughly congruent with patterns of overall diversity of phytophagous arthropods (Fig. 3, data of other groups taken from Brändle and Brandl 2001). For example, *Salix*, *Quercus*, *Betula*, *Populus*, *Prunus* (Rosaceae) and *Alnus* (Betulaceae), in the same order, have the greatest numbers of species, both of Auchenorrhyncha and other phytophagous arthropods, indicating that host selection mechanisms in sap-feeders principally do not differ from other feeding guilds. Remarkable incongruencies, with relatively species-poor guilds of Auchenorrhyncha, are found in all genera of conifers [*Abies*, *Larix*, *Picea*, *Pinus* (all Pinaceae), including *Juniperus* (Cupressaceae)], some fruit trees [*Malus*, *Pyrus* (both Rosaceae)] and two main forest trees [*Fagus* (Fagaceae), *Fraxinus* (Oleaceae)]. Conversely, almost all remaining forest trees, including *Salix*, are utilised proportionately more by Auchenorrhyncha than by other arthropods.

At host species level, species richness and composition of Auchenorrhyncha guilds were uneven and highly plant-specific. In the following section, the most prominent patterns found in Auchenorrhyncha will be identified (Fig. 4, see also Nickel 2003), and some *ad hoc* explanations will be discussed in brief. A more detailed analysis will be published elsewhere.

(i) Most abundant, widespread and/or tall-growing trees have species-rich Auchenorrhyncha guilds, for example *Quercus robur*, *Q. petraea*, *Betula pendula*, *Alnus glutinosa*, *Ulmus* spp. and *Acer pseudoplatanus* (Aceraceae). In comparison with other herbivorous arthropods (Fig. 3), this tendency appears to be even more pronounced in Auchenorrhyncha. Conversely, less apparent plants, which are small, less dominant, rare and/or geographically restricted are not attacked or only attacked by very few species, many of

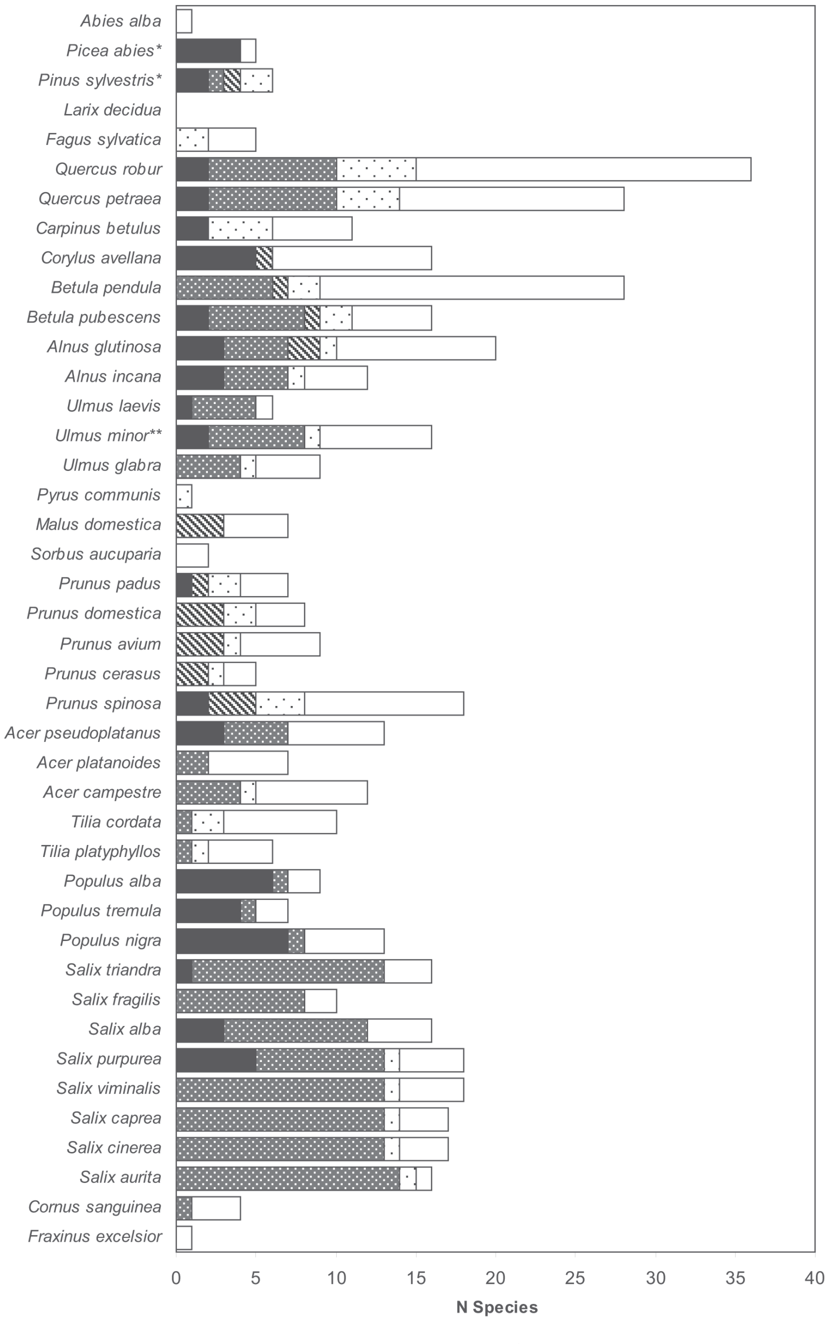

Fig. 4: Auchenorrhyncha guilds on important trees and shrubs in Germany. Black = monophagous 1st degree (feeding on one plant species), cross-hatched = monophagous 2nd degree (on one plant genus), hatched = oligophagous 1st degree (on one plant family), dotted white = oligophagous 2nd degree (on no more than 2 plant families or 4 plant species of no more than 4 families), white = polyphagous. * = except overwintering species. ** *U. minor* was not distinguished in the field from hybrid *U. x hollandica*.

which are host generalists. Examples include *Acer monspessulanum*, *Amelanchier ovalis, Cotoneaster integerrimus, Prunus mahaleb* (all three Rosaceae), *Buxus sempervirens* (Buxaceae), *Berberis vulgaris* (Berberidaceae), *Daphne mezereum* (Thymelaeaceae), *Hippophae rhamnoides* (Elaeagnaceae), *Ilex aquifolium* (Aquifoliaceae), *Lonicera* spp., *Sambucus* spp., (both Caprifoliaceae), *Myrica gale* (Myricaceae), *Myricaria germanica* (Tamaricaceae), *Rhamnus* spp. (Rhamnaceae), *Ribes* spp. (Grossulariaceae), *Staphylea pinnata* (Staphyleaceae) and *Taxus baccata* (Taxaceae). *Fagus sylvatica* and *Fraxinus excelsior* are both enigmatic, being attacked by only few and unspecialised species, despite their large size, wide distribution and abundance all over central Europe (Nickel 2003).

(ii) Species-rich plant taxa tend to be attacked by more insect herbivores (in total as well as per plant species) than species-poor taxa, indicating that host diversity favours herbivore diversity. This is particularly evident in Salicaceae and Rosaceae, which contain the highest numbers of woody species in central Europe (approximately 30 and 60 spp., respectively). In contrast, species-poor plant taxa tend to have only species-poor insect guilds or to be not attacked at all, e.g. Aquifoliaceae (only *Ilex aquifolium*), Berberidaceae (native only *Berberis vulgaris*), Buxaceae (only *Buxus sempervirens*), Elaeagnaceae (native only

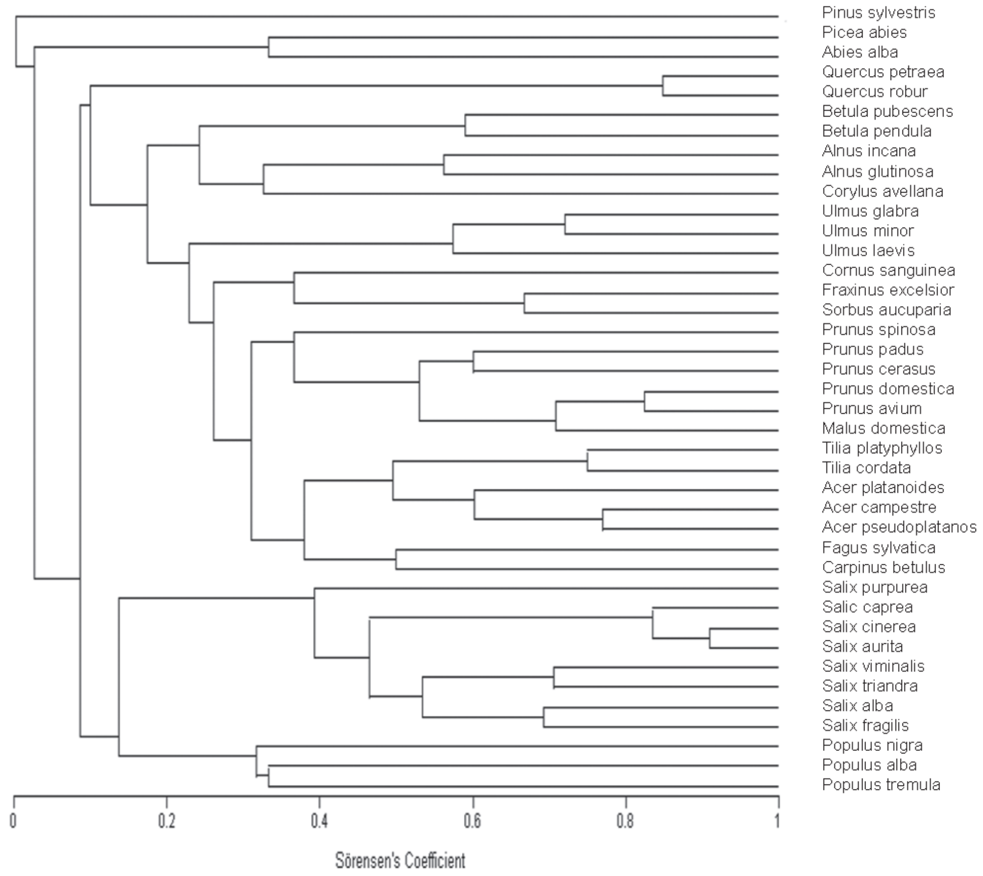

Fig. 5: Similarities of Auchenorrhyncha guilds on main tree species of the European deciduous forest zone (Sørensen's index).

Hippophae rhamnoides), Myricaceae (only *Myrica gale*), Oleaceae (native only *Fraxinus excelsior* and *Ligustrum vulgare*), Staphyleaceae (only *Staphylea pinnata*), Tamaricaceae (native only *Myricaria germanica*), Taxaceae (only *Taxus baccata*) and Tiliaceae (2 native species in central Europe).

(iii) Absolute and in comparison with total herbivore numbers (Fig. 3), evergreens have only species-poor feeding guilds. This is true for conifers (e.g. *Abies*, *Picea*, *Pinus*, *Taxus*) as well as broad-leaved species [e.g. *Buxus*, *Ilex*, *Hedera* (Araliaceae), *Ligustrum*]. It should also be noted that some conifers, particularly *Picea* and *Pinus*, provide winter hosts for some typhlocybid and idiocerine leafhoppers, which otherwise reproduce on deciduous trees.

(iv) Mountain species have less diverse insect guilds than their lowland congeners [e.g. *Pinus cembra* and *P. mugo* vs. *P. sylvestris*, *Alnus alnobetula* (= *viridis*) vs. *A. incana* vs. *A. glutinosa*, alpine and subalpine *Salix* spp. vs. lowland *Salix* spp.].

(v) Within plant families, woody species are clearly more favoured than herbs, although there are only two important families in the central European flora that comprise both phanerophytes and herbs, namely Rosaceae and Fabaceae.

(vi) Leaf properties, such as shape and hairiness, did not appear to provide a further clue for the understanding of leafhopper-host relationships. There may be trend of compound (in particular pinnate and palmate) leaves having fewer Auchenorrhyncha compared to simple leaves. For instance, *Fraxinus, Staphylea, Sambucus, Juglans, Acer negundo* and *Aesculus* are all very poor in leafhoppers, and even poorer in monophagous leafhoppers. But in all examples listed here, there may be alternative and perhaps more powerful explanations (see above).

Several of the factors listed above are interrelated, for example tree abundance and range size (Kelly and Southwood 1999). Further, the genus *Salix* is rich in plant species, all of which are deciduous, and within the genus all widespread, abundant, and tall-growing lowland species were attacked by diverse leafhopper guilds (Fig. 4). In contrast, fewest leafhoppers were found on geographically restricted, rare and low-growing mountain species such as *Salix bicolor*, *S. glabra*, *S. hastata*. Also, most other woody plants found to be largely devoid of leafhoppers are all rare, geographically restricted, small, evergreen, and/or belong to species-poor families, for example *Buxus sempervirens*, *Ilex aquifolium* and *Taxus baccata*. A more detailed analysis is necessary to ascertain the relative importance of each of these factors. For example, Brändle and Brandl (2001) found that species richness of phytophagous arthropods on tree

Tab. 1: Overwintering strategies of arboreal Auchenorrhyncha in European deciduous forests. Roman numbers in brackets refer to the text.

type of migration	overwintering site	overwintering stage		
		egg	nymph	adult
none	host	*Aphrophora* spp., Macropsinae, many Idiocerinae, many Typhlocybinae (i)	*Ledra aurita*, *Pithyotettix abietinus*, *Colobotettix morbillosus*, *Perotettix pictus* (ii)	*Acericerus* spp., *Stenidiocerus poecilus*, *Metidiocerus* spp., *Liguropia juniperi* (iii)
horizontal	host	*Ficocyba ficaria*, *Edwardsiana rosae*, *Lindbergina aurovittata*, *Zygina rhamni*, *Z. Discolor* (iv)	-	-
horizontal	non-host	-	-	*Zygina* spp., *Empoasca vitis*, *Linnavuoriana*?, *Zyginella pulchra*?, few Idiocerinae (v)
vertical	herb layer*	*Aphrophora* spp., *Platymetopius* spp., *Lamprotettix nitidulus*, *Allygus* spp., *Allygidius* spp., *Hesium domino* (vi)	*Issus* spp., *Colladonus torneellus*, *Speudotettix subfusculus*, *Thamnotettix* spp. (vii)	-
vertical	soil	-	Cixiidae, Cicadoidea, Cercopidae (viii)	-

* = including creeping and low-growing shrubs

Tab. 2: Overwintering strategies of arboreal Auchenorrhyncha species in Germany (after data from Nickel 2003, only native obligate arboreal species considered)

strategy type (see Tab. 1)	total		Fulgoromorpha		Cicadomorpha	
	S	%	S	%	S	%
(i) overwintering as egg on host	126	60,5	0	0	126	67,4
(ii) overwintering as nymph on host	5	2,4	0	0	5	2,7
(iii) overwintering as adult on host	9	4,3	0	0	9	4,8
(iv) overwintering as egg, migration between winter and summer host	2	1,0	0	0	2	1,1
(v) overwintering as adult on non-host	25	12,0	0	0	25	13,4
(vi) overwintering as egg in herb layer, migration of adults into canopy	12	5,8	0	0	12	6,4
(vii) overwintering as nymph in herb layer, migration of adults into canopy	8	3,8	4	19,0	4	2,1
(viii) overwintering as nymph in soil, migration of adults into canopy	21	10,1	17	81,0	4	2,1
Total	208	100	21	100	187	100

genera was most strongly correlated with grid occupancy of trees (used as a surrogate for abundance), and less so with tree height and pollen abundance in Holocene deposits (as a surrogate for tree abundance before major human interference).

