Phylogenetic Relationships, Ecology, and Ecological Genetics of Cecidogenous Tephritidae

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ABSTRACT

In this chapter, we analyze the phylogenetic relationships, ecology and ecological genetics of cecidogenous and gallicolous species in the subfamilies and tribes of the family Tephritidae. A vast majority of the gall-inducing and gall-inhabiting species belong to the subfamily Tephritinae. Certain genera in the tribes Myopitini, Cecidocharini, Eutretini, and Tephritini, and the Tomoplagia group of genera include many species which induce galls on asteraceous plants. Other species of these genera live on plant tissues without inducing galls. Often, gall-inducing species occur sporadically among nongall-inducing relatives. Ability to induce galls arises independently in all these tribes, and more than once in the Myopitini, Eutretini, and Tephritini. In Oxyna, certain species have secondarily lost their ability to induce galls. The tribe Dithyrcini (= Oedaspidini) is apparently the most specialized group, comprising only gall-inducing species showing strict host-plant preferences.

The evolutionary path leading to galls of different degrees of complexity has been reconstructed for the species in Urophora. As for its origin we assume a ‘species’ mining the achenes in the flower heads of Asteraceae. Gall evolution possibly started with a primitive nonlignified ovary gall as in the little-specialized \textit{U. quadrifasciata} (Meigen). The fascicular parenchyma of the achene is stimulated to result in the proliferation of the tissue and to enrich the cells with nutritious substances. More advanced evolutionary stages are the lignified unilocular and multilocular ‘cup-shaped’ ovary-receptacle galls found in several Urophora species associated with species of Centaurea and Mantisalca. Protective tissue in such galls consists of relatively thin lignified layers, which extend from the achene into the upper tissues of the receptacle. In a yet more complex type of gall, a considerable part of the receptacle becomes firmly lignified tissue, which surrounds the gall cavity with its nutritive tissues, and an exit channel. These are the multilocular ‘block’ galls of the species of Urophora developing in the capitula of Carthamus, Cirsium, and Carduus. The most elaborate gall type is the multilocular shoot gall of closely related and highly specialized \textit{Urophora cardui} (Linnaeus) and \textit{U. misakiana} (Matsumura) on \textit{Cirsium}. Benefits of this evolutionary trend are an increased capacity of the larvae to obtain nutrients from their host plant and an increased protection against intraguild
predation and generalist parasitoids; costs, however, are a longer larval period and a reduced host range.

Of the 200 described cecidogenous tephritid species only three have been studied with respect to their evolutionary ecology: Eurosta solidaginis (Fitch), Tephritis conura (Loew), and Urophora cardui. Most of the ecological and evolutionary processes of these species occur in the ‘shell’ of the gall, and can, therefore, be easily studied and constructed.

E. solidaginis and T. conura exemplify parapatric or sympatric speciation that is facilitated by their ability to adapt to a novel host plant. Whereas this process is completed in E. solidaginis, with two genetically distinct host races on Solidago altissima and S. gigantea, T. conura is, most probably, still in the process of differentiation. In contrast to E. solidaginis, T. conura attacks at least nine host plants, which are partially sympatric, parapatric or allopatric, but are not attacked over their entire distribution range in central Europe.

U. cardui is monophagous in central Europe and attacks only Cirsiurn arvense. Partly conflicting observations are discussed with respect to the post-glacial invasion history and its consequences for the population genetic structure of U. cardui. Clinal variations of genotypes have been observed on different spatial scales from 50 to 1,000 km. Whether this is the result of a still ongoing colonization of Europe after the last ice age or a repeated colonization wave after local extinctions, or even of the immigration of a different host race from eastern Europe, remains a question.

INTRODUCTION

About 5 percent of the 4,300 described species of Tephritidae ('true' fruit flies) are cecidogenous, thus making the tephritids the second most important gall-inducing dipteran family after the Cecidomyiidae (Freidberg 1984, 1998). Several species of cecidogenous tephritids (e.g., Urophora spp.) have been used in biological control, and are therefore of economic interest. Compared with the overwhelming amount of information that is available on tephritids in general, especially for fruit flies of economic importance (see Aluja and Norrbom 1999), only a few species of cecidogenous tephritids have been investigated in detail, and “some of these works are very old, rare or otherwise not easily accessible” (Freidberg 1984). Even the recent reviews on gall-inducing tephritids (Freidberg 1984, 1998) are in books that are not widely disseminated.

The history of studies on the biology of gall-inducing tephritids and the recent information has been reviewed by Freidberg (1984, 1998). In this chapter, we present the developments since Freidberg’s reviews; the key aspect will be to analyze the phylogenetic relationships of gall-inducing tephritids, which, we believe, will serve as a basis for further conclusions on the evolutionary ecology of gall induction in this family. In the first section, each of the tribes and groups of genera of the subfamily Tephritinae is considered with respect to occurrence of cecidogeny, including those with no gall-inducing capacity.

Preliminary cladistic analyses of certain taxa have been used to produce the trees, on which the distribution of cecidogeny and its evolution are explained. The program TreeGardener 2.2 (Ramos 1997) was used for preparation of the character matrices, which were then analyzed with use of the program HENNIG’86 (Farris 1988). The ‘mhennig’ option combined with
branch swapping (‘mh bb’ command) was used to generate the most parsimonious trees and, in each example, the Nelson consensus trees from numerous trees obtained from such an analysis itself or in combination with the successive character weighting procedures. Resulting treeplots were obtained from TreeGardener 2.2.

**TAXONOMIC POSITION AND PHYLOGENETIC RELATIONSHIPS OF CECIDOGENOUS TEPHRITIDAE**

Most gall-inducing tephritids belong to the subfamily Tephritinae. The concept of this subfamily has been altered recently (Hancock 1986, 1990, 2001, Foote et al. 1993, Norrbom et al. 1999, Korneyev 1986, 1988, 1999) to include the tephritid taxa associated with the flower heads of Asteraceae, and also certain other closely related fruit fly groups that feed on nonasteraceous plants. Some of these groups were previously considered either separate subfamilies Terelliinae, Myopitinae, Schistopterinae, Acirinae, and Oedaspidinae (e.g., R.H. Foote 1967, Hardy 1973, Freidberg 1984, Freidberg and Kugler 1989) or were merged into the tribe Tephritini (Hardy and Drew 1996). In this chapter, we follow the most detailed scheme based on phylogenetic analysis (Fig. 1) (Korneyev 1999), with some additions and corrections based on new data. To understand the origin of cecidogeny in the Tephritinae, we will also analyze those tribes that include only nongall-inducing flies.

![Diagram of phylogenetic relationships in the subfamily Tephritinae](image)

*Fig. 1* Scheme of phylogenetic relationships in the subfamily Tephritinae (adapted from Korneyev 2000) showing distribution of cecidogeny (shaded lines) in main suprageneric groupings.
The subfamily Tephritinae is divided into two groups of taxa, the Lower Tephritinae (Terelliini, Xyphosini, Noetini, Myopitini, Axiotaumatinii, and possibly Cecidocharini) and the Higher Tephritinae (Dithrycini, Eutretini, Acrotaeniini, Schistopterini, Tephritini, and Tephrellini). The Higher Tephritinae are believed to be a monophyletic group, while the Lower Tephritinae, a paraphyletic cluster. Because of numerous homoplasies, use of morphological characters has not helped in resolving the relationships among the constituent tribes. However, the monophyly of most of the suprageneric groups, discussed later in this section, remains established (Foote et al. 1993, Korneyev 1999).

Morphological characters of adults, such as the shape of the aculeus (the terminal joint of ovipositor) and cuticular structures of the eversible membrane between the oviscape (ovipositor sheath) and the aculeus, show certain regularities in differences between genera and species in each tribe, which can be considered adaptations for phytophagy. Blunt and wide aculei are therefore assumed to be less specialized for penetration into plants, whereas the sharply pointed and narrow aculei are considered to be more specialized. Tephritids with blunt aculei (certain species-groups of Terellia, Icterica, Procecidochares) oviposit between intact florets in flower heads or leaflets of buds (V.K., personal observation, Goeden and Teerink 1997a, B.A. Foote 1967), while those flies possessing needlelike, sawlike, or combined shapes of aculeus tips sometimes pierce or cut plant tissues to insert their eggs. The needlelike aculei occur in both cecidogenous (Urophora of the Myopitini, some Oedaspidina and most Dithrycina of the Dithrycini) and noncecidogenous tephritids (some Terelliini, most Tephrellini). Aculei with serrate posterolateral margins (often sharply pointed at the tip) are common in leaf-mining tephritids (Trypetinae: Trypetini), and also in both gall-inducing (most Dithrycini: Oedaspidina and Eutretini), and nongall-inducing tephritines (some Xyphosini, Eutretini, and Tomoplaga). As these characters have arisen independently in several distantly related lineages of the Tephritinae, they are subject to homoplasy, and are rarely used in phylogenetic reconstruction. However, polarity of this character is rather unambiguous, and the plesiomorphic condition is postulated in the analysis below as blunt aculei. In cecidogenous genera, the blunt aculei usually indicate generalists.