A taxonomic comparison of guilds on different plant taxa suggests that insect and host radiation are only partially congruent at a low taxonomic level, and that host shifts must be common. For example, most species of Idiocerinae and *Macropsis* feed on Salicaceae, and the genus *Oncopsis* is confined to Betulaceae. However, there are also numerous cases of genera which comprise ecologically distinct species groups feeding on different plant families. For example, the members of the typhlocybid genus *Ribautiana* have specialised on certain species of Fagaceae, Rosaceae and Ulmaceae, respectively. Members of the closely related genus *Edwardsiana*, all of which strongly resemble each other morphologically and can be distinguished only by their internal genital morphology, are found on numerous trees and shrubs across most plant groups, e.g. Betulaceae, Ulmaceae, Rosaceae, Aceraceae, Salicaceae and Cornaceae. A few species of the typhlocybid genera *Arboridia* and *Zygina* have even left the canopy layer and colonised taxonomically distant herbaceous plants such as *Geranium* (Geraniaceae), *Hypericum* (Clusiaceae) and *Potentilla* (Rosaceae), some of which are well known for their toxic secondary compounds.

Nevertheless, a cluster analysis (similarity after Sørensen) showed that closely related trees, generally, have similar phytophage guilds, even based on simple occurrence of species and without weighting host specialisation (Fig. 5). This was particularly evident in *Quercus*, *Betula*, *Alnus*, *Ulmus*, *Tilia*, *Acer*, *Salix* and *Populus*. The only exceptions could be found in the pairing of *Fagus sylvatica*/*Carpinus betulus* and *Fraxinus excelsior*/*Sorbus aucuparia*. However, these pairings were caused by the shared occurrence of a few polyphagous species, and their similarity values are relatively low. Conversely, in the genus *Salix*, similarities are high within broad-leaved (*S. caprea*, *S. cinerea*, *S. aurita*) and some narrow-leaved species (*S. viminalis*, *S. triandra*, *S. alba*, *S. fragilis*), but low between these two groups, and between *S. purpurea* and all other species. As within *Populus* species, these low similarity values were caused by the high number of strictly monophagous feeders. It should be noted, however, that Sørensen's index does not consider the taxonomic relationship between the phytophage species.

Life cycles

Leaf fall in autumn exerts a severe constraint upon all canopy animals. In winter, assimilate content in the phloem sap is reduced almost to nil, and green leaves, as a food source for leaf chewers and parenchyma feeders, are entirely absent. In European deciduous forests, food resources are present, if at all, only on a few intermingled coniferous trees and a handful of broad-leaved evergreens such as *Hedera*, *Buxus* and *Ilex*, which, however, contain resins or toxic secondary compounds. Conversely, most conifers are naturally largely confined to mountains, and thus, absent from lowland regions of the nemoral forest zone. Broad-leaved evergreens, which dominate in Mediterranean climates, are only poor in species number and biomass to the north of the Alps, and they are almost devoid of leafhoppers.

Principally, poikilothermic animals and those which rely exclusively on them as a food source (e.g. insect-feeding birds) can either endure the unfavourable season in a dormant stage or migrate to places where conditions are less severe (Müller 1992). In insects, dormancy may occur in the egg, nymph or adult stage, and it may be consecutive (i.e. as a direct and immediate response to unfavourable environmental factors) or prospective (i.e. before conditions become severe, usually induced by an environmental signal) (Witsack 1988, 2002). Migration can cover long or only short distances; the latter is relatively common, although usually combined with some form of dormancy, whereas long-distance migration is rare in insects. Possible and realised combinations of overwintering strategies are shown in Tab. 1 and discussed below. Numbers of species utilising these strategies are given in Tab. 2.

(i) The most common strategy is overwintering in the host canopy as egg, usually in sheltered sites such as buds, under bark or in crevices. This strategy is found in all Macropsinae and about half of the Idiocerinae. Within Typhlocybinae, it is common or predominating in Alebrini, Empoascini (*Kybos* spp., *Kyboasca*) and Typhlocybini. Within Deltocephalinae it is found in *Fieberiella* spp., *Grypotes puncticollis* (Herrich-Schäffer, 1834), *Opsius stactogalus* Fieber, 1865, *Japananus hyalinus* Osborn, 1900, and *Sagatus punctifrons* (Fallén, 1826). Further, it occurs in the spittlebug genus *Aphrophora pectoralis* Matsumura, 1903 and *A. salicina* (Goeze, 1778), although some species of that genus do not oviposit in the canopy layer, but in herbaceous vegetation, dwarf shrubs or tree saplings, and therefore belong to type (vi).

In arboreal Auchenorrhyncha of central Europe, this is the only strategy which is commonly associated with bivoltinism, particularly in mesophyll-feeding Typhlocybinae (e.g. *Kybos*, *Fagocyba*, *Edwardsiana*, *Ribautiana*, *Alnetoidia*). Most, if not all, species of other groups have only a single annual generation, or their bivoltinism is not properly documented. It should also be noted that single individuals even in small and delicate species may be rather long-lived, e.g. in *Empoasca vitis* (Göthe, 1875), which usually emerges in July and is frequently found until next May, making phenological studies of annual generation numbers in the field a difficult task. For this species, systematic studies (Böll and Herrmann 2004) and numerous field records of freshly emerged adults (Nickel 2003) indicate a single generation per year even in warmer regions of southern Germany, although three generations have been reported to occur in Italy (Vidano et al. 1988, Bosco et al. 1996).

There is wide agreement that seasonal variation in the nitrogen content of food resources is of great importance for the control of insect life cycles (McNeill and Southwood 1978, Mattson 1980, White 1993). For example, aphids synchronise egg hatching in spring with bud burst, and egg laying in autumn with leaf fall, when the content of soluble amino acids in phloem sap is highest (Dixon 1998), although more recent studies also discuss other processes, such as increased pressure of natural enemies, leading to higher rates of emigration and mortality in summer (Karley et al. 2004). Similarly, the performance of many arboreal phloem-feeding auchenorrhynchan species discussed here also peaks in spring, usually with the first adults emerging until mid June (see Nickel 2003). However, unlike in aphids, which have very short-lived generations, maturation feeding and oviposition in many Auchenorrhyncha must persist until mid or late summer when phloem and xylem nitrogen content is low. A number of species, including some Idiocerinae, *Fieberiella* spp. and *Japananus hyalinus*, are even typical mid and late summer feeders with adults appearing not before mid July. Likewise, the univoltine typhlocybid leafhopper *Ossiannilssonola callosa* (Then, 1886) has its maximum density exactly between the two peaks of the aphid *Drepanosiphum platanoidis* (Schrank, 1801), i.e. when the content of soluble nitrogen is lowest (Whittaker et al. 1988), and the same should be expected in other univoltine mesophyll-feeders, e.g. *Alebra*, *Eupterycyba* and *Eurhadina.* According to White (1993) who classified herbivores into flush and senescent feeders, these species should be classified as the latter.

Therefore the constraint imposed by seasonality and the species' intrinsic flexibility to adapt its life cycle may be a greater force for the evolution of an insect's life strategy than variations in nitrogen availability, which may be countered by small-scale movements towards more nutritious plant parts or individuals.

(ii) Overwintering in the host canopy layer as a nymph is another, though relatively rare strategy. It is found only on evergreen trees, mostly conifers, which are, however, rare in the native vegetation of central European lowlands. The only gymnosperms native in this area are *Taxus baccata*, *Juniperus communis* and *Pinus sylvestris*, none of which is utilised by any Auchenorrhyncha species in winter, except by those which migrate there from other plants (see below). In contrast, the extrazonal *Picea abies* is the exclusive host of the deltocephaline leafhoppers *Pithyotettix abietinus* (Fallén, 1806), *Perotettix pictus* (Lethierry, 1880), and *Colobotettix morbillosus* (Melichar, 1896), all of which overwinter as nymphs. Finally, the polyphagous *Ledra aurita* (Linnaeus, 1758), one of the few corticolous leafhoppers in Europe, overwinters even twice as nymph on the bark of its hosts.

(iii) Overwintering in the host canopy as an adult is also relatively rare. As in the preceding group, species following this strategy must face the adverse conditions of winter weather and the lack of green biomass. The underlying mechanisms have not been studied. However, the fact that some of them are attracted by light in winter nights suggests that at least some species may perform a non-prospective dormancy (see Witsack 1988, 2002), allowing food uptake and perhaps other activities during warmer winter periods. Most of the few examples belong to the cicadellid subfamily Idiocerinae. Members of the genus *Acericerus* are recorded frequently in winter nights at light near host trees, and it is likely that these species, the coloration of which is reminiscent of bark, overwinter in crevices in the trunk or on branches, although their feeding biology during this period is unknown. A similar overwintering strategy may be assumed for other idiocerine species such as *Stenidiocerus poecilus* (Herrich-Schäffer, 1835), *Metidiocerus* spp., and *Idiocerus herrichii* (Kirschbaum, 1868) all of which breed on members of the Salicaceae, although winter host records are only few. A last example is the invasive Mediterranean typhlocybid *Liguropia juniperi* (Lethierry, 1876), which is restricted to *Chamaecyparis lawsoniana* (an evergreen Nearctic species) planted in gardens and cemeteries.

(iv) A few species show a heteroecious life cycle that involves development on a winter host, where eggs overwinter and give rise to a spring generation, and a shift to a summer host, where one or two summer generations develop. The explanation for such host shifts in leafhoppers must remain speculative. Unlike phloem-feeding aphids that, typically, show heteroecious life cycles, all leafhoppers involved belong to the subgroup of Typhlocybinae and are mesophyll-feeders. In some cases winter hosts are evergreen [e.g. *Rubus fruticosus* (Rosaceae) a winter host for *Lindbergina aurovittata* (Douglas, 1875) and *Zygina rhamni* Ferrari, 1882], but other species shift between deciduous hosts [e.g. *Ficocyba ficaria* (Horváth, 1897) on *Lonicera* spp. and *Ficus carica* (Moraceae) or *Zygina discolor* Horváth, 1897 and some populations of *Edwardsiana rosae* (Linnae-

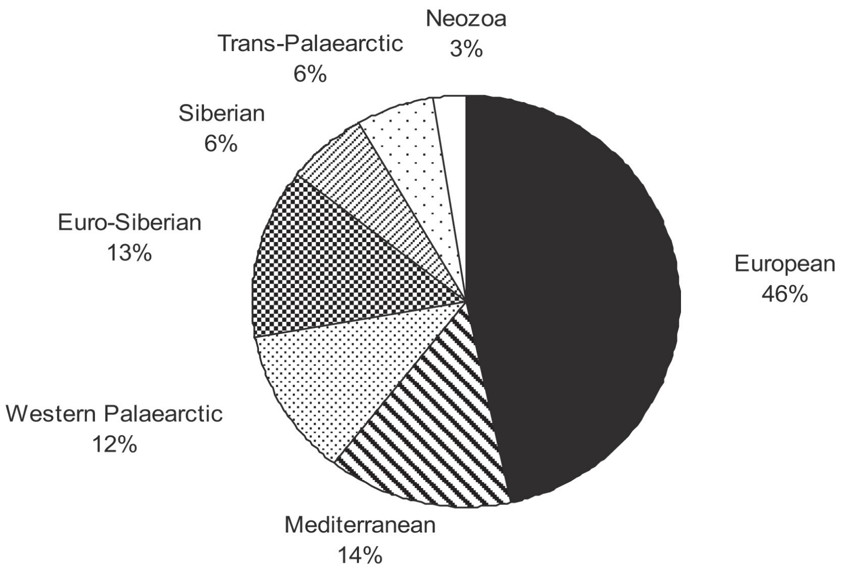

Fig. 6: Distribution of arboreal Auchenorrhyncha of the deciduous forest zone of Europe (Austria, Baltic states, Belarus, Benelux, Czech Republic, Denmark, Germany, Great Britain, Ireland, Poland, Switzerland; S = 310, see Table Appendix). Explanations see text. Category Siberian includes a few transboreal species. Ranges compiled after Nast (1972, 1987) and literature thereafter.

us, 1758) from *Rosa* spp. to other species of Rosaceae] (Claridge and Wilson 1978; Mazzoni pers. comm., Vidano 1960, Vidano et al. 1987, 1990). Most examples are reported from Italy and Wales. Therefore, this type of host shift may be associated with mild winter climates.

(v) Some adult typhlocybid leafhoppers perform a horizontal migration in late summer and autumn, usually from deciduous hosts to evergreen plants, with *Picea abies* and *Pinus sylvestris*, and to a lesser extent, *Juniperus communis* being the most important winter hosts. This strategy is found in most species of the genus *Zygina*, and perhaps in other genera such as *Linnavuoriana* and *Zyginella*. Spruce is also the winter host of some idiocerine species, notably *Tremulicerus fulgidus* (Fabricius, 1775) and *Metidiocerus rutilans* (Kirschbaum, 1868). The most abundant winter leafhopper all over central Europe is certainly the grape leafhopper *Empoasca vitis*, which may then be found in large numbers on all kinds of conifers as well as *Taxus baccata*, *Hedera helix* and other evergreen plants.

(vi) Another strategy involves overwintering as an egg in the herb layer. Adults migrate up to the canopy shortly after emergence and maturation feeding occurs in the canopy, but oviposition on herbs or grasses. It is found in some deltocephaline leafhoppers (see Tab. 1) and the spittlebugs *Aphrophora alni* (Fallén, 1805), *A. major (*Uhler, 1896) and *A. corticea (*Germar, 1821). In the latter group, vertical migration may be advantageous since these insects feed on xylem sap, which, unlike phloem, is under negative pressure, this last increasing notably with height above ground. Therefore, it is plausible that the small and weak nymphs feed on herbs, and the stronger adults feed higher up (Raven 1983; Novotný and Wilson 1997).

(vii) A similar strategy is found in the deltocephaline leafhoppers *Colladonus torneellus* (Zetterstedt, 1828), *Speudotettix subfusculus* (Fallén, 1806), and *Thamnotettix* spp., but overwintering takes place in the nymphal stage, probably largely on grasses and sedges. Adults of this group occur rather early in the season and may be found from late April onwards. Likewise, in the issid planthopper

Tab. 3: Introduced arboreal Auchenorrhyncha in central Europe and adjacent regions, and some features of their biology. mp1 = 1st degree (= strictly) monophagous, 1 host species, mp2 = 2nd degree monophagous, 1 host genus, op1 = 1st degree oligophagous, 1 host family, op2 = 2nd degree oligophagous, 2 food plant families or up to 4 species of no more than 4 plant families, pol = polyphagous, * = Exotic host. Author and year of species see Appendix list.

species	earliest record in Europe	origin	central European host	diet width	hibernation stage
Flatidae					
Metcalfa pruinosa	1979, N Italy	eastern nearctic	mainly trees and shrubs	pol	egg
Acanaloniidae					
Acanalonia conica	2003, N Italy	eastern nearctic	mainly trees and shrubs	pol	egg
Membracidae					
Stictocephala bisonia	1912, Hungary	eastern nearctic	Fabaceae, Rosaceae, Salicaceae et al.	pol	egg
Cicadellidae					
Macropsis elaeagni	1958, Romania	central palaearctic	*Elaeagnus angustifolia**	mp1?	egg
Graphocephala fennahi	1932?, England	eastern nearctic	*Rhododendron** (Ericaceae)	mp2?	egg
Kyboasca maligni	1997, E France	eastern nearctic	*Malus domestica*	op1?	egg
Igutettix oculata	1986?, Moscow	eastern palaearctic	*Syringa* spp.*	mp2?	egg?
Erythroneura vulnerata	2004, N Italy	eastern nearctic	*Vitis vinifera* (Vitaceae)	pol?	adult
Scaphoideus titanus	1958, S France	eastern nearctic	*Vitis vinifera*	mp1?	egg
Orientus ishidae	1998, N Italy	eastern palaearctic	deciduous shrubs	pol	egg

Sources: Morcos (1953), Zangheri and Donadini (1980), Arzone *et al.* (1987), della Giustina (1989), Tishechkin (1989, 2000, and pers. comm.), Wilson and Lucchi (2001), Lauterer (1984), Lauterer and Malenovsky (2002), Seljak (2002), Dmitriev and Dietrich (2003 - 2005), Duso *et al.* (2005), Guglielmino (2005), Söderman (2005), D'Urso and Uliana (2006), Nickel (2003)

Issus coleoptratus (Fabricius, 1781), and probably *I. muscaeformis* (Schrank, 1781), nymphs spend the winter mostly on low-growing evergreen shrubs and trees, at least some of which are also host plants. However, unlike the species mentioned above, they are widely polyphagous and utilise biochemically peculiar or even toxic plants, including *Hedera helix*, *Taxus baccata*, *Buxus sempervirens*. Eggs are laid in or onto the soil (Müller 1942).

(viii) Overwintering of nymphs in the soil and vertical migration into the canopy in spring is certainly the strategy with deepest implications for evolution, because living in the soil requires special adaptations. Maturation feeding of adults takes place in the canopy. Downward migration is performed either by adults which oviposit in the herb layer, or by first instars climbing or falling down from oviposition sites in branches. All cicadas and cixiid planthoppers follow this strategy. In cercopids, *Haematoloma dorsatum* (Ahrens, 1812) is the only species that obligatorily ascends into tree canopies, whereas the remaining cercopids mostly feed on herbs and grasses.

Geographic distribution

The European zone of deciduous forests is an important centre of endemism of forest biota, although species richness is lower than in similar zones of eastern North America or eastern Asia (Schaefer 1991). In arboreal Auchenorrhyncha, many species' geographic ranges are more or less congruent with those of their host plants (see e.g. Meusel et al. 1965, Nast 1987) and, therefore, typically extend from Britain, France and the northern half of Spain, through southern Scandinavia, central Europe and Italy, eastward to central Russia, the Balkan peninsula, the Caucasus and/or northern Anatolia, usually being absent from Mediterranean lowlands and the Pontic region. Host examples include *Corylus avellana* (Corylaceae), *Quercus robur*, *Ulmus glabra* and *Acer platanoides* (Walter and Straka 1970).

Such European distribution patterns are found in almost half of the arboreal Auchenorrhyncha species known from central Europe. Another 12% of the species are widespread in the Western Palaearctic. Of the latter, usually, their ranges include both the deciduous forest zone and the Mediterranean region (where sclerophyllous forests predominate), and may extend more or less far into western or even central Asia, without being bound to a certain vegetation zone. A further 13% show a typically Mediterranean distribution, extending locally into southern parts of the deciduous forest zone. The remaining species have a wider distribution, either through both the European deciduous forest zone and the Siberian coniferous forest zone (Eurosiberian), throughout the Palaearctic from the Pacific to the Atlantic coast (trans-Palearctic), or their ranges extend from the Siberian zone of coniferous forests into eastern and central Europe (Siberian) - see Fig. 6.

Therefore, Auchenorrhyncha support the general pattern of the distinctiveness of the European forest fauna, with a high proportion of endemic species and a relatively small influence of other biogeographic regions.

Alien species

Most of the alien species in the central European fauna of arboreal Auchenorrhyncha belong to the Cicadomorpha and include such well-known examples as the Nearctic *Stictocephala bisonia* Kopp & Yonke, 1977, and *Graphocephala fennahi* Young, 1977, but also very recent invaders such as the eastern Palaearctic *Orientus ishidae* (Matsumura, 1902) and the Nearctic *Kyboasca maligni* (Walsh, 1862). Further species are expanding their ranges from neighbouring regions, including the Nearctic species *Metcalfa pruinosa* (Say, 1830), *Erythroneura vulnerata* Fitch, 1851 and *Scaphoideus titanus* Ball, 1932 and the eastern Palaearctic *Igutettix oculatus* (Lindberg, 1929). Some details of their biology and colonisation history are summarised in Tab. 3.

Tab. 4: Exotic trees and shrubs in Central Europe attacked by stenophagous native leafhoppers. For explanations of diet width see Tab. 3. Author and year of species see Appendix list.

exotic host	origin	leafhopper	native leafhopper host	diet width in central Europe
Acer palmatum	Japan	*Japananus hyalinus*	*Acer campestre*	mp2?
Aesculus hippocastanum	south-eastern Europe	*Edwardsiana lethierryi*	*Acer campestre*, *Tilia* spp.	op2?
Corylus colurna, *C. maxima*	south-western palaearctic	*Alebra coryli*	*Corylus avellana*	mp1
Pyracantha coccinea	mediterranean	*Zygina angusta*	*Prunus*, *Rosa*, *Crataegus*	op2
Rosa rugosa	eastern palaearctic	*Edwardsiana sociabilis*	*Filipendula ulmaria*	mp1
Tamarix spec.	south-western palaearctic	*Opsius stactogalus*	*Myricaria germanica*	mp1

There are three cases of alien leafhoppers breeding on alien plants (Tab. 3). For example, the macropsid leafhopper *Macropsis elaeagni* Emelyanov, 1964 is likely to have been introduced on its original host *Elaeagnus angustifolia* (Elaeagnaceae) from the southwestern Palaearctic. It is probable that the two remaining species, *Graphocephala fennahi* and *Igutettix oculatus*, have performed a within-genus host shift. The Nearctic *G. fennahi* has colonised ornamental and invasive rhododendron, which is taxonomically complicated, but is thought to be of Palaearctic origin, primarily. The lilac-feeding *I. oculatus*, now locally common in middle Russia and southern Finland, originally lives on *Syringa amurensis* (Oleaceae), but has shifted to the southeast European *S. josikaea* and *S. vulgaris* (Tishechkin 2000, and pers. comm., Söderman 2005). Another interesting case, though no transcontinental spread is involved, is the typhlocybid leafhopper *Liguropia juniperi*, which has expanded its range within Europe. It is likely that this species performed a host shift at the generic level, since none of its native Mediterranean hosts (scaly species of Cupressaceae, notably *Cupressus sempervirens*, *J. phoenicea*, *Tetraclinis articulata*; Remane, pers. comm.) occurs in central Europe. Instead, it has colonised *Chamaecyparis lawsoniana*, which is grown as an ornamental plant in gardens and parks. Therefore, this is one of the very rare cases of a specialised neozoan insect colonising a neophytic plant originating from somewhere else outside their native ranges.

Due to the small number of species involved, it is difficult to detect any pattern which might allow predictions for future introductions. For example, there is no apparent systematic clumping, except perhaps an over-representation of typhlocybid leafhoppers. With reference to life history, species overwintering in the egg stage appear to be favoured, simply because these species spend most of their time as an egg, sheltered in host plant tissue, and, thus, are least susceptible to disturbance such as herbicide application, cold and wind during transport over long distances.

Habitat requirements of these species are in accordance with some patterns common to neozoa. In particular, none of them has succeeded in colonising near-natural habitats. Instead all are confined to open anthropogenic habitats such as gardens, orchards, cultivations, parks or river floodplains. Further, all species introduced to Europe, including all grass and herb feeders, are monomorphic macropterous. This is also a feature of arboreal species in general (Waloff 1983, Nickel 2003) and, thus, it is difficult to weight the significance of each factor individually. However, macropterous species account for 77% of the Old World species introduced to North America (48 out of a total of 62), but only for 58% of the Old World pool of central Europe (after data from Hamilton 1983a, Nickel 2003). Therefore macroptery clearly seems to be advantageous for potentially invasive species, disregarding their stratification.

Conversely, concerning the utilisation of exotic woody plants by native Auchenorrhyncha, it can be stated that there is a lack of systematically collected data, and therefore, the conclusions drawn here should be considered as preliminary. There has been much occasional and random sweeping which produced some positive host records, but most negative results have neither been published nor even noted. For example the author’s database includes only negative data collected after 1998, but not between 1990 and 1997, though hundreds of ornamental trees and shrubs have been swept.

Extensive and long-term collecting activity by Wagner (e.g. 1935, 1939), Müller (1956, 1972), Schiemenz (1987, 1988, 1990), Schiemenz et al. (1996), Remane (e.g. 1987, 2003) and Nickel (2003) has produced only a very small number of positive records. This leads to the general impression that introduced trees and shrubs, including most congeners of native trees, are almost free of leafhoppers. This is particularly true for *Pseudotsuga menziesii* (Pinaceae), *Thuja* spp. (Cupressaceae), *Platanus* spp. (Platanceae), *Juglans regia, Pterocarya* spp. (both Juglandaceae), *Ailanthus altissima* (Simaroubaceae), *Catalpa* spp. (Bignoniaceae), *Quercus rubra*, *Prunus serotina*, *Robinia pseudacacia* (Fabaceae), *Syringa*

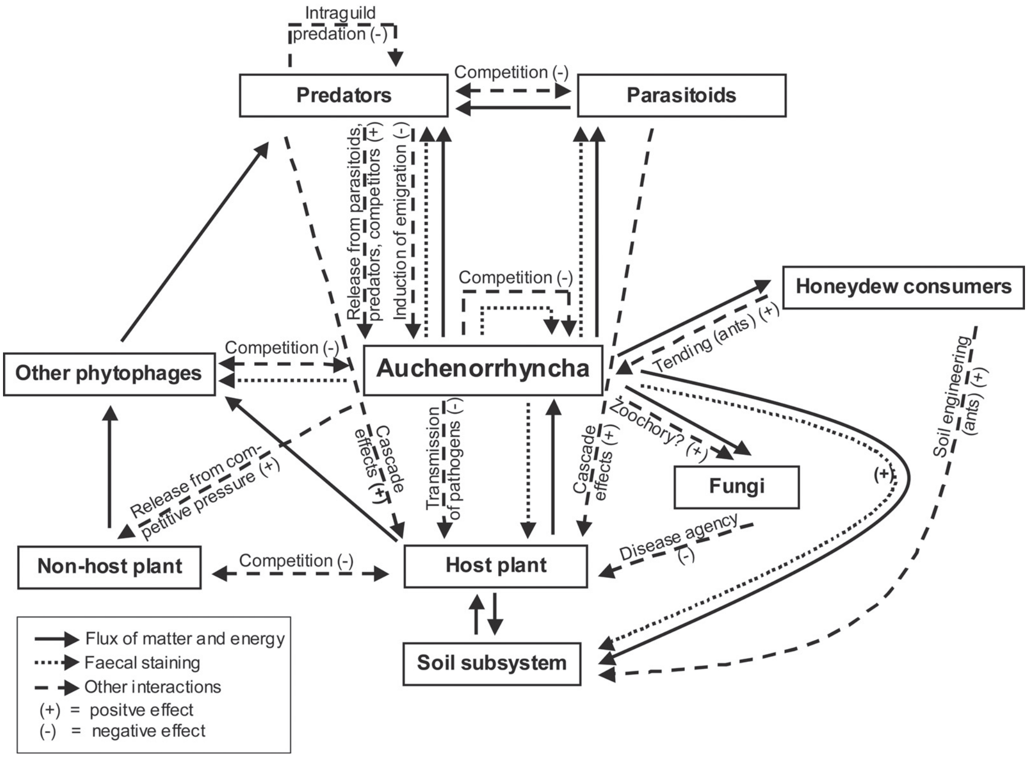

Fig. 7: Relationships between Auchenorrhyncha and their associated ecosystem components. Interactions are only shown if relevant for Auchenorrhyncha.

spp., and *Acer negundo*. Sweeping these trees frequently produces no more than a handful of specimens, most of which are vagrants, except the broadly polyphagous leafhoppers *Empoasca vitis* and, less commonly, *Alebra wahlbergi* (Boheman, 1845), *Fagocyba cruenta* (Herrich-Schäffer, 1838) and *Alnetoidia alneti* (Dahlbom, 1850). This pattern is supported by studies of other taxa of phytophagous insects in central Europe (e.g. Frenzel et al. 2000).