Lower Tephritinae

This group is defined by the presence of long lateral (external) vertical seta and no gap in the row of setulae on the vein R<sub>4+5</sub>, and consists of Terelliini, Xyphosini, Noetini, Axiotaumatinii, Myopitini, and a suprageneric group of unclear rank, the Tomoplaga group (Acrotaeniini, pro parte major). The tribe Cecidocharini shows an intermediate state of the Lower and Higher Tephritinae characters and has been placed here tentatively (Korneyev 1999).

All tribes of lower Tephritinae include noncecidogenous species infesting flower heads of asteraceous plants. Adult oviposition and larval feeding behavior, which were described by Goeden and Headrick (1991b) for Tomoplaga cressoni Aczél, are rather common in generalist capitulum-infest-
ing Lower and Higher Tephritinae, and are believed to show the biological
groundplan features of the subfamily, which are (1) the female oviposits
from the apex of an open flower head after anthesis by inserting the aculeus
between the corolla tubes or into the florets, for example, some Terelliiini,
Neaspilota, and Tomoplagnia (Rozhkov 1956, Goeden 2000, Goeden and
Headrick 1991b); and (2) the third instar excavates a cuplike depression in
the surface of the receptacle without any tissue proliferation (no gall induction),
and feeds by imbibing sap, which collects in the feeding cavity, for
example, in Terellia, Xyphosia (V.K., personal observation), Neaspilota,
Tomoplagnia, Goedenia, Paracantha (Goeden and Headrick 1991b, 1992, Goeden
et al. 1995, Headrick and Goeden 1990a, b), and Tephritis (Romstöck 1987).

Terelliiini

This tribe, considered the sister group to the other Tephritinae, differs from
other members of the subfamily by the rather complex structure of the
phallic glans, which is close to the ground plan of the Higher Tephritidae as
a whole. Most species are associated with the flower heads of Palearctic
plants of the tribe Cardueae, and the most primitive of them are apparently
the species infesting flower heads of Echinops in the southwestern Palearctic
Region including North Africa (Korneyev 2004, B. Merz, unpublished data).
A few species are indigenous to the Nearctic, Oriental, and Afrotropical
Regions, and all belong to groups derived from Palearctic terelliiini. The
tribal position of the New World Neaspilota is still not clear, and is believed
to be related to the Xyphosiini or to the Tomoplagnia group rather than to the
Terelliiini (Korneyev 1999). Females of Terelliiini species basically have rather
blunt and broad oviscapes and oviposit between florets in large flower
heads. Larvae in most cases have well-developed creeping welts, a reticulated
facial mask, and are active borers in flower-head receptacles, often
penetrating into the stem and boring it. This strategy of resource use by
these larvae is apparently the least specialized in the Tephritinae, but
terelliiini tolerate competition with more specialized gall inducers of
Myopitini and Tephritini only in resource-rich, large flower heads. Some
Terellia, and all species of Chaetostomella, Chaetorellia, and Craspedoxantha,
have acute aculei and apparently are able to oviposit by piercing plant
tissues. Chaetorellia species introduce their eggs between the bracts of the
flower heads (H.Z., personal observations). Stem-boring behavior occurs in
species of Terelliiini that share flower-head resources with Urophora
(Myopitini), which form lignified galls limiting resources of terelliiini lar-
vae. Almost all species of Cerajocera show a similar specialized larval behav-
ior. None of the Terelliiini species has ever been reported to induce galls.

Tomoplagnia Group of Genera  This group includes Tomoplagnia, Polionota,
Neotaracia and Caenoriata. The male genitalia also possess quite a primitive
structure. Its members infest predominantly large or moderate-sized flower
heads of Vernonieae and allied genera of the tribe Vernonieae, as well as some
Mutisieae, and may displace the terelliiini in the Western Hemisphere.
However, the aculeus shape in females is more acute, often serrate, and the
known larvae are bulkier and less mobile than those of most terelliiini
(Benjamin 1934, Goeden and Headrick 1991b). A few cecidogenous *Tomoplaga*
are known, among them *T. vernoniae* Hering from Brazil, which induce
dolithalamous stem galls (Hering 1938).

**Xyphosini**

None of the genera (*Xyphosia, Icterโคides, Icterea*, and the apparently related
*Neaspilota* and *Gymnocarena*) includes gall-inducing representatives. The lar-
vae feed mostly on ovules, achenes, pappi and receptacle parenchyma. Com-
pared with Terelliini, larvae of *Xyphosia miliaria* Schrank feed on younger
floral buds and male flower heads of *Cirsium* (Angermann 1986); they have
cylindrical bodies, moderately developed reticulation of the facial mask,
and the acanthae on abdominal segments generally form no distinct creeping
welts (Goeden and Headrick 1999).

**Noeetini**

Most representatives are associated with a few Holarctic genera of the tribe
Lactuceae. Except for *Ensina sonchi* (Linnaeus) whose numerous, small elong-
gate cylindrical larvae feed on ovules without visible deformation, the
noeetine larvae (*Jamesomyia, Noeta, Xenochaeta, Acidogona, Paracanthella*, and
*Hyphenidium*) have their bodies either short and cylindrical or thickened at
the posterior end, and feed singly in rather small flower heads, sometimes
causing deformation, which prevents opening, but without pronounced gall
induction.

**Myopitini**

Among the Lower Tephritinae, this tribe apparently contains the most gall-
inducing species. Phylogenetic relationships of the tribe are poorly under-
stood, and possible connections either with the Noeetini or Axiothaumatini
have been tentatively postulated (Korneyev 1999). The relationships among
the genera of this tribe have been recently analyzed (Freidberg and Norrbom
1999), and a treeplot received from reanalysis of the characters they discussed
is provided (Fig. 2). Korneyev and White (2000) analyzed relationships among
the species of *Urophora*. Figure 3 shows the resulting treeplot received from
the analysis of the data listed in Tables 1 and 2.

A summary of the review of host-plant associations and distribution of
gall-inducing species of the Myopitini (Freidberg and Norrbom 1999) is
provided here: species of *Eurasimona, Myopitora, Inuromaesa*, and *Neomyopites*
may not induce evident galls, or at most, the larvae cause swellings usually
in nonlignified achenes. This is true for the *nigricornis, dzieduszyckii*, and
*quadrifasciata* groups of species of *Urophora* (Harris and Myers 1984, Freidberg
and Norrbom 1999, Korneyev and White 2000, A.L. Norrbom, personal ob-
servations, V.K., unpublished data). This type of larval feeding is believed to
be the basic pattern in the tribe.

Larval feeding in the *Eurasimona–Goedenia* lineage, ranked the sister group
to the other Myopitini in some analyses, is well-examined in Nearctic spe-
cies, which belong to *Goedenia*, but is poorly known in *Eurasimona*. How-
ever, there is a dry specimen of the flower head of *Achillea* infested by
Fig. 2  Cladogram showing phylogenetic relationships in the Myoptini based on reanalysis of morphological characters data matrix (Freidberg and Norborn 1999). Parsimony analysis using HENNIG86 Nelsen consensus tree from the mhennig bb* options combined with successive weighting of characters.