There is only a handful of exceptions from this rule: examples of specialised native leafhoppers shifting to exotic trees or shrubs include *Rosa rugosa*, being attacked by the typhlocybid *Edwardsiana sociabilis* (Ossiannilsson, 1936), originally a rare species feeding on the tall herb *Filipendula ulmaria* (Rosaceae) and *Acer palmatum* (and probably other introduced maples) colonised by the leafhopper *Japananus hyalinus*. This insect was thought to have been exotic in itself (Arzone et al. 1987, Seljak 2002), but several authors have argued that most European records are from the native *Acer campestre* in near-natural woodland sites, and that it is probable that the species is indigenous (Remane and Fröhlich 1994, Nickel 2003). In Britain, *Nothofagus obliqua* and *N. procera* (Fagaceae), originating from Chile and now planted widely as forest trees, have been colonised by at least six typhlocybid species, including the *Quercus* specialist-feeders *Eurhadina kirschbaumi* W. Wagner, 1937 and *E. concinna* (Germar, 1831) (Claridge and Wilson 1981). Further examples are summarised in Tab. 4. Accordingly, leafhoppers are principally capable of performing a spontaneous shift just on encountering a new plant. Such host shifts are rare, but may imply a trespass of the insect's original systematic host range and a colonisation of new plant genera or even families, making predictions about new insect-plant relationships a difficult task.

To conclude, most alien Auchenorrhyncha on European woody plants originate from temperate regions of eastern North America or eastern Asia. All are macropterous, most of them overwinter in the egg stage and typhlocybid leafhoppers are slightly over-represented. Although the quality of survey has improved, the increase of new invasions during recent decades is unlikely to be a sampling artefact, but is likely to have been caused by the improvement of worldwide logistics. Conversely, alien woody plants are only rarely colonised by native leafhoppers, most of which are broadly polyphagous. The few documented cases of specialists involve host shifts only between closely related hosts.

The functional role of Auchenorrhyncha

Generally, functional relationships of Auchenorrhyncha are poorly known, and much of what we know is inferred from barely a handful of studies. This is particularly true for arboreal systems, where access is physically constrained. Documented and inferred relationships of Auchenorrhyncha with other biotic components of their environment are summarised in Fig. 7. Due to the paucity of studies, this model is also based on evidence from herb-feeding species (e.g. Carson and Root 1999, Olmstead et al. 1997, Gratton and Denno 2003), tropical forests (Delabie 2001, Del-Claro and Oliveira 2000, Del-Claro 2004) and related sap-feeding groups such as aphids (e.g. Dixon 1998, Stadler et al. 1998, 2001), as well as from general considerations on Auchenorrhyncha biology.

Most Auchenorrhyncha tap the phloem vessels of their hosts, whereas a few groups, notably cicadas, spittlebugs and sharpshooters (Cicadoidea, Cercopoidea, Cicadellinae) have specialised on xylem sap. Therefore, they rely on a highly imbalanced and diluted diet that must be complemented through the help of symbiotic microorganisms (Müller 1956, Raven 1983, Strong et al. 1984). Some groups, notably the Achilidae and Derbidae, are no longer phytophages, but feed on fungal hyphae that live in deadwood (Wilson et al. 1994). In contrast, the Typhlocybinae, a subgroup of the Cicadellidae, have shifted from vessel feeding to leaf tissue, which implies extraction from and damage to palisade and spongy parenchyma, but, unlike chewing insects, the external leaf structure remains intact (Smith 1926, Pollard 1968). These leafhoppers must tolerate or overcome the adversities of secondary plant chemistry (Claridge 1986), whereas feeders of phloem, and particularly, xylem live on a substrate that has much lower concentrations of toxic or digestability-reducing compounds (Raven 1983). Another difference between these two feeding strategies is that resources of tissue-feeders are principally limited, but less so in vessel-feeders. Therefore, Typhlocybinae have been used as model organisms for the study of interspecific competition between closely related species (McClure and Price 1975, 1976, Hunter and Yeargan 1989, Settle and Wilson 1990).

Auchenorrhyncha occupy a central position in many above-ground food webs. They are important consumers of plant material, and may affect their host's growth significantly. A comparative study of the damaging effects of a xylem-feeding spittlebug (*Philaenus spumarius*) and a leaf-chewing beetle on the North American tall herb *Solidago altissima* (Asteraceae) showed that only after three weeks spittlebugs had significantly affected leaf and root biomass, and their impact was more than five times greater than that of the beetle (Meyer 1993, Meyer and Root 1993). In a similar study of early successional plant communities, Carson and Root (1999) found a severe feeding impact of *Philaenus spumarius*, which significantly altered the course of early succession. Whittaker (1984) found that a single adult individual of the typhlocybid *Ossiannilssonola callosa*, a host specialist of *Acer pseudoplatanus*, consumed the mesophyll contents of 4cm^2 within ten days. Moreover, in these stippled leaf areas, net photosynthesis was reduced to one third of the former rate, and water vapour conductance was increased due to the numerous feeding punctures by 18% during daytime and 75% at night.

In grasslands, Auchenorrhyncha densities frequently exceed 1000 individuals per m^2 (Biedermann et al. 2005), and there is evidence that similar values occur in tree canopies. A single stem eclector in a dense stand of 25 year-old *Populus tremula* in Germany caught 33.000 individuals of the permantly arboreal idiocerine leafhopper *Populicerus laminatus* (Flor, 1861), implying that only those specimens which had fallen down through leaf vibration were caught (Nickel 2003). Extrapolating this number on ground area would result in densities of at least 3,000 per m^2. On the North American *Platanus occidentalis*, densities of adult and juvenile *Erythroneura* leafhoppers ranged from one to eight per leaf (McClure and Price 1975). On the European *Carpinus betulus*, average densities of 0.5-1 individuals on a 2000mm^2 leaf have been recorded (Nickel, pers. obs.). Assuming a leaf-area index of 5 would result in an overall density of 1250-2500 per m^2 ground area. Based on Whittaker's (1984) calculations of feeding rates (see above), 1000 typhlocybid individuals per m^2, within an assumed feeding period of 30 days could damage nearly one quarter of a tree's leaf mass, decreasing its net photosynthesis by one sixth. This estimate is supported by a locally high proportion of stippled leaf area on *Ulmus*, *Acer*, *Carpinus*, *Prunus* and other trees visible in late summer. However, at that time of the season, the actual damage to the plant may be low, and typhlocybid distribution on trees have been shown to be rather heterogenous, with higher densities on sun-exposed leaves (Claridge et al. 1981, Claridge 1986), though contrasting opinions have been published after extensive studies on typhlocybid biology (Claridge and Wilson 1976). Finally, it should be mentioned that biomass estimates of periodical cicadas in an Illinois floodplain forest were among the highest recorded for any terrestrial animal in a natural system, ranging from 1.9 to nearly 3.7 tons per ha (Dybas and Davis 1962). Such high cicada densities have also been found to cause fertilising pulses for soil microbia through dead bodies at the end of a 17-year cycle, which, in turn, may be beneficial for the host (Yang 2004).

Further, there are direct interactions with many other ecosystem components, notably with a diverse array of predators such as birds, spiders, ants and sphecid wasps (Andrzejewska 1979, Whittaker 1984, Moreby and Stoate 2001, Zolda and Holzinger 2002), as well as parasitoids such as pipunculid flies, dryinid and myrmarid wasps and strepsipterans (Sander 1985, Waloff and Jervis 1987, Giordano et al. 2002, Böll and Herrmann 2004), some of which may reduce the density of their prey considerably.

An important point is the preference of Auchenorrhyncha for abundant and, therefore, competitively superior host plants (see above). Excessive feeding may cause a reduction of host vitality which, in turn, may allow more resources for non-host plants, ultimately increasing overall plant diversity, as has been found in the spittlebug *Philaenus spumarius* in stands of the tall herb *Solidago altissima* (Carson and Root 1999).

Auchenorrhyncha have long been known as disease vectors of cereals and other crops, including cultures of perennial woody plants such as grapevines and raspberry (de Fluiter and van der Meer 1953, Müller 1956, 1972, Schvester et al. 1963, Maramorosch and Harris 1979, Weber and Maixner 1998). However, only relatively recently, it was found that they also play a role in the transmission of tree diseases that may weaken or even kill host trees and, therefore, exert a crucial impact on the composition and diversity of forest communities (Maixner and Reinert 1999, Carraro et al. 2004).

Another peculiarity of Auchenorrhyncha biology is the production of honeydew, which is the cause of mutualistic relations mainly with tropical ants (Wood 1984, 1993, Delabie 2001). Although in Europe this phenomenon is known only from the treehopper *Gargara genistae* (Fabricius, 1775) and a handful of other species (Schedl 1998, Lehouck et al. 2004, Steiner et al. 2004), it may be much more important at an ecosystem level than thought previously. Unlike gregarious and largely sedentary aphids, auchenorrhynchan honeydew is thinly distributed all over the vegetation, and may be quickly consumed also by a variety of other organisms such as soil microbes, fungi, Diptera and further groups of Hymenoptera. The Nearctic flatid *Metcalfa pruinosa* has even gained economic importance as a bee honey source in northern Italy (Gazziola et al. 2000). Ants, which are widely known as soil engineers with a profound impact on the vegetation, may compensate the suction damage to host plants by enhancing microbial growth in the soil (Jones et al. 1994, Dauber and Wolters 2000, Platner 2004). Conversely, faecal pollution and physical damage through oviposition enhance fungal growth on leaves and twigs and their loss (Lauterer 2002, Ferracini et al. 2004) and causes deterioration of habitat conditions for most other arthropods, regardless of their food web position.

Finally, there are interactions between other biotic food web components that may affect auchenorrhynchan performance indirectly. For example, intra-guild predation between ants and spiders in grasslands has been found to reduce top-down control of Auchenorrhyncha, and hence, to reduce positive cascade effects of these predators on plants (Finke and Denno 2004), and similar effects may occur, when predators exert control of parasitoids. Through increased predation rates on other phytophages, predators may also release Auchenorrhyncha from competitive pressure.

To conclude, at present the evidence is too scattered to gain a comprehensive idea of how important these insects are in shaping their environment. As in many other ecological studies, the main problem is to assess, on the basis of rather limited findings, where, when, how long, and under which circumstances effects occur, and how important these are ultimately for crucial ecosystem processes. Nevertheless, the variety of potential effects in combination with high field densities suggest that the ecological impact of Auchenorrhyncha has strongly been underestimated and deserves more attention.

Some thoughts on the evolution of arboreal life habits

It appears that permanently arboreal insects are relatively rare in temperate deciduous forests, because autumn leaf fall reduces shelter, moisture and available food in the canopy. As a consequence, many species utilise tree crowns only during the growing season, when green leaf biomass is abundant and when nutrient transport through phloem and xylem is activated. For oviposition, nymphal development or pupation they descend into the detritus or herb layer and must therefore perform a vertical migration (see above). This is particularly true in many species-rich holometabolous insect groups such as curculionid and chrysomelid beetles (Trautner et al. 1989, Böhme 2001), geometrid moths (Skou 1986) and sawflies (Pschorn-Walcher 1982, Viitasaari 2002). The dichotomy of life habits between adults and larvae in these groups should be seen correlated with the evolution of diverging morphological traits through holometaboly (Wilbur 1980).

In contrast, most hemimetabolan nymphs develop adult characters progressively, without undergoing the dramatic external and internal transformation of holometabolan metamorphosis and, as a consequence, differences between immature and adult life habits are often minute. Such a life history is particularly widespread among Hemiptera, in which habitat and food requirements are usually identical through all developmental stages. For this insect group, and Fulgoromorpha and ancestral Cicadomorpha in particular, epigaeic life in the shelter of the detritus layer and near the base of host plants is thought to be the primitive condition (Schaefer 1988, Bourgoin 1997 - but see Wilson et al. 1994), and the ascent of Cicadellidae into higher vegetation has been seen in correlation with the evolution of the jumping apparatus and the peculiar habit of anointing the body surface with brochosomes as a protection against water, drought and other adverse forces (Dietrich 2002, Rakitov 2002). The morphological and ecological similarity of successive life stages in Hemimetabola may, therefore, have acted as a constraint for the evolution of vertical migration, selecting for a permanent life either near the ground or, as a derived trait, in the canopy layer, but not for a shift between both. Conversely, seasonality should have been a strong opposite force selecting for the ability to leave the tree canopy when conditions become unfavourable.