*Eurasimona stigma* in the collection of the Naturhistorisches Museum Wien (V.K., personal observation) (Fig. 4A). It has a long chimneylike opening; this flower head was not dissected and has no external signs of galling. Goeden et al. (1995) and Goeden (2002d) described the larvae of *Goedenia timberlakei* (Blanc and Foote) (as *Urophora timberlakei*) and *G. setosa* (Foote) as confined in their feeding to ovules and soft achenes, but apparently not feeding on sap, as the larval chamber remained dry. This difference from the primary feeding type has not yet been described for other members of the tribe. *Goedenia rufipes* (Curran) eggs are inserted between the outer phyllaries of closed, preblossom flower heads of *Isocoma*; larvae of this species and of *Goedenia stenoparia* (Steyskal) on *Gutierrezia californica* (DC.) Torrey and A. Grey and *Goedenia steyskali* Goeden on *Grindelia hirsutula* Hooker and Arnott feed on ovules; third instars also feed on receptacles: sap constitutes at least part of their diet (Goeden 2002c, e, f). All the host plants of *Goedenia*
belong to the subtribe Solidagininae of the tribe Astereae, and those of *Eurasimona* in the Anthemideae.

Larvae of *Spinicosta*, a genus considered closely related to *Urophora* (Freidberg and Norrbom 1999), feed within the achenes of species *Berkheya* spp. (Arctotaceae) and *Vernonia* spp. (Vernonieae) and excavate the achene totally (Clark 1989) (as *Urophora agromyzella* Bezzi). They induce no galls.

*Stammophora*, *Myopites* and most *Urophora* larvae induce conspicuous galls, which differ in structure from each other. *Myopites* and *Stammophora* galls usually comprise a swollen receptacle; *Stammophora*-induced flower-head galls have a common exit channel ('chimney'), through which adults escape. Such a chimney does not include achenes. *Stammophora*-induced flower-head galls (on *Vernonia hymenolepis* A. Rich. and *V. adoensis* Schulz Bip. ex Walp.) are large (diameter up to about 3 cm) and comprise 50 to 100 individual
Table I  Character states of taxa used in analysis of relationships among the species of *Urophora*

1. Flagellomere 1: 0, blunt, rounded; 1, acute.
2. Flagellomere 1: 0, yellow; 1, apically darkened; 2, black.
3. Upper orbital bristle: 0, not inclinate; 1, inclinate.
4. Upper orbital bristle: 0, present; 1, absent.
5. Lateral yellow strips: 0, narrow; 1, broad, covering notopleura and area of mesonotum bordering to them; 2, mesonotum mostly yellow.
6. Microtrichosity of mesonotal scutum: 0, dense, covering all the scutum; 1, somewhat sparse laterally; 2 four strips of sparse microtrichia medially; 3, absent.
7. Mesopleuron: 0, uniformly microtrichose; 1, medial area shining.
8. Veins $R_{4+5}$ and $M$: 0, divergent or parallel apically; 1, conspicuously convergent.
9. Intercalary crossband: 0, present; 1, absent.
10. Cell bc: 0, hyaline or yellow; 1, brown.
11. Cell Cu$_A2$ closed: 0, with a postero-apical lobe (at least short); 1, with arcuate vein.
12. Subbasal crossband: 0, very long, reaching posterior margin; 1, well developed, reaching middle of anal vein; 2, reduced to small spot; 3, absent.
13. Discal and preapical crossband: 0, convergent posteriorly; 1, parallel or subparallel.
15. Preapical crossband, when apical band present: 0: present; 1: reduced.
16. Subapical and apical crossbands: 0, isolated distally of $R_{2+3}$ apex; 1, fused; 2, isolated proximally of $R_{2+3}$ apex.
17. Hypandrium and vanes of fultella: 0, narrowly touching; 1, narrowly fused; 2, broadly fused.
18. Glans of phallus: 0, with developed acrophallic sclerites; 1, with subapical gonopore (no acrophallic sclerites).
19. Glans of phallus: 0, not long and tubular; 1, long and tubular.
20. Glans of phallus: 0, with the pillowlike 'juxta' and sclerotized apicodorsal rod; 1, without these structures.
21. Aculeus: 0, rounded or acute apically; 1, truncate or incised.
22. Aculeus: 0, longer than abdomen; 1, shorter.
23. Aculeus: 1, with primary steps; 0, without.
24. Aculeus: 0, without secondary steps; 1, with deep secondary steps; 2, with smoothed secondary steps.
25. Secondary steps, if present: 0, well-expressed; 1, smoothed.
26. Aculeus: 0, with rather long portion after primary steps; 1, with short projection apicad of primary steps (in *impicta* and *hermonis*).
27. Host-plants: 0, not of tribe Cardueae; 1, of tribe Cardueae.
28. Host-plants: 0, not of Inuleae; 1, of Inuleae.
29. Host-plants: 0, not of subtribe Echinopsidinae; 1, of Echinopsidinae.
30. Host-plants: 0, not of subtribe Carduineae; 1, of Carduineae.
31. Host-plants: 0, not of the subtribe Centaureinae; 1, of Centaureinae.
32. Host-plants: 0, not of the genus *Centaurea*; 1, of the genus *Centaurea*.
33. Host-plants: 0, not of subgenus *Centaurea*; 1, of *Centaurea s. str.*
34. Host-plants: 0, not of the genus *Cousinia*; 1, of the genus *Cousinia*.
35. Host-plants: 0, not of the *Centaurea (Acrolophus), Cent. (Jacea), Cent. (Phalolepis), Cent. (Cyanus)*; 1, of *Centaurea (Acrolophus), Cent. (Jacea), Cent. (Phalolepis), Cent. (Cyanus)*.
36. Host plants: 0, not *Carduus; 1, Carduus*.
37. Forming lignified achenes galls: 0, no; 1, yes.
cells, each leading to a common exit channel opening at the tip (Munro 1955). Unlike the parallel orientation of the tunnels in Urophora and Myopites galls, the orientation here is radial (Figs. 4B, C) (Freidberg 1998). In Myopites galls, each chamber has an individual exit channel formed by lignified achenes. Galls of Urophora are formed partially by lignified achenes, and partially of receptacle tissue: having mined through the ovary (or the very young achene), the larva enters the receptacle and induces the development of gall parenchyma, nutritive tissue, and subsequently, the lignified tissue. The path through the receptacle in which the young larva feeds constitutes the exit channel.

The ability to form lignified galls arises within the Urophora and in the group of species associated with the flower heads of plants of the subtribes Carduinae and Centaureinae. This peculiarity is the main constituent of the adaptive zone of the largest part of Urophora. The multichamber galls are induced on Cirsium stems and branches by Urophora cardui (Linnaeus) and

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U. misakiana (Matsumura) (Han and Kwon 2000), which form a monophyletic clade in the *stylata* group of species. Sister species of this clade, *U. coronata* Basov and *U. chakassica* Shcherbakov, induce lignified flower-head galls on *Serratula* spp. *coronata* L. agg. and *Cirsium heterophyllum* (L.) Hill. The ability of *U. cardui* to induce flower-head galls typical for other members of this group was shown experimentally (Lalonde and Shorthouse 1985), proving that stem-gall induction in *Urophora* is derived from the lignified flower-head gall induction. Gall induction in *Urophora* and its evolution is described in detail in the section entitled ‘Evolution of Gall Induction in *Urophora*,’ later in this chapter.

In the *Stammophora–Myopites* lineage, which is monophyletic (Freidberg and Norrbom 1999), the origin of gall induction is more difficult to trace, considering the vague relationships of this clade. Simpler galls with a common exit channel without achenes (like the galls of *S. vernoniicola* Bezzi on *Vernonia hymenolepis* A. Rich. and *V. adoensis* Schulz Bip) are believed to be the least specialized type of galls. Both stem galls, known for some *Stammophora* (see Freidberg 1998, Freidberg and Norrbom 1999), and flower-head galls, typical of *Myopites* species with known host plants (Freidberg 1980, 1984), are derived from the simpler galls. Flower-head galls may not be universal for the whole genus, since galls of certain species now assigned to *Myopites* have not been described yet: *Myopites flavovarria* Becker (= *Nearomyia flavovaria*), *M. delottoi* Munro, *M. sp. B*, and *M. sp. C* (Freidberg and Norrbom 1999). These species are distinct morphologically and sometimes have very distantly related host plants: according to Freidberg and Norrbom (1999), the *Myopites* sp. B and *M. sp. C* were reared from flower heads of *Echinops* of the tribe Cardueae, and *M. delottoi* from *Sphaeranthus* of the Plucaeeae (or Inuleae sensu lato). Presumably, they may induce different types of galls.

Apparently the only other gall-inducing member of the tribe is *Asimoneura petiolata* (Munro), which was originally reported to cause swelling in the capitulum base. Species of other Myopitini genera have not been reported to induce galls (see Freidberg and Norrbom 1999). Therefore, in Myopitini, the gall induction rises independently after separation of the tribe, into at least two lineages (Fig. 2).

**Axiothaumatini**

Korneyev (1999) has recognized Axiothaumatini as the *Axiathauma* group of genera, and later Hancock (2003) formally named it as the tribe Axiothaumatini to include *Axiathauma, Terpnodesma, Orthocanthoides*, and *Cryptophorellia*. A previously unplaced oriental genus *Soraida* also belongs here (V.K., unpublished data). Most known host records are Senecioneae, but galls have not been reported (see Freidberg and Hancock 1989).

**Cecidocharini**

This tribe (which we consider separately from the Dithyrcini), includes over 30 species of the genera *Cecidochares, Neorhagoletis, Procecidochares* and, probably, *Procecidocharoides* from Neotropical and Nearctic Regions (Korneyev 1999). Such a strict concept of the tribe differs from that of Norrbom et al. (1999), who placed them with some superficially similar genera now
transferred into tribes Dithrycini and Eutretini of the Higher Tephritinae. We define the Cecidocharini largely based on Procecidochares and its supposed relationships with Cecidochares. Most species, whose hosts are known, induce galls on plants of the tribes Eupatoriae, Astereae, and Heliantheae (Freidberg 1984, Foote et al. 1993). Some species, however, have a wider range of host plants. Localization of the gall and its presence or absence vary among species. Procecidochares anthracina (Doane) inserts eggs between leaflets within prominent rhizome axillary buds of Solidago californica buried 3–10 cm under the soil surface (Goeden and Teerink 1997a); the bud tissues remain intact until larvae emerge. Oviposition between the young oppositely placed leaves at the tip of the shoots and the gall induction along the growing shoots have been described for Procecidochares utilis Stone (Bess and Haramoto 1958), and such a localization of galls is the most common (Goeden and Teerink 1997a). In some multivoltine gall inducers a sequential change in choice of plant part occurs: from flower head to stem in Procecidochares australis Aldrich (Huettel and Bush 1972) and P. blancoi Goeden et Norrbom (Goeden and Norrbom 2001). Procecidocharoides penelope (Osten Sacken) infests flower heads of Eupatorium without inducing galls. Even if primary association with flower heads is hypothesized from its occurrence in most Lower Tephritinae, the strategy of larval feeding of Cecidocharini in general appears to be highly plastic and with a tendency to revert, and lacks morphological adaptations of female aculei for deep penetration, piercing, or cutting of plant tissues.

**Higher Tephritinae**

This group is defined by the presence of short lateral (external) vertical seta and a conspicuous gap in the row of setulae on the vein R$_{4+5}$ at the Sc apex (synapomorphies) (Korneyev 1999).

**Dithrycini (= Oedaspidini)**

This is apparently the most specialized group, comprising only gall-inducing species with strict host-plant preferences. Ovipositing into buds and inducing monothalamic galls are usual habits throughout this tribe, and are believed to be its apotopy. Monophyly of the tribe is supported by a unique pattern of scales on the eversible membrane in species examined (Korneyev 1999). All species examined possess aculei with needlelike or serrate apices for inserting their eggs into plant tissues. Considering that a sister group of the Dithrycini is unknown, such an aculeus type may be either an autapomorphy of the tribe or a synapomorphy (for instance, with some Eutretini subgroups).

The scheme of phylogenetic relationships in the Dithrycini considered by Korneyev (1999) did not include numerous Australian species recently described by Hardy and Drew (1996), and is critically revised below. Many species of the tribe are rare in collections and often known as males or females only. We therefore emphasize that the phylogenetic proposals are preliminary and must be used with caution. The list and matrix of characters used in the analysis are provided in Tables 3 and 4.
<table>
<thead>
<tr>
<th></th>
<th>Character states of taxa used in analysis of relationships among the species of <em>Dithrycini</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Flagellomere 1, 0, rounded apically, 1, slightly pointed and incised dorsoapically, 2, strongly pointed and incised dorsoapically</td>
</tr>
<tr>
<td>2</td>
<td>Arista, 1, setulose, 0, bare</td>
</tr>
<tr>
<td>3</td>
<td>Number of unicolorous frontal setae 1, four, 2, two, 0, three</td>
</tr>
<tr>
<td>4</td>
<td>Additional white setula before unicolorous frontal setae 1, present, 0, absent</td>
</tr>
<tr>
<td>5</td>
<td>Mesofrons 1, finely setulose, 0, bare</td>
</tr>
<tr>
<td>6</td>
<td>Vertical plates 1, long, reaching the middle of frons length, 0, restricted to posterior 1/3 of frons length</td>
</tr>
<tr>
<td>7</td>
<td>Outer vertical setae 0, acuminate, black to yellow, 1, white, short</td>
</tr>
<tr>
<td>8</td>
<td>Outer vertical seta 0, long, 1, short</td>
</tr>
<tr>
<td>9</td>
<td>Posterior orbital bristles 1, whitish, 0, yellow to brown</td>
</tr>
<tr>
<td>10</td>
<td>Proboscis 0, reduced, 1, normal, capitate, 2, long, geniculate, 3, very long</td>
</tr>
<tr>
<td>11</td>
<td>Shorter setulae between longer setae of postorbital row present 1, yes, 0, no</td>
</tr>
<tr>
<td>12</td>
<td>Presutural part of mesonotum 1, shortened, 0, of normal length</td>
</tr>
<tr>
<td>13</td>
<td>Setulae of mesonotal scutum 1, mixed yellow and black, 2, black, 0, unicolorous yellow to white</td>
</tr>
<tr>
<td>14</td>
<td>Tomentum of mesonotum 1, sparse, 2, absent, 0, dense</td>
</tr>
<tr>
<td>15</td>
<td>Scutellum 2, suncated, 1, sparsely microtrichose, 0, densely microtrichose</td>
</tr>
<tr>
<td>16</td>
<td>Apical scutellar setae 1, absent, 0, present</td>
</tr>
<tr>
<td>17</td>
<td>Presutural dorsocentral setae 1, present, 0, absent</td>
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<td>18</td>
<td>Scutellum 1, convex, 0, flat or very slightly convex, 2, bilobate apically</td>
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<td>19</td>
<td>Scutellum yellow with apical black spot 0, no, 1, yes</td>
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<td>20</td>
<td>Gap in setulae on R1 0, absent, 1, present</td>
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<tr>
<td>21</td>
<td>Vein R-M 0, distinctly proximally of R1 apex, 1, at R1 level or slightly (one R-M length) distal of R1 apex, 2, distal of R1 apex (more than R-M length)</td>
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<tr>
<td>22</td>
<td>Cell r1 0, without hyaline spots, 1, with one hyaline spot, 2, with two, 3, with 3</td>
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<tr>
<td>23</td>
<td>Vein R4+5 above 1, at least with 4-6 setulae basally, at most to R-M, 2, bare, or at most with 1-3 setulae basally, 0, setulose to DM-Cu vein level</td>
</tr>
<tr>
<td>24</td>
<td>Wing pattern 1, reticulate, 2, radiate, 3, striate or dark with hyaline wedges</td>
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<td>25</td>
<td>Distance between R-M and DM-Cu 0, exceeding or as long as DM-Cu, 1, shorter than DM-Cu</td>
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<td>26</td>
<td>Wing 1, with a transverse hyaline crossband distally of dm-cu, 0, without such a crossband</td>
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<td>27</td>
<td>Dark stripe along Cu vein 1, present, 0, absent</td>
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<td>28</td>
<td>Cell r2+3 1, with a hyaline spot behind R2+3 apex, 0, without such a spot</td>
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<td>29</td>
<td>Apex of r+4+5 cell 0, without hyaline spots, 1, with a small hyaline spot, 2, mostly hyaline</td>
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<td>30</td>
<td>Abdominal tergites 1-4 1, densely microtrichose, 2, shunng, 0, subshining</td>
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<td>31</td>
<td>Surstyl 1, narrow and elongate, 0, not such</td>
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<td>32</td>
<td>Posterior lobe (flange) of surstylus 1, densely microtrichose, 0, setulose</td>
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<td>33</td>
<td>Phallic glans 0, with a tail-like flagellum, 1, without a tail-like flagellum</td>
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<td>34</td>
<td>Dorsal surface of the eversible membrane 1, with shallow medial groove, devoid of scales, 0, not such</td>
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<td>Ventral surface of the eversible membrane 1, with scales restricted to medial area, 0, not such</td>
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<td>36</td>
<td>Aculcus 1, arrowlike, barbed, 0, not such</td>
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<td>37</td>
<td>Aculcus in preapical portion 1, serrate, 0, smooth</td>
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<td>38</td>
<td>Aculcus 1, as long as abdomen, 0, not longer, than 4-6 tergites altogether</td>
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<td>Host-plants 1, Anthemideae, 0, not such</td>
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(Contd.)
Table 4 (Contd.)