Obligate vertical migration

It is concluded here that obligate vertical migration in Hemimetabola must be considered as a derived attribute, one which is confined to only very few taxa, and some of these have evolved derived holometaboloid characters (i.e. specific either to nymphal or adult stages) enabling them to cope with this new strategy. For example, in cicadas (Cicadoidea) nymphs bear enlarged fossorial fore legs for locomotion in the ground (Kudryasheva 1979, Boulard and Mondon 1995). In spittlebugs (Cercopoidea) nymphs live in a foamy cover consisting of proteinaceous and mucopolysaccharide secreta of the Malpighian tubules, and they breathe through a ventral cavity formed by ventrolateral extensions of the tergites (e.g. Guilbeau 1914, Rakitov 2002). It is highly probably that this habit, and the associated morphological adaptations, are derived. In Cercopoidea, vertical migration is not found throughout the group, but root-feeding (implying a vertical migration after completion of the nymphal phase) has been suggested as an ancestral trait (Evans 1940, Emelyanov 1987). Accordingly, a permanent life in epigaeic herbal vegetation, as is common in extant species of the family Aphrophoridae (e.g. *Neophilaenus*, *Lepyronia*, *Philaenus*), should be interpreted as an attribute which evolved secondarily, perhaps as a response to a colder climate since the mid Tertiary, one that was unfavourable for endogaeic nymphal development. In Cixiidae, which is the third important group of vertical migrants, autapomorphic characters related with dichotomous life habits are more difficult to assess, but may include the wax plates and glands of females which are likely to provide defence for eggs, that are oviposited on or into the soil, against moisture, fungal mould, bacteria and perhaps other adverse factors (Müller 1942, Holzinger et al. 2002). Fossorial fore legs have evolved in some subgroups only, whereas the ability to jump should be interpreted as primitive (Emelyanov 2002, and pers. comm.).

Vertical migration is often, and perhaps always, associated with a shift of food plant species. This is evident in all species which spend their nymphal stage in the herbaceous vegetation, but ascend into the tree layer as adults. Conversely, food plants of endogeic nymphs are known insufficiently. The cixiid *Cixius nervosus* (Linnaeus, 1758) has been reared on *Bellis perennis* (Asteraceae) (Müller 1942), but laboratory rearings are never equivalent to field conditions, and many hopper species exposed exclusively to non-field hostplants in the laboratory may thrive surprisingly well even through many generations (e.g. Strübing 1966, Müller 1973, Witsack 1985). In fact, most endogaeic nymphs should have a rather small host range at least at the individual level, because their mobility in soil substrates is reduced.

Vertical shifts

Nevertheless, the evolutionary step for an insect from the ground surface up to the tree top was apparently small. Principally, it required no profound morphological adaptations, but only a shift from moving, sucking and ovipositing on herbaceous shoots to woody twigs and, perhaps, some physiological adaptations related to tolerance to drought and cold. Therefore, there are no conspicuous morphological differences between inhabitants of the arboreal and herbaceous layers. It is not surprising that such shifts may have occurred several times within low-ranking Auchenorrhyncha taxa from subfamilies downwards, although it is not always evident whether the primitive attribute in a particular subgroup was epigaeic and the derived attribute arboreal, or *vice versa*. Thus, both attributes are found within one or few closely related genera in Cicadellinae (Nielson and Knight 2000), the typhlocybid taxa Dikraneurini and Erythroneurini as well as in Deltocephalinae. Many species from most groups show transitional life habits involving the facultative utilisation of both herbs and trees (see Appendix, Nickel 2003). Furthermore, it is likely that formerly arboreal taxa returned to the herb layer, notably in *Edwardsiana*, *Zygina* and *Arboridia*. The former is one of the most diverse arboreal typhlocybid genera of the northern hemisphere. A single species, however, *E. sociabilis*, is in natural habitats confined to the tall herb *Filipendula ulmaria*, but has secondarily colonised th introduced shrub *Rosa rugosa*. Similarly, in the largely arboreal genus *Zygina*, members of the subgenus *Hypericella* [*Z. hyperici* (Herrich-Schäffer, 1836), *Z. hypermaculata* Remane & Holzinger, 1995, *Z. frauenfeldi* Lethierry, 1880, see Lauterer 1980] are monophagous on low-growing herbs, namely *Hypericum* spp., *Sanguisorba minor* (Rosaceae). Likewise, *Arboridia* is mostly confined to trees or shrubs, but *A. pusilla* (Ribaut, 1936) and *A. kratochvili* Lang, 1945 have colonised *Geranium sanguineum* (Geraniaceae) and *Potentilla arenaria* (Rosaceae) respectively. Another example may be found in the cicadellid tribe Macropsini, which is almost exclusively arboreal and probably originated from the Oriental region (Hamilton 1980, 1983b). The genera *Hephathus*, *Macropsidius* and *Batracomorphus*, however, with most species occurring in central Asian steppe and semi-desert regions, mostly feed on low-growing herbs and dwarf shrubs (Dlabola 1963, Mityaev 1971, Anufriev and Emeljanov 1988, Tishechkin 1999). Since the climate in this region has become dry only in the Caenozoic, it is likely that the ancestors of these leafhopper taxa were arboreal. It is remarkable that most of these secondary herbaceous hosts contain derived secondary compounds, at least some of which have been shown to have toxic effects on herbivorous insects (Frohne and Jensen 1998, Guillet et al. 2000, Ayoub 2003).

Permanently arboreal groups

Some supraspecific taxa, at a conventional subfamily level, have largely or even exclusively adapted to a permanently arboreal life, for example Idiocerinae, Iassinae, Macropsinae, Penthimiinae, as well as some other groups confined to warmer latitudes (Nielson and Knight 2000). This indicates that tree canopies have been offering a considerable resource for Auchenorrhyncha and other Hemiptera at least since angiosperms have gained dominance in the world's forests in the mid and late Cretaceous. However, unlike in aphids, many of which are thought to have phylogenetically older feeding relations to coniferous trees (Shaposhnikov 1985, Heie 1996, von Dohlen and Moran 2000), the number of Auchenorrhyncha feeding on gymnosperms (as well as those living on other primitive plants) is rather small. Moreover, most if not all of these belong to more derived leafhopper groups, which largely feed on angiosperms, providing clear evidence for a secondary colonisation of ancestral plants from more derived plants. For example, a few species of the typhlocybid leafhopper genus *Aguriahana* feed on gymnosperms, but most species (as well as most related genera) feed on deciduous trees belonging to Betulaceae, Fagaceae and Aceraceae (Dworakowska 1972), all of which belong to the much more derived rosid clade (see Angiosperm Phylogeny Group 2003). Such dramatic host shifts within the same genus are apparently not uncommon in Auchenorrhyncha and even involve shifts from monocot grasses to non-spermatophyte horsetails or ferns (Nickel 2003).

Geological history

Geological dating of the auchenorrhynchan ascension to the tree layer can be estimated by extrapolation only. Opinions about the systematic position of many fossils and, therefore, the geological age of many groups are contradictory (e.g. Szwedo 2002 *contra* Blocker 1996) and sometimes rather speculative. Generally, Eocene amber and Palaeocene fossil beds provide the most reliable records and produced almost the full range of extant Auchenorrhyncha diversity at family level (Rust 1999, Szwedo 2002, Szwedo et al. 2004). Although the morphology of these fossils does not offer clues for their host plants, it must be considered highly likely that most species found in amber inclusions lived on trees, since herbaceous plants do not produce such a type of resin. Earlier fossils are more scarce and do not permit any conclusions about host relations. Moreover, their systematic positioning is often less well supported, though Tettigarctidae were satisfiably documented from the late Triassic, and primitive Cixiidae and Achilidae from the late Jurassic or early Cretaceous, respectively (Shcherbakov 2002, Szwedo 2002).

Nevertheless, it is probable that modern Auchenorrhyncha diversified almost synchronously with modern plants. This leads us to the assumption that the well-documented rise of woody angiosperms enhanced the radiation of arboreal leafhoppers and planthoppers greatly, at least since the mid Cretaceous. We can speculate further that earlier Hemiptera (including ancestral Fulgoromorpha and Cicadomorpha) did not avoid the huge tree ferns and conifers which dominated Earth's vegetation during the late Paleozoic and much of the Mesozoic (see Strong et al. 1984, Labandeira 1997, Schoonhoven et al. 1997), although the very few extant Auchenorrhyncha species feeding on conifers and ferns belong to more derived groups (see above). Shcherbakov (2000), after summarising the limited evidence, suggested that earlier Hemiptera mainly fed on gymnosperms but, given the great importance of plant apparency for host choice, there appears to be no particular reason why they should have avoided tree ferns.

Altogether we can assume that a considerable radiation of arboreal Hemiptera, particularly Typhlocybinae, Idiocerinae, and Macropsinae, occurred in the early Caenozoic, correlating with the rise of woody angiosperms. Permanently arboreal life habits in Cicadomorpha may have originated during this period, although earlier utilisation of tree ferns and gymnosperms by extinct taxa is likely. Nevertheless, ecological conclusions drawn from such early fossils must remain speculative.

Conclusions and perspectives

Leafhoppers and planthoppers form an important component of the canopy fauna of temperate deciduous forests; they are rich in species and individual numbers, and contain a high proportion of host specialists. Plant apparency, and particularly, plant size, plant abundance, and plant diversity, are major determinants of host choice. It is probable that plant chemistry is of secondary importance only, since most tree species and genera in European deciduous forests belong to a single plant clade and, therefore, biochemical differences should be little.

The historical dominance of research in insect-host relations may lead to the conclusion that bottom-up control in Auchenorrhyncha is dominant. On the other hand, the few studies which concentrated on their relations with predators and parasitoids indicate that top-down forces may have been underestimated.

At present, we are far from evaluating the functional significance of canopy leafhoppers and planthoppers, since there are no reliable figures of abundance and biomass. However, we do know that their impact may be much more than just the quantity of tissue or plant sap removed. We have reasonable evidence that they are an important component of the canopy food web, that interacts in many ways with other animals and fungi through removal of sap and biomass, faecal staining, honeydew production, and as a food source for ants, spiders, birds and a diverse array of parasitoid hymenopterans, dipterans and strepsipterans. Recent studies have indicated that some species are vectors of plant diseases that may eventually affect their host's distribution, and therefore, forest tree composition. In particular, the impact of consumption, honeydew production and transmission of pathogens deserves more attention, because it potentially affects key functions of the forest ecosystem.

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Appendix: Overview of arboreal planthoppers and leafhoppers of central Europe (Austria, the Baltic and Benelux countries, Belarus, Czech Republic, Denmark, Germany, Ireland, Poland, Switzerland, UK). Distribution data taken mainly from Nast (1972, 1987) and literature thereafter. Data on biology mainly after Nickel (2003). Asterisks indicate taxonomically critical species or published records that should be revised. P = Phloem, X = Xylem, M = Mesophyll. mp1 = 1st degree (= strictly) monophagous, 1 host species, mp2 = 2nd degree monophagous, 1 host genus, op1 = 1st degree oligophagous, 1 host family, op2 = 2nd degree oligophagous, 2 food plant families or up to 4 species of no more than 4 plant families, pol = polyphagous, ( ) refers to nymphal stage only. Nymphal and adult hosts are separated by a slash.

taxon	geographic range	period of arboreality	host range	resource	host or food plant(s)	remark
Fulgoromorpha Evans, 1946 - Planthoppers						
Cixiidae Spinola, 1839						
Cixius nervosus (Linnaeus, 1758)	eurosiberian	adult	pol?	P	deciduous woody plants	nymphs in soil; also in alpine belt
Cixius cunicularius (Linnaeus, 1767)	eurosiberian	adult	pol?	P	deciduous woody plants	nymphs in soil
Cixius simplex (Herrich-Schäffer, 1835)	european?	adult	pol?	P	shrubs	nymphs in soil
Cixius wagneri China, 1942	mediterranean?	adult	pol?	P	shrubs	nymphs in soil
Cixius distinguendus Kirschbaum, 1868	eurosiberian?	adult	pol?	P	deciduous woody plants	nymphs in soil
Cixius sticticus Rey, 1891	mediterranean	adult	op2?	P	shrubs	nymphs in soil
Cixius alpestris W. Wagner, 1939*	european	adult	pol?	P	shrubs, tall herbs	conspecific with *C. sticticus* ?
Cixius heydenii Kirschbaum, 1868	european	adult	pol?	P	shrubs et al.	nymphs in soil; also in alpine belt
Cixius beieri W. Wagner, 1939	european	adult	mp1?	P	*Picea abies*, *Abies alba*?	nymphs in soil; Syn.: *C. haupti* Dlab.
Cixius cambricus China, 1935	european	adult	pol?	P	shrubs	nymphs in soil; also in alpine belt
Cixius stigmaticus (Germar, 1818)	european	adult	pol?	P	deciduous woody plants	nymphs in soil
Cixius dubius W. Wagner, 1939	european	adult	pol?	P	deciduous woody plants	nymphs in soil
Cixius similis Kirschbaum, 1868	siberian	adult	op2?	P	*Betula, Pinus*, *Vaccinium*?	nymphs in soil
Tachycixius pilosus (Olivier, 1791)	european	adult	pol?	P	deciduous woody plants	nymphs in soil
Trigonocranus emmeae Fieber, 1876	european	adults occasionally	?	P	deciduous shrubs (roots)?	mainly epigeic
Myndus musivus (Germar, 1825)	western palaearctic?	adult	mp2?	P	*Salix* spp., narrow-leaved	nymphs in soil
Apartus michalki (W. Wagner, 1948)	european	adult	op1?	P	*Pinus sylvestris*, *P. nigra*, *Picea abies*	nymphs in soil
Pentastiridius beieri (W. Wagner, 1970)	european	adult	op2?	P	*Salix* spp., narrow-leaved (et al.?)	nymphs in soil
Setapius apiculatus (Fieber, 1876)	european	adult	pol?	P	unknown	nymphs in soil
Setapius cuspidatus (Fieber, 1876)	mediterranean	adult	pol?	P	various shrubs	nymphs in soil
Reptalus melanochaetus (Fieber, 1876)	western palaearctic	adult	pol?	P	shrubs et al.	nymphs in soil
Reptalus panzeri (P. Löw, 1883)	european	adult	pol?	P	shrubs et al.	nymphs in soil
Reptalus quinquecostatus (Dufour, 1833)	western palaearctic?	adult	pol?	P	shrubs	nymphs in soil
Hyalesthes obsoletus Signoret, 1865	western palaearctic	adults occasionally	pol	P	mainly forbs	mainly in herb layer, nymphs in soil
Hyalesthes luteipes Fieber, 1876	mediterranean	adults occasionally	pol	P	various trees and shrubs	nymphs in soil
Hyalesthes philesakis Hoch, 1986	mediterranean	adults occasionally	pol	P	various trees and shrubs	nymphs in soil
Delphacidae Leach, 1815						
Asiraca clavicornis (Fabricius, 1794)	western palaearctic	occasionally	pol	P	herbs, (shrubs)	mainly in herb layer
Achilidae Stål, 1866						
Cixidia pilatoi D'Urso & Guglielmino, 1995	mediterranean?	adult	pol?	F	Fungi	nymphs in litter or topsoil
Cixidia confinis (Zetterstedt, 1828)	european?	adult	mp1?	F	fungi in dead wood of *Pinus sylvestris*	nymphs in decaying wood
Tettigometridae Germar, 1821						
Tettigometra macrocephala Fieber, 1865	western palaearctic	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra atra Hagenbach, 1825	western palaearctic	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer

taxon	geographic range	period of arboreality	host range	resource	host or food plant(s)	remark
Tettigometra fusca Fieber, 1865	western palaearctic?	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra griseola Fieber, 1865	western palaearctic	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra impressopunctata Dufour, 1846	mediterranean	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra laeta Herrich-Schäffer, 1835	mediterranean	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra leucophaea (Preyssler, 1792)	trans-palaearctic	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra sulphurea Mulsant & Rey, 1855	western palaearctic	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Tettigometra virescens (Panzer, 1799)	mediterranean	occasionally	pol?	P	forbs, (woody plants)	mainly in herb layer
Issidae Spinola, 1839						
Issus coleoptratus (Fabricius, 1781)	mediterranean?	nymph/adult	pol	P	woody plants (et. al.?)	oviposition into soil
Issus muscaeformis (Schrank, 1781)	european?	nymph/adult	pol?	P	woody plants (et. al.?)	oviposition into soil
Flatidae Spinola, 1839						
Metcalfa pruinosa (Say, 1830)	nearctic	permanent	pol	P	mainly trees and shrubs	neozoon
Cicadomorpha Evans, 1946 - Leafhoppers *s. l.*						
Cicadidae Leach, 1815 – Cicadas						
Cicada orni Linnaeus, 1758	mediterranean	adult	pol?	X	various woody plants	nymphs in soil
Cicadatra atra (Olivuer, 1790)	mediterranean	adult	pol?	X	various woody plants	nymphs in soil
Lyristes plebejus (Scopoli, 1763)	mediterranean	adult	pol?	X	various woody plants	nymphs in soil
Tibicina haematodes (Scopoli, 1763)	mediterranean	adult	pol?	X	various woody plants	nymphs in soil
Tibicina steveni (Krynicki, 1847)	mediterranean	adult	pol?	X	various woody plants	nymphs in soil
Cicadetta brevipennis Fieber, 1876	european?	adult	pol	X	various woody plants	nymphs in soil
Cicadetta cerdaniensis Puissant & Boulard, 2000	european?	adult	pol?	X	various woody plants	nymphs in soil
Cicadetta montana (Scopoli, 1772)	trans-palaearctic?	adult	pol	X	various woody plants	nymphs in soil
Cicadetta podolica (Eichwald, 1830)	european	adult	pol?	X	various woody plants	nymphs in soil
Cicadivetta tibialis (Panzer, 1788)	western palaearctic	adult	pol?	X	various woody plants	nymphs in soil
Cercopidae Leach, 1815						
Cercopis arcuata Fieber, 1844	european	adults occasionally	pol?	X	forbs et al.	mainly in herb layer
Cercopis sanguinolenta (Scopoli, 1763)	mediterranean?	adults occasionally	pol	X	herbs et al.	mainly in herb layer
Cercopis vulnerata Rossi, 1807	european	adults occasionally	pol	X	herbs et al.	mainly in herb layer
Haematoloma dorsatum (Ahrens, 1812)	mediterranean	adult	(op1)	X	Poaceae/*Pinus sylvestris*	nymphs in soil
Aphrophoridae Amyot & Serville, 1843 - Froghoppers						
Lepyronia coleoptrata (Linnaeus, 1758)	trans-palaearctic	adults occasionally	pol	X	mainly Poaceae and herbs	mainly in herb layer
Neophilaenus campestris (Fallén, 1805)	mediterranean?	adults occasionally	op1	X	Poaceae	mainly in herb layer
Aphrophora alni (Fallén, 1805)	trans-palaearctic	adult	pol	X	herbs/deciduous woody plants	nymphs in herb layer
Aphrophora major Uhler, 1896	siberian	adult	pol	X	herbs/deciduous woody plants	nymphs in herb layer
Aphrophora corticea Germar, 1821	european	adult	pol	X	*Pinus sylvestris*, nymphs also on dwarf shrubs	nymphs on dwarf shrubs and young trees
Aphrophora pectoralis Matsumura, 1903	eurosiberian	permanent	mp2	X	*Salix* spp.	
Aphrophora salicina (Goeze, 1778)	eurosiberian	permanent	mp2	X	*Salix* spp.	
Aphrophora similis Lethierry, 1888	siberian	adult?	pol?	X	*Betula pubescens* et al.?	nymphs in herb layer?
Peuceptyelus coriaceus (Fallén, 1826)	siberian	permanent	mp1	X	*Picea abies*	
Philaenus spumarius (Linnaeus, 1758)	trans-palaearctic	adults occasionally	pol	X	mainly herbs and grasses	mainly in herb layer
Membracidae Rafinesque, 1815 – Treehoppers						
Gargara genistae (Fabricius, 1775)	trans-palaearctic	locally summer	op1	P	*Cytisus scoparius*, *Ononis spinosa* et al.	both on dwarf shrubs and shrubs
Centrotus cornutus (Linnaeus, 1758)	eurosiberian?	occasionally	pol	P	herbs, shrubs	mainly in herb layer
Stictocephala bisonia Kopp & Yonke, 1977	nearctic	adult	pol	P	Fabaceae, Rosaceae, Salicaceae et al.	neozoon
Cicadellidae Latreille, 1825 - Leafhoppers *s. str.*						
Ledrinae Kirschbaum, 1868						
Ledra aurita (Linnaeus, 1758)	european	permanent	pol	P	deciduous trees	corticolous
Macropsinae Evans, 1935						