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</table>

[c(ode *1* 1' 1* 18/*10 35/*10 36/*10 37]

This analysis shows unresolved polytomy of subdivision of the tribe into three basal lineages (Fig. 5). *Gerrhaceras,* in the Andes, with two species inducing stem galls on *Piqueria* (Eupatoriaceae), forms one lineage. Its species have four scutellar setae and a phallic glans with well-developed tail-like apico-dorsal process (pleiomeromorphies). The two other lineages are based predominantly on the apomorphic state either of scutellar setae number (two instead of four) or the phallic glans (apico-dorsal process lacking).

Monophyly of the lineage containing the subtribes Dithrycina and Eurostina (Fig. 5) is supported by the presence of two scutellar setae (synapomorhpic character of low weight, occurring also in a few *Oedaspis* species, in *Eurosta cribra* and some others with four scutellars, apparently due to reversal) combined with a similar phallus glans structure (moderately developed tubular acrophallus; apico-dorsal rod long, tail-like) and moderately developed paraoboscs (sympleiomorphies). Furthermore, all species examined possess a sharply pointed aculeus apex, which is neither barbed nor latero-apically serrated.

Most species in this group induce monothalamic bud galls on rhizomes, stems or crowns, except for *Valentibulla* and possibly *Placaciura.* Species whose phenoology is known overwinter as larvae in *Acirina* spp., these are the first instars (Goeden and Teerink 1996a, b, c), and this may also be true for Palearctic *Hendrella* species (V.K., personal observation).

Nearctic species form a monophyletic lineage, which corresponds to the subtribe Eurostina; it is supported by at least one synapomorphy (long narrow setae). These species are associated with asteraceous perennial herbs and undershrubs of the subtribe Solidagininae (tribe Astereae) (Wasbauer 1972, Wangberg 1978, 1980, 1981, Novak and Foote 1980, Foote et al. 1993). While larger flies of the *Eurosta* occur mainly in the humid areas of eastern North America (see Maps 20–22 in Foote et al. 1993) and *infest mesic species of Solidago,* members of *Acirina* and *Valentibulla* are gall inducers on xeric *Chrysothamnuus* (and occasionally *Gutierrezia*) plants in semi-arid western North America (including southwestern Canada and northwestern Mexico) (see Maps 2–3 in Foote et al. 1993). The two main trends in evolution of the Eurostinae are apparently adaptation to mesic and xeric plants, which have resulted in the *Eurosta* and *Acirina–Valentibulla* lineages, respectively.
Fig. 5  Cladogram showing phylogenetic relationships in the tribe Dithrycini based on analysis of data matrix (Tables 3 and 4). Parsimony analysis using HENNIG86 Nelsen consensus tree from the *mhemng bb* options combined with successive weighting of characters. Abbreviations: Eur = Eurostina; Dith = Dithrycina; AT = Afrotropical Region; AU = Australasian Region; OR = Oriental Region; NA = Nearctic Region; NT = Neotropical Region; PA = Palearctic Region.

The Palearctic group of genera with one pair of scutellar setae was not found to be monophyletic, despite being uniform in the structure of female aculeus and male epandrium and phallus. All known host plants belong to the tribe Anthemideae (Achillea, Artemisia, and Santolina). Hendrella sordida Korneyev induces monothalamic bud galls in the crown of undershrubs of Artemisia (Seriphidium) (Fig. 4F), and Dithryca guttulosa (Loew) induces similar galls on Santolina rosmarinifolia (Houard 1909; see Fig. 5.3 in Korneyev 2002). By extrapolation, H. basalis (Loew), a sister-species of H. sordida, is assumed to have similar habits. On the contrary, galls of H. caloptera (Loew) and allied species have never been found in crowns of Artemisia spp. near limonifolia, from which the flies were usually collected by sweeping (V.K., personal observation); they are suspected to induce galls on rhizomes. 'Root galls' of D. guttularis (Meigen) on Achillea millefolium L. ha·e not been rediscovered since Kaltenbach (1874), and are probably rhizome galls. The stem
galls of *Placaciura alacris* (Loew) are apparently nonbud galls (Pak and Mamaev, unpublished data on a label). Like the North American Eurostina, the Dithrycina form two unequal groups of different climatic preferences: *Hendrella* and *Placaciura* species occur exclusively in dry wormwood mountain steppes and semideserts, whereas *Dithryca guttularis* inhabits a moderately humid belt from England and northern Spain in the west to Magadan in northeastern Russia. *D. guttulosa*, quite distant from *D. guttularis* in its morphological features, occurs in drier areas of Spain and Portugal.

*Ptiloedaspis* from the Iberian Peninsula fits the diagnosis of the subtribe Dithycina (Korneyev 2002). The shape of a dry gall suggests that *Ptiloedaspis* induces stem-bud galls on *Artemisia* (B. Merz, unpublished data); however, *Ptiloedaspis* does not share synapomorphies with other dithrycines, which induce stem galls on *Artemisia*. *Peronyma* from the southeastern United States is similar to *Ptiloedaspis* in the thorax shape, pattern of shiny black spots, and oblique position of the discal band, enabling it to be considered a sister group of *Ptiloedaspis* (Korneyev 1999). Like Eurostina species, *Peronyma* induces galls on plants of Solidagininae (Asteraceae). The scutellum of *Peronyma* bears four scutellar setae; this character is either a reversal, or a plesiomorphic condition, when compared with the other Dithycina and Eurostina species. If the plesiomorphic condition is acceptable, *Peronyma* and *Ptiloedaspis* form a lineage, which apparently arose from the main lineage of Dithrycini before the Eurostina. If independent reduction of apical scutellar seta is assumed for Eurostina, Dithycina, and *Peronyma*-*Ptiloedaspis*, then the idea of monophyly of this whole cluster has to be rejected.

The larger lineage corresponds to most of the subtribe Oedaspidina (Fig. 5). Its monophyly is supported by the presence of the comparatively small glans of the distiphallus with a very short acrophallus and without any trace of the apico-dorsal projection (synapomorphies). The presence of four scutellar setae is the sympleiomorphy that distinguishes most species of the subtribe from both Eurostina and Dithycina. Except for *Oedoncus* and *Xenodorella*, recently assigned to Tephrellini (Hancock 2000), the subtribe is rather homogeneous and all included species fit within the widest generic concept of *Oedaspis*, proposed by Freidberg and Kaplan (1992).

Oedaspidina covers *Oedaspis* (with all the species formerly assigned to *Tylaspis*, *Embaspis*, *Oedaspoides*, *Chrysotrypaneia* and *Chejuparia*), and also *Liepana*. *Oedaspis* and *Liepana* have not been formally synonymized yet. Monophyly of such a group was assumed because of the strong reduction of the apparently nonfunctional labellum (Freidberg and Kaplan 1992). However, the degree of reduction differs among species, so the labellum of *Oedaspis quinquefasciata* Becker is not shorter than that of *Dithryca*; also, this character remains undescribed for many Australian species, including those of *Liepana*. Generic concepts need be reconsidered in a worldwide revision of Oedaspidina. Therefore, we maintain the limits of genera as following Norrbom et al. (1999).

Most of the examined species of Oedaspidina have latero-apically serrated or barbed aculei, either sharply or less pointed at the apex (Freidberg and Kaplan 1992, Hardy and Drew 1996, Korneyev 2002). This character
allows us to hypothesize that females always pierce plant tissues to insert eggs, as described for Acturina (Goeden and Teerink 1996a, b, c) and Eutreta (Goeden 1990a, b). The bud gall of Oedaspis multifasciata Loew (Fig. 4G) (V.K., personal observation) is very similar to those in Hendrella and some Acturina.

Out of 50 species of Oedaspidina, 32 are now known to occur in Australian and Afrotropical Regions. In the tropics, they inhabit montane areas; although some species in both regions are certainly related, showing connections between the two faunas, no species of the subtribe has been found yet in India, Indochina, Sunda Islands or New Guinea. Apparently the only Asian species that have connections with these regions are three species of the pibaria group from Taiwan, mainland China, and Korea (Korneyev 2002). Both Afrotropical and Australian species are extremely different from each other and large gaps in the knowledge of their morphology and biology prevent the arrangement into groups. The only apparent groundplan characters of the subtribe are the wing pattern with two hyaline wedges at the anterior margin (like in Stenopa; see Figs. 401–402 in Foote et al. 1993) and a serrate aculeus, neither barbed nor acutely pointed at the apex.

Six of 15 recorded hosts in Australia and the Afrotropics belong to Asteraceae Inuleae (including Plucheae), others belong to Astereae, Heliantheae, and Goodeniaceae; one more species associated with Inuleae occurs in Palearctic Region (Canary Islands). Oedaspidines probably were primarily connected to Inuleae plants, which are widespread over the Paleotropics and Australia, and their association with other plant taxa is derived.

The complex of species with serrate aculeus (without a narrowly pointed apex) and two hyaline spots in r₁ cell, is predominantly Australian. In some species tentatively placed here, the aculeus serration is lacking, probably due to reversal.

Species assigned to Liepana resemble certain species of Oedaspis, like O. hardyi Norrbom (= O. serrata Hardy and Drew), in having wing base and subcostal cell completely dark (synapomorphies?); however, these relationships, hypothesized from incomplete descriptions only, must be treated with caution. Only Liepana helichrysysi Hardy and Drew is known to induce stem galls on Helichrysum (Inuleae) (Hardy and Drew 1996). Hancock (2001) has added Liepana apicilcara (Hardy and Drew) (= Oedaspis apicilcara Hardy and Drew), but diagnosis of the genus needs further clarification.

The pibari group of species occurring in eastern Asia (Korea, southern mainland China, and Taiwan) contains O. pibari (Kwon), O. wolongata (Wang), and O. schachti Korneyev; O. fini Freidberg apparently also fits this group (Korneyev 2002). Its monophyly is supported by having a dark anal lobe (synapomorphy), and dark brown wing pattern with hyaline spots, which may be considered a type derived from the banded wings known in O. hardyi or related to those of Liepana. However, species of the pibari group differ in having unicolor brown–black orbital and vertical setae synapomorphies?). Host plants are not known.

The escheri group of species includes species with the dark medial H-like mark well-defined, almost parallel-sided, and separated from the double
apical crossband by an almost straight hyaline crossband, either joined anteriorly with the second hyaline spot in r1 or separate. O. apicalis Hardy and Drew, O. escheri Bezzi, O. trimaculata Hardy and Drew, O. sp. E, and apparently O. perkinsi Hardy and Drew belong here. Only the O. sp. E of Hardy and Drew 1996 is known to have serrate aculeus, though nonbarbed (see Fig. 138 in Hardy and Drew 1996). Host plants are not known.

The whitei group contains three species (O. continua Hardy and Drew, O. semihyalina Hardy and Drew, O. whitei Hardy and Drew) with strongly sexually dimorphic wing pattern (see Figs. 85–86, 114–115, 126–127 in Hardy and Drew 1996) (synapomorphy), but judging from the female wing pattern, which is very similar in the whitei and the escheri groups, the first may be a derived group of the latter. In O. whitei, the aculeus is neither barbed nor serrate (Fig. 132 in Hardy and Drew 1996); host plants are not known, but all the species are collected in association with goodeniaceous plants, believed to be their hosts (Hardy and Drew 1996).

O. goodenia Hardy and Drew reared from stem galls on Goodenia (Goodeniaceae) shows no definite connections with any of the known groups, partially because of its incomplete description (aculeus said to be slender, sharply pointed, but not figured) and partially because of strongly swollen scutellum and rather sclerotized phallic glans (Hardy and Drew 1996). This is the only proven instance of a shifting to host plants of another family in the tribe Dithrycini.

A group of Afrotropical species including O. trapezoidalis Munro, O. plucheivora Freidberg and Kaplan, and O. serrata Freidberg and Kaplan forms a lineage whose monophyly is proven by having a proximal position of the R-M crossvein and similar wing pattern, consisting of four very wide transverse crossbands, and a hyaline apex with one to two dark spots (see Figs. 22–24 in Freidberg and Kaplan 1992). The narrowly pointed apex of the aculeus, in addition to serrate preapical margins, is apparently a synapomorphy of this and some other species groups (see later in this chapter). O. amani Freidberg and Kaplan is another species that is probably a member of this group because it has similar wing venation and pattern characters, as well as body coloration, but differs mostly by having rather long, narrow, neither serrated, nor spearlike barbed apex of aculeus (see Fig. 53 in Freidberg and Kaplan 1992). Within the trapezoidalis group, O. trapezoidalis and O. serrata are sister species sharing the absence of katepisternal seta (synapomorphy). Species of the trapezoidalis group induce stem galls on asteraceous plants in Pluchea and Blumea (tribe Inuleae, sometimes placed into a separate tribe, Plucheae). O. russa Munro, which induces stem galls on Helichrysum (Inuleae), nearly fits the diagnosis of this group, especially in the banded wing pattern, but differs in a much more distal position of R-M and in an aculeus gradually tapered, rather than barbed (though finely serrate). If the last characters are plesiomorphies, then O. russa is sister group to the trapezoidalis group, as they have one synapomorphy (apical brown crossband wide and straight). If these characters are hypothesized to be reversals, O. russa belongs to the group, but its relationships remain unresolved.
Another group of species (the *austrina* group) that have the saw-edged spearlike aculei (not sharply pointed at apex), along with elongate apical crossbands separated from the remaining dark pattern by an oblique hyaline crossband (apomorphy), includes three Australian species, *O. austrina* Hardy and Drew, *O. mouldsi* Hardy and Drew, and *O. olearia* Hardy and Drew. Two are stem gallers in asteraceous plants (*Olearia*). Sharing these characters with Afrotropical *O. maraisi* Munro, a galler on stems of *Othonna* (Asteraceae: Senecioneae), they comprise a possibly monophyletic group of wider distribution.

Palearctic species of *Oedaspis* with known hosts are associated with *Artemisia* (Asteraceae: Anthemideae), except *O. quinquefasciata* Becker from the Canary Islands, which induces stem galls on *Schizogyne* (Inuleae).

Mainland western and central Palearctic species (plus *O. dorsocentralis* Chen from the Far East) apparently constitute a morphologically uniform group of species, referred as the group of species near *Oedaspis* (*Oedaspis*). It differs from all other species of the genus by at least one synapomorphy: the length of the apical, arrowhead-like portion of aculeus more than twice its width. Also, the labellum is rudimentary and the wing pattern has 1 (~0) hyaline spot in *r*₁ cell and an oblique hyaline crossband between the cubital and preapical crossbands (these wing-pattern characters are probably the synapomorphies shared also with the *austrina* group (see above), and with the Afrotropical *O. crocea* and *O. inflata*). This group corresponds to the subgenera *Dichoedaspis*, *Melanoedaspis*, and most *Oedaspis* (*Oedaspis*) (sensu Hendel 1927). The presence of the three dark spots in the pterostigma shared by some eastern Asian (*O. chinensis* Bezzi, *O. formosana* Shiraki) and Australian species (*O. mouldsi* Hardy and Drew) is apparently a homoplasys. Otherwise, the monophyly of the group of species near *Oedaspis* (*Oedaspis*) is very likely, and its connections with Afrotropical oedaspidines are more probable. In addition, the numbers of species of this group in the Mediterranean and Far East Asian regions are equal (six species in each), but the morphological diversity in the Mediterranean species is conspicuously greater.

Hancock (2001) has transferred the genera *Platensina*, *Malaisinia*, *Euthauma*, *Bezzina*, *Australasina*, *Hyalopeza*, and *Colessomyia* into the Dithyrcini. This placement cannot be discussed until characters of the eversible membrane in these genera are examined.