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Oncopsis alni (Schrank, 1801)	european	permanent	mp2	P	*Alnus glutinosa*, *A. incana*	
Oncopsis appendiculata W. Wagner, 1944	european	permanent	mp2	P	*Betula pendula*, *B. pubescens*	
Oncopsis tristis (Zetterstedt, 1840)	eurosiberian	permanent	mp2	P	*Betula pendula*, *B. pubescens*	
Oncopsis avellanae Edwards, 1920	european	permanent	mp1	P	*Corylus avellana*	
Oncopsis carpini (J. Sahlberg, 1871)	european	permanent	mp1	P	*Carpinus betulus*	
Oncopsis flavicollis (Linnaeus, 1761)	trans-palaearctic	permanent	mp2	P	*Betula pendula*, *B. pubescens*	
Oncopsis subangulata (J. Sahlberg, 1871)	european	permanent	mp2	P	*Betula pendula*, *B. pubescens*	
Pediopsis tiliae (Germar, 1831)	european?	permanent	mp2	P	*Tilia cordata*, *T. platyphyllos*	
Macropsis ocellata Provancher, 1872	western palaearctic	permanent	mp1	P	*Salix alba*	
Macropsis gravesteini W. Wagner, 1953	european?	permanent	mp1	P	*Salix alba*	
Macropsis prasina (Boheman, 1852)	european?	permanent	mp2	P	*Salix* spp., grey-leaved	
Macropsis viridinervis W. Wagner, 1950	european	permanent	mp1	P	*Salix triandra*	
Macropsis notata (Prohaska, 1923)	eurosiberian	permanent	mp2	P	*Salix triandra*, *S. fragilis*	
Macropsis marginata (Herrich-Schäffer, 1836)	european?	permanent	mp1	P	*Salix purpurea*	
Macropsis infuscata (J. Sahlberg, 1871)	european?	permanent	mp2	P	*Salix caprea*, *S. myrsinifolia*	
Macropsis cerea (Germar, 1837)	eurosiberian	permanent	mp2	P	*Salix* spp.	
Macropsis najas Nast, 1981	european?	permanent	mp1	P	*Salix alba*	
Macropsis remanei Nickel, 1999	european	permanent	mp1	P	*Salix eleagnos*	
Macropsis haupti W. Wagner, 1941	european	permanent	mp1	P	*Salix purpurea*	
Macropsis impura (Boheman, 1847)	eurosiberian	permanent	mp2	P	*Salix repens*, *S. aurita*	
Macropsis fuscinervis (Boheman, 1845)	eurosiberian	permanent	mp1	P	*Populus tremula*	
Macropsis graminea (Fabricius, 1798)	western palaearctic?	permanent	mp1	P	*Populus nigra*	
Macropsis vicina (Horváth, 1897)	western palaearctic	permanent	mp1	P	*Populus alba*	
Macropsis glandacea (Fieber, 1868)	european	permanent	mp1?	P	*Ulmus minor*, *U. laevis*?	
Macropsis elaeagni Emelyanov, 1964	central palaearctic	permanent	mp1?	P	*Elaeagnus angustifolia*	neozoon
Macropsis brabantica W. Wagner, 1964*	european	permanent	mp1	P	*Rubus caesius*	species status in need of revision
Macropsis fuscula (Zetterstedt, 1828)	western palaearctic	permanent	mp2	P	*Rubus idaeus*, *R. caesius*, *R. fruticosus*	
Macropsis scotti Edwards, 1920	european	permanent	mp1	P	*Rubus fruticosus*	
Macropsis megerlei (Fieber, 1868)	western palaearctic	permanent	mp2	P	*Rosa rubiginosa*, *R. spinosissima* et al.	
Macropsis mulsanti (Fieber, 1868)	western palaearctic	permanent	mp1	P	*Hippophae rhamnoides*	
Agalliinae Kirkaldy, 1901						
Dryodurgades antoniae (Melichar, 1907)	european	permanent	mp1	P	*Cytisus scoparius*	
Idiocerinae Baker, 1915						
Rhytidodus decimusquartus (Schrank, 1776)	western palaearctic	permanent	mp1	P	*Populus nigra* and hybrids	
Rhytidodus wagneri Dlabola, 1965	western palaearctic?	permanent	mp1	P	*Populus nigra*	
Idiocerus lituratus (Fallén, 1806)	western palaearctic	permanent	mp2	P	*Salix* spp.	
Idiocerus vicinus Melichar, 1898	european	permanent	mp2	P	*Salix purpurea*, *S. eleagnos*	
Idiocerus similis Kirschbaum, 1868	european?	permanent	mp1	P	*Salix purpurea*	
Idiocerus stigmaticalis Lethierry, 1874	european	permanent	mp2	P	*Salix* spp.	
Idiocerus herrichii (Kirschbaum, 1868)	western palaearctic?	permanent	mp2	P	*Salix alba*, *S. fragilis*	
Metidiocerus elegans (Flor, 1861)	siberian?	permanent	mp2	P	*Salix cinerea*, *S. caprea*, *S. aurita*	
Metidiocerus rutilans (Kirschbaum, 1868)	eurosiberian	permanent	mp2	P	*Salix* spp.	horizontal migrant?
Metidiocerus impressifrons (Kirschbaum, 1868)	siberian	permanent	mp2	P	*Salix viminalis*, *S. purpurea*	
Sahlbergotettix salicicola (Flor, 1861)	eurosiberian?	permanent	mp2?	P	*Salix* spec.	
Stenidiocerus poecilus (Herrich-Schäffer, 1835)	western palaearctic	permanent	mp1	P	*Populus nigra*	
Tremulicerus tremulae (Estlund, 1796)	eurosiberian	permanent	mp1	P	*Populus tremula*	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Tremulicerus vitreus (Fabricius, 1803)	european	permanent	mp1	P	*Populus nigra* and hybrids	
Tremulicerus distinguendus (Kirschbaum, 1868)	european	permanent	mp1	P	*Populus alba*	
Tremulicerus fulgidus (Fabricius, 1775)	western palaearctic	permanent	mp1	P	*Populus nigra*, hybrids?, evergreens in winter?	horizontal migrant?
Tremulicerus fasciatus (Fieber, 1868)*	european	permanent	?	P	?	species status in need of revision
Viridicerus ustulatus (Mulsant & Rey, 1855)	western palaearctic	permanent	mp1	P	*Populus alba*	
Bugraia ocularis (Mulsant & Rey, 1855)	mediterranean	permanent	mp2?	P	*Populus alba*, *P. nigra*?	
Populicerus albicans (Kirschbaum, 1868)	western palaearctic	permanent	mp1	P	*Populus alba*	
Populicerus confusus (Flor, 1861)	trans-palaearctic	permanent	mp2	P	*Salix* spp., grey-leaved	
Populicerus nitidissimus (Herrich-Schäffer, 1835)	western palaearctic?	permanent	mp1	P	*Populus nigra*	
Populicerus laminatus (Flor, 1861)	eurosiberian	permanent	mp1	P	*Populus tremula*	
Populicerus populi (Linnaeus, 1761)	trans-palaearctic	permanent	mp1	P	*Populus tremula*	
Acericerus heydenii (Kirschbaum, 1868)	european	permanent	mp2	P	*Acer pseudoplatanus* (and other *Acer* spp.)	
Acericerus ribauti Nickel & Remane, 2002	european	permanent	mp2	P	*Acer campestre* (and other *Acer* spp.)	
Acericerus vittifrons (Kirschbaum, 1868)	european	permanent	mp2	P	*Acer campestre* (and other *Acer* spp.)	
Balcanocerus larvatus (Herrich-Schäffer, 1835)	european	permanent	mp1	P	*Prunus spinosa*	
Balcanocerus pruni (Ribaut, 1952)	mediterranean	permanent	mp1	P	*Prunus spinosa*	
Iassinae Amyot & Serville, 1843						
Batracomorphus allionii (Turton, 1802)	eurosiberian?	locally summer	op1	P	*Cytisus scoparius*, *Genista tinctoria*	both on dwarf shrubs and shrubs
Iassus lanio (Linnaeus, 1761)	european	permanent	mp2	P	*Quercus robur*, *Qu. petraea*	
Iassus mirabilis Orosz, 1979	european	permanent	mp1	P	*Quercus cerris*	
Iassus scutellaris (Fieber, 1868)	european	permanent	mp1?	P	*Ulmus minor*, *U. laevis*?	
Penthimiinae Kirschbaum, 1868						
Penthimia nigra (Goeze, 1778)	mediterranean	permanent	pol	P	deciduous shrubs and trees	
Cicadellinae Latreille, 1825						
Graphocephala fennahi Young, 1977	nearctic	permanent	(mp2)?	X!	*Rhododendron* (et al.?)	neozoon
Typhlocybinae Kirschbaum, 1868						
Alebra neglecta W. Wagner, 1940	eurosiberian?	permanent	op2	M	*Carpinus betulus*, *Prunus padus*, *Crataegus* spp.	
Alebra coryli Le Quesne, 1977	european	permanent	mp2	M	*Corylus avellana*, (*C. maxima*, *C. colurna*)	
Alebra sorbi W. Wagner, 1949*	european	permanent	mp1	M	*Sorbus aria*	species status in need of revision
Alebra wahlbergi (Boheman, 1845)	european	permanent	pol	M	deciduous woody plants	
Alebra albostriella (Fallén, 1826)	european	permanent	op2	M	*Quercus robur*, *Alnus glutinosa*	
Alebra viridis Rey, 1891	european	permanent	mp1?	M	*Quercus petraea*, *Qu. cerris*, *Castanea sativa* (et al.?)	
Liguropia juniperi (Lethierry, 1876)	mediterranean	permanent	mp1?	M	*Chamaecyparis lawsoniana* (et al.?)	Invasive in central Europe?
Igutettix oculatus (Lindberg, 1929)	eastern palaearctic	permanent	mp2	M	*Syringa* spp.	neozoon
Kybos austriacus (W. Wagner, 1949)*	european	permanent	mp2?	M	*Betula* spec.	species status in need of revision
Kybos butleri (Edwards, 1908)	eurosiberian	permanent	mp2	M	*Salix triandra*, *S. repens*, *S. cinerea*, *S. aurita*	
Kybos rufescens Melichar, 1896	eurosiberian	permanent	mp1	M	*Salix purpurea*	
Kybos limpidus (W. Wagner, 1955)	european?	permanent	mp2	M	*Salix viminalis*, *S. triandra*	
Kybos abstrusus (Linnavuori, 1949)	european	permanent	mp1	M	*Populus nigra italica*, *P. n. nigra*	
Kybos populi (Edwards, 1908)	eurosiberian	permanent	mp2	M	*Populus tremula*, *P. alba*, *P. nigra*	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Kybos sordidulus (Ossiannilsson, 1941)	siberian	permanent	mp2	M	*Salix myrsinifolia* et al.	
Kybos lindbergi (Linnavuori, 1951)	siberian	permanent	mp2	M	*Betula pendula*, *B. pubescens*	incl. *K. betulicola* (W. Wg.)
Kybos digitatus (Ribaut, 1936)	european	permanent	mp1?	M	*Salix eleagnos*?	
Kybos smaragdula (Fallén, 1806)	eurosiberian	permanent	mp2	M	*Alnus glutinosa*, *A. incana*	
Kybos calyculus (Cerutti, 1939)	european?	permanent	mp1?	M	*Betula pubescens*?	
Kybos strigilifer (Ossiannilsson, 1941)	european	permanent	mp2	M	*Salix caprea*, *S. cinerea*, *S. myrsinifolia*	
Kybos perplexus (Ribaut, 1952)*	western palaearctic	permanent	mp1?	M	*Salix caprea* (et al.?)	perhaps conspecific with *K. strigilifer*
Kybos mucronatus (Ribaut, 1933)	european	permanent	mp1?	M	*Alnus glutinosa*	
Kybos verbae Zachvatkin, 1953*	european?	permanent	?	M	*Salix*?	perhaps conspecific with *K. mucronatus*
Kybos strobli (W. Wagner, 1949)	european	permanent	mp1?	M	*Alnus incana*?	
Kybos virgator (Ribaut, 1933)	eurosiberian?	permanent	mp2	M	*Salix alba*, *S. fragilis* et al.	
Kybos volgensis Vilbaste, 1961*	european?	permanent	?	M	*Salix* spec.	species status in need of revision
Empoasca affinis Nast, 1937	siberian	occasionally	pol	M?	forbs, (woody plants)	mainly in herb layer
Empoasca apicalis (Flor, 1861)	siberian	permanent?	op1?	M?	*Sambucus ebulus*, *Lonicera xylosteum*?, *L. nigra*?	horizontal migrant
Empoasca decipiens Paoli, 1939	ealaearctic, oriental?, ethiopian?	occasionally	pol	M?	forbs, (woody plants)	mainly in herb layer
Empoasca dealbata Cerutti, 1939	european	?	pol?	M?	*Prunus padus* et al.?	known from only 2 specimens
Empoasca ossiannilssoni Nuorteva, 1948*	siberian	permanent	pol?	M?	various trees and shrubs?	perhaps conspecific with *E. dealbata*
Empoasca kontkaneni Ossiannilsson, 1949	siberian	winter and spring	pol	M?	trees and herbs, *Picea abies* in winter	horizontal and vertical migrant
Empoasca vitis (Göthe, 1875)	trans-palaearctic	permanent	pol	P!	trees and shrubs, evergreens in winter	horizontal migrant
Asymmetrasca decedens (Paoli, 1932)	mediterranean	permanent	pol?	M?	*Salix* spp. et al.	
Kyboasca bipunctata (Oshanin, 1871)	eurosiberian	permanent	op2	M	*Ulmus minor*, *U.* x *hollandica*, *Glycyrrhiza glabra*	
Kyboasca maligna (Walsh, 1862)	nearctic	permanent	op1?	M	*Malus domestica*, *Crataegus* spec.?	neozoon
Fagocyba carri (Edwards, 1914)	european	permanent	mp2	M	*Quercus robur*, *Qu. petraea*	
Fagocyba cerricola Lauterer, 1983	european	permanent	mp1	M	*Quercus cerris*	
Fagocyba cruenta (Herrich-Schäffer, 1838)	european	permanent	pol	M	deciduous woody plants	syn.: *F. douglasi* (Edw.)
Ficocyba ficaria (Horváth, 1897)	nediterranean	permanent	op2	M	*Lonicera spp.*, *Ficus carica*	heteroecious
Ossiannilssonola callosa (Then, 1886)	european	permanent	mp1	M	*Acer pseudoplatanus*	
Edwardsiana alnicola (Edwards, 1924)	european	permanent	mp2	M	*Alnus incana*, *Alnus glutinosa*	
Edwardsiana avellanae (Edwards, 1888)	european	permanent	mp1	M	*Corylus avellana*	syn.: *E. staminata* (Rib.)
Edwardsiana bergmani (Tullgren, 1916)	eurosiberian	permanent	op1	M	*Betula*, *Alnus*	
Edwardsiana candidula (Kirschbaum, 1868)	european	permanent	mp1	M	*Populus alba*	
Edwardsiana martigniaca (Cerutti, 1939)*	european	permanent	mp1	M	*Populus alba*	perhaps conspecific with *E. candidula*
Edwardsiana crataegi (Douglas, 1876)	eurosiberian?	permanent	op1	M	Rosaceae	
Edwardsiana diversa (Edwards, 1914)	western palaearctic	permanent	mp2	M	*Cornus sanguinea*, *C. mas*	
Edwardsiana flavescens (Fabricius, 1794)	european	permanent	op2	M	*Carpinus betulus*, *Fagus sylvatica* (u.a.?)	
Edwardsiana flexuosa (Ribaut, 1931)	european	permanent	mp1?	M	*Salix eleagnos*?	
Edwardsiana rhodophila (Cerutti, 1937)	european	permanent	mp1	M	*Rosa rubiginosa*	
Edwardsiana nicolovae Dlabola, 1967	european	permanent	mp1?	M	*Rosa spinosissima*	
Edwardsiana sociabilis (Ossiannilsson, 1936)	european	permanent (some populations)	op1	M	*Rosa rugosa*, *Filipendula ulmaria*	both on a native tall herb and a neophytic shrub
Edwardsiana frustrator (Edwards, 1908)	european	permanent	pol	M	deciduous woody plants	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Edwardsiana ampliata (W. Wagner, 1948)	european	permanent	op2?	M	*Tilia*?, *Acer*?, *Corylus*?, *Quercus*?	
Edwardsiana geometrica (Schrank, 1801)	european	permanent	mp2	M	*Alnus glutinosa*, *A. incana*, *A. alnobetula*?	
Edwardsiana gratiosa (Boheman, 1852)	european	permanent	mp1	M	*Alnus glutinosa*	
Edwardsiana lamellaris (Ribaut, 1931)	european	permanent	op2?	M	*Rosa canina*?, *Quercus*?	
Edwardsiana lethierryi (Edwards, 1881)	european	permanent	op2	M	*Acer campestre*, *Tilia spp.* (et al.?)	
Edwardsiana plurispinosa (W. Wagner, 1935)	european?	permanent	op1	M	*Corylus avellana*, *Alnus glutinosa*	
Edwardsiana ulmiphagus Wilson & Claridge, 1999	european?	permanent	mp2	M	*Ulmus minor*, *U. laevis*, *U. glabra*	
Edwardsiana ishidai (Matsumura, 1932)	eurosiberian	permanent	mp2?	M	*Ulmus minor*, *U. laevis*, *U. glabra*, *Corylus avellana*?	
Edwardsiana lanternae (W. Wagner, 1937)*	european?	permanent	op2?	M	*Alnus glutinosa*, *Sorbus aucuparia*?	species status in need of revision
Edwardsiana menzbieri Zachvatkin, 191948	siberian	permanent	mp2?	M	*Salix* spec.	
Edwardsiana soror (Linnavuori, 1950)	siberian	permanent	mp1?	M	*Alnus incana*	
Edwardsiana nigriloba (Edwards, 1924)	european	permanent	mp1	M	*Acer pseudoplatanus*	
Edwardsiana platanicola (Vidano, 1961)	european	permanent	mp2	M	*Platanus* spp.	
Edwardsiana plebeja (Edwards, 1914)	western palaearctic	permanent	mp2	M	*Ulmus minor*, *U. laevis*, *U. glabra*	
Edwardsiana prunicola (Edwards, 1914)	european	permanent	op2	M	*Prunus*, *Salix* spp., grey-leaved	
Edwardsiana rosae (Linnaeus, 1758)	trans-palaearctic	permanent	op1	M	*Rosa*, *Prunus spinosa* et al.	
Edwardsiana rosaesugans (Cerutti, 1939)	european	permanent	mp1?	M	*Rosa pendulina*, *R. canina*?	
Edwardsiana salicicola (Edwards, 1885)	siberian	permanent	mp2	M	*Salix* spp., grey-leaved	
Edwardsiana smreczynskii Dworakowska, 1971	european	permanent	mp2?	M	*Ulmus minor*, *U. laevis*?	
Edwardsiana spinigera (Edwards, 1924)	european	permanent	mp1	M	*Corylus avellana*	
Edwardsiana stehliki Lauterer, 1958	european	permanent	mp1?	M	*Corylus avellana* (et al.?)	
Edwardsiana tersa (Edwards, 1914)	siberian	permanent	mp2?	M	*Salix viminalis*, *S. pentandra*?	
Edwardsiana kemneri (Ossiannilsson, 1942)*	eurosiberian?					a dubious species
Eupterycyba jucunda (Herrich-Schäffer, 1837)	european	permanent	mp1	M	*Alnus glutinosa*	
Linnavuoriana decempunctata (Fallén, 1806)	siberian	permanent	mp2	M	*Betula pendula*, *B. pubescens*	horizontal migrant
Linnavuoriana intercedens (Linnavuori, 1949)	european?	permanent	mp1	M	*Alnus incana*	horizontal migrant?
Linnavuoriana sexmaculata (Hardy, 1850)	eurosiberian?	permanent	mp2	M	*Salix* spp.	
Lindbergina aurovittata (Douglas, 1875)	mediterranean	permanent	pol?	M	*Rubus*, *Quercus*, *Fagus* et al.	heteroecious
Lindbergina loewi (Lethierry, 1884)	mediterranean	permanent	mp1?	M	*Quercus cerris*	
Ribautiana alces (Ribaut, 1931)	european	permanent	mp2	M	*Quercus* spp.	
Ribautiana debilis (Douglas, 1876)	mediterranean	permanent	op1?	M	*Rubus fruticosus*, *R. caesius* et al.	
Ribautiana scalaris (Ribaut, 1931)	european	permanent	mp2	M	*Quercus* spp.	
Ribautiana tenerrima (Herrich-Schäffer, 1837)	european	permanent	op2?	M	*Rubus* et al.	
Ribautiana ognevi (Zachvatkin, 1948)	european	permanent	mp1	M	*Ulmus laevis*	
Ribautiana cruciata (Ribaut, 1931)	mediterranean	permanent	mp1?	M	*Ulmus minor* (et al.?)	
Ribautiana ulmi (Linnaeus, 1758)	european	permanent	mp2	M	*Ulmus minor*, *U. laevis*, *U. glabra*	
Typhlocyba quercus (Fabricius, 1777)	western palaearctic	permanent	op2?	M	*Prunus*, *Quercus* (et al.?)	
Zonocyba bifasciata (Boheman, 1851)	european	permanent	op2	M	*Carpinus betulus*, *Ulmus minor*, *U. glabra*	
Eurhadina concinna (Germar, 1831)	european	permanent	op1?	M	*Quercus* spp.	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Eurhadina kirschbaumi W. Wagner, 1937	european	permanent	op1?	M	mainly *Quercus petraea*	
Eurhadina loewii (Then, 1886)	european	permanent	mp1	M	*Acer pseudoplatanus*	
Eurhadina pulchella (Fallén, 1806)	trans-palaearctic?	permanent	mp2	M	*Quercus robur*, *Qu. petraea*	
Eurhadina ribauti W. Wagner, 1935	european	permanent	mp2	M	*Quercus robur*, *Qu. petraea*	
Eurhadina saageri W. Wagner, 1937	european	permanent	mp1?	M	*Quercus robur* (et al.?)	
Wagneripteryx germari (Zetterstedt, 1840)	eurosiberian	permanent	mp2	M	*Pinus sylvestris*, *P. mugo*	
Aguriahana pictilis (Stål, 1853)	siberian	permanent	mp1?	M	*Betula pubescens*?, *Vaccinium myrtillus*?	
Aguriahana stellulata (Burmeister, 1841)	eurosiberian?	permanent	pol?	M	*Tilia*, *Prunus*, *Populus*, *Betula*, *Acer*	
Zyginella pulchra P. Löw, 1885	european	permanent	mp2	M	*Acer* spp.	horizontal migrant?
Alnetoidia alneti (Dahlbom, 1850)	eurosiberian	permanent	pol	M	deciduous woody plants	
Zygina lunaris (Mulsant & Rey, 1855)	mediterranean	permanent	(mp2)?	M	*Salix alba*, *S. fragilis*, *S. purpurea* (et al.?)	horizontal migrant
Zygina nivea (Mulsant & Rey, 1855)	mediterranean	permanent	mp1?	M	*Populus alba* (et al.?)	horizontal migrant?
Zygina tithide Ferrari, 1882	european	permanent	mp1?	M	*Populus alba* (et al.?)	vagrant in Germany?
Zygina angusta Lethierry, 1874	eurosiberian	permanent	op2	M	*Crataegus*, *Rosa*, *Prunus*, *Quercus*, *Fagus* (et al.?)	horizontal migrant
Zygina discolor Horváth, 1897	western palaearctic	permanent	op1?	M	Rosaceae spp. (et al.?)	heteroecious
Zygina flammigera (Geoffroy, 1785)	eurosiberian?	permanent	(op1)?	M	*Prunus* et al.	horizontal migrant
Zygina ordinaria (Ribaut, 1936)	eurosiberian?	permanent	mp2	M	*Salix* spp., narrow-leaved	horizontal migrant?
Zygina rhamni Ferrari, 1882	mediterranean?	permanent	pol	M	*Rosa, Rubus, Vitis* (et al.)	heteroecious
Zygina rorida (Mulsant & Rey, 1855)	mediterranean	permanent	(mp2?)	M	*Quercus* spp. (et al.)	horizontal migrant
Zygina rosea (Flor, 1861)	european?	permanent	(mp1)?	M	*Betula pubescens*, *Pinus sylvestris*?	horizontal migrant
Zygina salicina Mityaev, 1975*	eurosiberian?	permanent	mp1?	M	*Salix repens*	European records in need of revision
Zygina suavis Rey, 1891	eurosiberian?	permanent	op1	M	*Rhamnus cathartica*, *Frangula alnus*	horizontal migrant
Zygina schneideri (Günthart, 1974)	european	permanent	op1	M	*Prunus spinosa*, *Rosa* spp. (et al.?)	
Zygina tiliae (Fallén, 1806)	european	permanent	op2	M	*Alnus glutinosa*, *A. incana*, *Tilia cordata*	horizontal migrant
Zygina rosincola (Cerutti, 1939)	european?	permanent	(op1)?	M	*Rosa* spec. (et al.?)	horizontal migrant
Zygina griseombra Remane, 1994	european	permanent	(mp1)	M	*Carpinus betulus*	horizontal migrant
Zygina nigritarsis Remane, 1994	european?	permanent	(mp1)	M	*Prunus padus*	horizontal migrant
Arboridia erecta (Ribaut, 1931)	european	permanent	op2?	M	*Acer campestre*? (et al.?)	horizontal migrant?
Arboridia parvula (Boheman, 1845)	trans-palaearctic	locally	op2?	M	Rosaceae spp., deciduous trees	mainly in herb layer
Arboridia ribauti (Ossiannilsson, 1937)	european	permanent	op2	M	*Carpinus betulus*, *Tilia cordata* (et al.?)	horizontal migrant?
Arboridia simillima (W. Wagner, 1939)	european	permanent	mp2	M	*Rosa spinosissima* et al.	horizontal migrant?
Arboridia velata (Ribaut, 1952)	european	permanent	mp2?	M	*Quercus* (et al.?)	horizontal migrant?
Arboridia spathulata (Ribaut, 1931)	european	permanent	mp2?	M	*Quercus* spp.	horizontal migrant?
Fruticidia bisignata (Mulsant & Rey, 1855)	mediterranean	permanent	op1?	M	*Crataegus, Malus, Rosa* et al.	
Fruticidia sanguinosa (Rey, 1891)	mediterranean	permanent	op1?	M	*Crataegus, Prunus* et al.	
Deltocephalinae Fieber, 1869						
Fieberiella bohemica Dlabola, 1965	european	permanent	pol	P	?	
Fieberiella florii (Stål, 1864)	mediterranean	permanent	pol	P	deciduous shrubs	
Fieberiella septentrionalis W. Wagner, 1963	eestern palaearctic?	permanent	pol	P	deciduous shrubs	
Synophropsis lauri (Horváth, 1897)	mediterranean	permanent	pol	P	Evergreen shrubs	
Placotettix taeniatifrons (Kirschbaum, 1868)	mediterranean	permanent	pol?	P	*Rhododendron,* other evergreen shrubs	
Phlogotettix cyclops (Mulsant & Rey, 1855)	trans-palaearctic	adult?	pol?	P	various	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Scaphoideus titanus Ball, 1932	nearctic	permanent	mp1	P	*Vitis vinifera*	neozoon
Grypotes puncticollis (Herrich-Schäffer, 1834)	western palaearctic	permanent	mp1	P	*Pinus sylvestris*	
Japananus hyalinus (Osborn, 1900)	eurosiberian	permanent	mp2	P	*Acer campestre* u.a.	
Opsius stactogalus Fieber, 1866	mediterranean	permanent	op1	P	*Myricaria germanica*, *Tamarix* spp.	
Balclutha boica W. Wagner, 1950	siberian?	winter?	op1?	P	Poaceae/coniferous trees?	
Balclutha punctata (Fabricius, 1775)	trans-palaearctic?	winter?	(op1)	P	Poaceae/coniferous trees?	
Sagatus punctifrons (Fallén, 1826)	eurosiberian	permanent	mp2	P	*Salix* spp., narrow-leaved	
Platymetopius complicatus Nast, 1972	mediterranean?	adult?	pol?	P	?	
Platymetopius dorsofenestratus Dlabola, 1958	mediterranean?	adult?	pol?	P	?	
Platymetopius filigranus (Scott, 1876)	mediterranean	adult?	pol?	P	?	
Platymetopius guttatus Fieber, 1869	western palaearctic	adult	pol?	P	?/*Betula pendula*, *Quercus* spp.	nymphs in herb layer?
Platymetopius henribauti Dlabola, 1961*						taxonomically dubious
Platymetopius rostratus (Herrich-Schäffer, 1834)	western palaearctic	adult?	pol?	P	?	
Platymetopius major (Kirschbaum, 1868)	european	adult	pol	P	herbs/*Betula*, *Quercus*	nymphs in herb layer
Platymetopius undatus (De Geer, 1773)	trans-palaearctic?	adult	op2?	P	*Quercus*?, *Betula*?	nymphs in herb layer
Anoplotettix fuscovenosus (Ferrari, 1882)	mediterranean	adult	pol	P	deciduous shrubs and trees (incl. *Vitis*)	nymphs in herb layer
Anoplotettix horvathi Metcalf, 1955	european	adult?	pol?	P	deciduous shrubs and trees	nymphs in herb layer?
Idiodonus cruentatus (Panzer, 1799)	eurosiberian	adult	pol	P	herbs/woody plants	nymphs in herb layer; also in alpine belt
Colladonus torneellus (Zetterstedt, 1828)	eurosiberian	adult	pol?	P	*Melica uniflora*?/trees and shrubs?	nymphs in herb layer
Lamprotettix nitidulus (Fabricius, 1787)	european	adult	pol?	P	herbs?/*Quercus*, *Ulmus* et al.	nymphs in herb layer
Allygus communis (Ferrari, 1882)	european	adult	pol?	P	Poaceae?/*Quercus*, *Betula*	nymphs in herb layer
Allygus mixtus (Fabricius, 1794)	european	adult	pol?	P	Poaceae?/deciduous trees and shrubs	nymphs in herb layer
Allygus maculatus Ribaut, 1952	european	adult	op2?	P	Poaceae?/*Quercus* spp.	nymphs in herb layer
Allygus modestus Scott, 1876	european	adult	pol?	P	Poaceae/deciduous trees	nymphs in herb layer
Allygidius commutatus (Fieber, 1872)	european	adult	(op1)?	P	Poaceae/*Quercus*, *Ulmus*, *Betula* et al.	nymphs in herb layer
Allygidius abbreviatus (Lethierry, 1878)	european	adult	(op1)?	P	Poaceae/deciduous shrubs and trees	nymphs in herb layer
Allygidius atomarius (Fabricius, 1794)	european	adult	(op1)?	P	Poaceae/*Ulmus*, *Quercus* (et al.?)	nymphs in herb layer
Allygidius furcatus (Ferrari, 1882)	european	adult	op1?	P	Poaceae?/deciduous shrubs and trees	nymphs in herb layer
Allygidius mayri (Kirschbaum, 1868)	european	adult	op1?	P	Poaceae?/deciduous shrubs and trees	nymphs in herb layer
Mimallygus lacteinervis (Kirschbaum, 1868)	european	permanent	mp1?	P	*Salix purpurea* (et al.?)	on very low shoots only
Orientus ishidae (Matsumura, 1902)	eastern palaearctic	permanent	pol	P	deciduous shrubs	neozoon
Selenocephalus obsoletus (Germar, 1817)	mediterranean	permanent?	pol	P	Evergreen and deciduous shrubs	
Speudotettix subfusculus (Fallén, 1806)	trans-palaearctic	adult	pol	P	*Carex*, Poaceae?/ deciduous woody plants	nymphs in herb layer; also in alpine belt
Hesium domino (Reuter, 1880)	european	adult	op2?	P	Poaceae/*Betula* et al.	nymphs in herb layer
Thamnotettix confinis (Zetterstedt, 1828)	eurosiberian	adult	pol	P	herbs/deciduous woody plants	nymphs in herb layer; also in alpine belt
Thamnotettix dilutior (Kirschbaum, 1868)	european	adult	pol?	P	Poaceae (et al.?)/*Quercus* et al.?	nymphs in herb layer
Thamnotettix exemtus Melichar, 1896	european	adult?	pol?	P	various broad-leaved trees and shrubs	
Pithyotettix abietinus (Fallén, 1806)	european	permanent	mp1?	P	*Picea abies*, *Abies alba*?	
Perotettix pictus (Lethierry, 1876)	european	permanent	mp1?	P	*Picea abies*, *Abies alba*?	