The position of the two Afrotropical oedaspidine genera with long proboscis, *Oedoncus* and *Xenodorella*, remains uncertain. From the wing pattern type and shining convex scutellum, Freidberg and Kaplan (1992) placed *Xenodorella* in Oedaspidinae, near *Oedaspis crocea*, *O. hyalibasis*, and *O. quinquefasciata*. Long mouthparts may be considered here as a reversal, derived from moderately, but not from strongly, reduced mouthparts occurring in some *Oedaspis* species. Hancock (2000) has recently transferred this genus into the *Euryphalara* genus-group then assigned to the 'Platensinin', while *Oedoncus* was provisionally placed into the *Sphaeniscus* group of the Tephrellini (Hancock 2001).
Eutretini (sensu Korneyev 1999)

The tribe includes over 75 species in at least 15 genera, occurring mainly in the Neotropical and Nearctic Regions. The concept of the tribe and its monophyly are still debated. Several groups of genera are recognized and better defined than is the tribe itself. Concepts of the genus Acrotaenia and tribe Acrotaenini need revision (Korneyev 1999), and we do not discuss them below.

The group of genera related to Stenopa also includes Cecidocharella and Dracontomyia. The three genera share broad wings with an apically widened, almost triangular discomedial cell and also strong costal spurs, vertical elongate eyes, shining scutellum, and sparse scalelike mesonotal setulae (synapomorphies). They are similar in their body vestiture and vertical eyes to Cecidochares; this genus, as well as Procicidochares, however, possesses long black lateral vertical setae (vte) and fits in the Lower Tephritoidea, whereas in Stenopa, Cecidocharella, and Dracontomyia the setae are short, as in other Eutretini. The two Nearctic species of Stenopa feed in Senecio spp.: St. vulnerata Loew induces galls in buds or young twigs in the lower part of the host plant (Novak and Foote 1975), whereas St. affinis Quisenberry mine the parenchyma in rosettes (underground stem and upper root) without tissue proliferation (Goeden and Headrick 1990). The biology of Neotropical Cecidocharella and Dracontomyia remains unknown. The female aculeus is acutely pointed and serrated laterally (V.K., personal observation); however, piercing of tissues during oviposition has not been reported yet. The egg is elongate, the anterior end not drawn into a pedicel (Fig. 9 in Novak and Foote 1975). Larvae, including the third instar, are moderately elongate, with an elongate reticulated gnathocephalon (Goeden and Headrick 1990), which is more characteristic of mining larvae than of gallicolous larvae. Unlike the Terelliini, Tomoplagia group, and Xyphosiini, larvae of Stenopa have no conspicuous oral ridges, sharing this apomorphic character with the Higher Tephritinae. The Stenopa group represents generalized Higher Tephritinae (V.K., in preparation).

The group of genera related to Paracantha is represented by the New World genera Paracantha (=Scriptotricha, =Neorhabdochaeta) and Laksyetsa, the Palearctic Acinia, and Dictyotrypetes, which occurs in the Neotropical Region and has also been recorded from the Oriental Region. The last records apparently belong either to that genus or to a closely related genus (V.K., personal observation). These genera share (1) enlarged palpi, long costal spurs, and sharply pointed aculei, which are tentative synapomorphies of the Eutretini (Korneyev 1999); (2) spotted wing pattern, which is characteristic for most of the remaining Higher Tephritinae; and (3) a setulose R₄₊₅; a symplesiomorphy that is absent in most Higher Tephritinae, except for some Dithrycini and most Eutretini. This group, therefore, includes rather generalized genera of the tribe and is assumed to be nonmonophyletic. Species of Acinia infest flower heads of Astereae, Inuleae, and Cardueae, and Paracantha feed in flower heads of Heliantheae and Cardueae. Females of Paracantha cultivaris Coquillett pierce phyllaries of capitula (Cavender and Goeden 1984);
P. gentilis Hering inserts the ovipositor into the central opening of the immature capitulum between the apices of bracts, puncturing one or more layers of bracts (Headrick and Goeden 1990a, 1990b). First instars feed in the florets and later on ovules and receptacles, but do not induce galls. A similar type of feeding was observed for Acinia biflexa (Loew) on Inula germanica and for A. corniculata (Zetterstedt) on Centaurea jacea (V.K., personal observation). We therefore hypothesize this type of larval feeding as the groundplan type for the remaining groups of the Higher Tephritinae.

Rachiaptera Bigot and Strobelia Rondani form a monophyletic lineage with 11 closely related species. The spotted head and the mesonotum clustered with white scalelike setulae are similar to those in Paracantha. Therefore, Rachiaptera + Strobelia and Paracantha are tentatively considered sister groups. All examined species have an acutely pointed aculeus apex, strongly narrowed before the apices of the ventral lobes of the aculeus (synapomorphy) (V.K., unpublished data). Their larvae develop inside a spongy mass of plant exudate (Fig. 4H) on Grindelia and Baccharis, in South America. Larvae feed on stem tissues, but true gall induction has not been detected (Freidberg 1984).

Eutreta includes 31 species in North and South America; all species whose biology was examined are ceacidogenous (Stoltzfus 1977, Norrbom et al. 1999). Cryptotreeta is probably closely related and forms a monophyletic lineage together with Eutreta. Its monophyly is based upon having a hyaline apical spot or crescentlike band and heavily darkened, wide wing with yellowish or brownish dots, but no true reticulate pattern. Position and relationships of Polymorphomyia and Pseudoeutreta need clarification.

Members of the subgenera Eutreta (Eutreta) and E. (Setosigena) share an apically pointed and latero-apically inconspicuously serrated aculeus, as in the Stenopa group. Species of the nominative subgenus show a wide diversity of host plants, which belong not only to the tribes Astereae, Heliantheae, Coreopsideae, Senecioneae, and Vernonieae of the Asteraceae, but also to Verbenaceae. Some species are widely oligophagous and infest plants which belong to different genera and tribes. Gall localization may vary from stem to crown in E. (Eutreta) angusta (Stoltzfus 1977). Unlike generalized E. (Eutreta), species of the subgenus Metatephritis (= Uncaculeus) have a peculiar double- or triple-barbed arrowlike, but more blunt, aculeus apex (see Figs. 52–71, 73 in Stoltzfus 1977) and are restricted to stem galls on Artemisia. Metatephritis is clearly monophyletic, possessing a synapomorphy (the aculeus shape) combined with characters either of plesiomorphic, or of reversal origin (unenlarged palpi and unspotted face). Both E. (Eutreta) simplex Thomas and E. (Metatephritis) diana insert a single egg into a bud, obviously by piercing tissues (Goeden (1990a, b) observed eggs surrounded by necrotic tissues). Known galls are monothalamic bud galls.

Polymorphomyia and Pseudoeutreta share a broad, widely darkened wing disc and general body coloration and vestiture with Eutreta. No unconditional synapomorphies have been found yet, and we provisionally place these genera together with Eutreta. Polymorphomyia and Pseudoeutreta share
the presence of white scalelike mesonotal setulae (synapomorphy?) and are believed to form a monophyletic lineage, which is then divided into two branches corresponding to genera, each possessing individual autapomorphies: the oblique DM-Cu vein in _Polymorphismia_ and the single pair of scutellar setae in _Pseudeutreta_. The aculeus of species examined are apically pointed, similar to that in _Eutreta_ (Eutreta). _Ps. falcigera_ (Kieffer) induces stem galls on _Baccharis_ (Kieffer, cited in Kieffer and Jorgensen 1910), and _Po. footei_ Korytkowski was reared from galls on leaves of _Tessaria integrifolia_ R. and P. (Korytkowski 1971); no further details are available.

_Xanthomyia_ is Holarctic; it includes two boreal–montane species occurring from Alaska and Northwestern Territories to higher altitudes in New Mexico and from northern Russia to the Alps, Pamirs, and mountains of Mongolia and Central China; and two more species known from the Russian Far East, Japan and northeastern China, and from the eastern USA (Korneyev 1990 and unpublished data; Norrbom et al. 1999). Species of _Xanthomyia_ share very narrowly acute aculei with two tiny apical steps, much more pointed than in most _Eutreta_ or _Dictyotrypeta_. _Xanthomyia alpestris_ (Pokorny) was collected (by sweeping) on higher altitudes (2500–4000 m) in association with _Erigeron_ or _Aster_ species (Asteraceae), but has never been reared from their flower heads (B. Merz, personal observation; V.K., personal observation); it may induce rhizome or stem galls. Its phylogenetic relationships with _Dictyotrypeta_ and _Rachiaptera_ group are probable.