taxon	geographic range	period of arboreality	host range	re-source	host or food plant(s)	remark
Colobotettix morbillosus (Melichar, 1896)	european	permanent	mp1?	P	*Picea abies*, *Abies alba*?	
Euscelis ohausi W. Wagner, 1939	european	locally summer	op1	P	*Cytisus scoparius*, *Genista anglica*	both on dwarf shrubs and shrubs

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Canopy Arthropod Research in Europe

Basic and applied studies from the high frontier

Edited by Andreas Floren (Univ. Würzburg) & Jürgen Schmidl (Univ. Erlangen-Nuremberg)

Foreword by K.E. Linsenmair, University of Würzburg, Dep. of Animal Ecology and Tropical Biology

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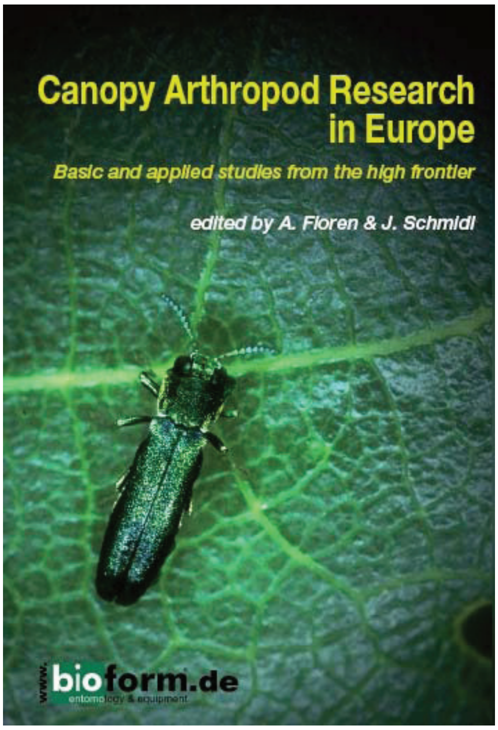

Aims & Scope: In contrast to tropical ecosystems, in temperate zones the importance of canopy ecology is underestimated and underrepresented in science projects. Recent surveys and studies show that also in temperate forest canopies a diverse arthropod fauna exists, containing specialized and endangered species and even species new to science. Species and guild compositions of canopy arthropods in European forests are not yet described sufficiently, and many functional aspects of temperate forests still are not understood or studied.
The present volume tries to reduce this gap by summarizing studies and papers dealing with canopy arthropods in Europe. Aspects of diversity, function, structure and dynamics of canopy arthropod as well as aspects of nature conservation and transmission of scientific results into forestry and management practice are central aims of this book.

Contents & Chapters: Foreword ● Introduction ● General forest ecological aspects ● Arthropod diversity, guilds and structure related communities ● Stratification and distribution of arthropods in tree habitats ● Anthropogenic and natural disturbance structuring arthropod communities ● Canopy research and its impact on forestry and nature protection practice.

The volume is fully refereed

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Canopy Arthropod Research in Europe

Basic and applied studies from the high frontier.

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"As the global community comes to realise that our climatic future is intimately tied up with the health of our forests so canopy studies take their rightful place in the forefront of forest science. This book will ensure that studies of temperate forest canopies no longer remain the 'poor cousins' of tropical canopy studies. The research described will stimulate new and exciting activities in temperate canopy studies as well as giving the newcomer to the field an invaluable insight into what has gone before." Roger Kitching, Professor of Ecology, Griffith University, Brisbane

Table of Content