A group of Afrotropical genera, related to _Afreutreta_, which includes also _Tarchonanthea_ and _Cosmetothrix_, fits in the tribe Eutretini well. These genera have apically pointed, often latero-apically serrated aculei, broad dark wings with numerous dots, three dark frontal setae and dark parafacial spots on head, and the glans of the phallus similar to those in the New World _Eutreta_. No indisputable synapomorphies unite them, and we may hypothesize their parallel origin from less specialized _Acinia-_ or _Dictyotrypeta_-like eutretines. Flies of both groups strongly resemble leaf or lady beetles and mimicry may explain such a parallelism. The larvae develop in stem galls or growing tips of Asteraceae: _Inuleae_ (Brachylaena and _Tarchonanthea_) and Vernonieae (Vernonia) (see Freidberg 1984 and Freidberg and Kaplan 1993 for references). Galls of _Afreutreta hemimelas_ (Bezzi) are monothalamous (Freidberg and Kaplan 1993). _Tarchonanthea frauenfeldi_ (Schiner) larvae are normally inquilines in galls of the gall midge _Afrodisiposis tarchonanthei_ Felt (Munro 1926), but may induce their own twig galls, although they are less conspicuous. Larvae of _T. coleoptera_ Freidberg and Kaplan live inside undeformed twigs (Freidberg and Kaplan 1993). _Cosmetothrix discoidalis_ (Bezzi), according to Munro (1925) oviposit into young shoots (apparently by piercing); young larvae burrow into these tissues inducing a monothalamous gall. Inclusion of _Euthauma ghentianum_ Munro in this group (Munro 1949, Freidberg and Kaplan 1993) is not definite, because it could also belong to the Tephritini.

The following tribes, Schistopterini, Tephrellini, and Tephritini whose less specialized representatives resemble some Eutretini genera, are assumed to be derivative taxa of Eutretini.
**Schistopterini**

The tribe includes about 65 described species assigned to 14 genera, and about 140 undescribed species (Freidberg 2002) from the Old World. Its relationships with the Eutretini need further clarification: two Oriental species of unresolved generic position, ‘*Dictyotrupeta* longiseta’ Hering from India and ‘*Xyphosia* malaiset’ Hering from Indochina, which are apparently congeneric with, or closely related to, the Afrotropical species *Perirhithrum marshalli* Bezzi, form a lineage that we consider a sister group to Schistopterini (V.K., unpublished data). Chaetotaxy and genital characters, however, can barely distinguish these species from the New World *Dictyotrupeta* (Eutretini). Most Schistopterini are known to feed as larvae in flower heads of various Asteraceae, inducing no galls. *P. marshalli* feeds in flowers of *Barleria* (Acanthaceae), also without gall induction (Munro 1947) and that was why this species was assigned to Tephrellini Platensinina (Norrbom et al. 1999). Concepts of Eutretini, Schistopterini, and Tephrellini, need revision.

**Tephrellini**

The tribe includes over 170 species of 40 genera occurring in the Old World, mainly Afrotropical and Oriental Regions, with a few species in Palearctic and Australasian Regions, and includes, almost without exception, species whose larvae feed in flowers and young fruits of Acanthaceae, Lamiaceae, and Verbenaceae. The aculeus is needlelike, narrow without any incisions, which is one of the main synapomorphies of the tribe. Cecidogeny is uncommon, but Munro (1947) reported *Isoconia atricoma* Munro inducing galls in an inflorescence of *Blepharis transvaalensis* (Acanthaceae). Hardy (1973) recorded a gall on *Jussiaea* (Onagraceae) induced by *Platensina acrostecta* (Wiedemann).

Radhakrishnan (1984) has described large stem galls induced by *Tephrella variegata* Radhakrishnan on *Inula cappa* (DC.) (Asteraceae: Inuleae). Recently, Hancock (2001) has transferred this species to the genus *Malaisinia*, which he placed into the Dithrycini with *Platensina, Australasina, Euthauma, Bezzina*, and *Colessomyia*. Oriental species assigned to *Pliomelaena* better fit the diagnosis of *Protephritis*, which was not mentioned in the discussion of *Malaisinia* (Hancock 2001), and may be a senior synonym. *Protephritis* generally resembles *Acinia* and *Dictyotrupeta* of the Eutretini and may be related to them (Korneyev 1999). Both gall-inducing Asteraceae-associated species and noncecidigenous species that are not associated with Asteraceae have a needlelike, possibly piercing, aculeus. The hypothesis of secondarily changed larval feeding mode—the shift from gall induction on Asteraceae to anthropagy on Acanthaceae and Lamiaceae (Korneyev 1999)—after separation of the tribe Tephrellini appears reasonable.

**Tephritini**

The tribe includes over 1,000 species in 80 genera, with numerous gallers occurring in many genera and generic groupings.
Sphenella Group of Genera  This group is a rather small (over 50 species belonging to six or seven genera) and well-defined cluster of Old World genera associated with plants of the tribe Senecioneae. The group was recognized by Munro (1957), reviewed by Freidberg (1987) and Freidberg and Hancock (1989), then redefined in the strict sense by Korneyev (1999). Most Sphenella, Oedosphenella, Orotava, Afrotropical species assigned to Paratephritis, and possibly Telateles and Bevismyia feed as larvae in flower heads, sometimes inducing the achenes to swell (Munro 1957), but no detailed descriptions of their galls are available.

East Asian (but not all of the Afrotropical) species of Paratephritis and Parafeutreta form large polythalamous stem galls, which can be from spherical to spindlelike. Depending on their numbers, larvae pupate in a common chamber or in separate chambers, with a single exit from the gall (Munro 1953, Kandybina et al. 1967). The New Zealand 'Tephritis' fascigera Malloch clearly belongs to this group, but generic placement has not been resolved yet; the biology was discussed by Gourlay (1955). Both genera belong to the group which includes also Sphenella and Oedosphenella. Monophyly of this group is based on the presence of antero-ventral setae on the hind femur. Otherwise, Paratephritis and Parafeutreta share plesiomorphic features (setulose frontal vitta, setulose vein $R_{4+5}$, two prensisetae) or synapomorphies of the Sphenella group as a whole (phallus glans type and long posterior lobe of the epandrium, or the flanges). Therefore, monophyly of the group of gall-inducing species remains unresolved. Aculeus shape is similar in the gallicolous Pseudotephritis transitoria (Rohdendorf) and species ovipositing into flower heads, although conspicuously narrower and longer in P. transitoria, but not sharply pointed at its apex. Ovipositional behavior has not been described.

Campiglossa Group of Genera  This group is apparently monophyletic. In most genera, the preglans area of distiphallus bears acanthae, the apico-dorsal projection of the glans is almost universally reduced, the labellum is elongate, and two frontal setae are present. At least the first character is certainly a synapomorphy of Antoxya, Mesoclados, Scedella, Oxyna, Homoeotricha, Oxyparna, Campiglossa (= Paroxyyna), Lethyna, and Desmella. The genus Dioxyna and the Australian species assigned to Campiglossa by Hardy and Drew (1996) apparently belong elsewhere. The group includes about 260 species. The richest and the most diverse fauna is in the Afrotropical Region, followed by the Palearctic, whereas only two species of Oxyna and 20 of Campiglossa inhabit the Nearctic Region. The larvae of most species infest flower heads of Asteraceae, feeding on ovules or achenes and usually inducing no galls. Oxyna, Homoeotricha, Campiglossa (Campiglossa) (irrorata and grandinata groups), and most Campiglossa (Pseudacinia) species have never been reared from flower heads. Four Oxyna species, and one or two Campiglossa (Campiglossa) induce rhizome or stem galls. Other species may induce subterranean galls. Five Palearctic species of Oxyna live in stems without inducing galls (Korneyev 1990; V.K., personal observation; Freidberg, personal communication). The Nearctic O. aterrima (Doane) (= O. utahensis
Quisenberry) induce galls on apical and axillary buds, and *O. palpalis* (Coquillett) lives as an inquiline (Goeden 2002a, b). *Mesoclania bruneata* Munro has been reared from stems, where its larvae feed either without inducing any deformation or swellings (Munro 1950), while the other species infest flower heads. Phylogenetic polarity of the shoot–flowerhead larval localization remains unresolved and, probably, in some cases is reciprocal.

As in some *Procecidochares*, the second generation of two sister bivoltine species of *Campiglossa* (*Campiglossa*), *C. misella* (Loew), and probably its sister species *C. melaena* (Hering) feeds in the flower heads of *Artemisia* spp. (*vulgaris* aggr.) (V.K., personal observations). The first generation larvae of *C. misella* were reported to feed gregariously in unilocular stem galls on the same plant species (Uffen and Chandler 1978). These data have not been confirmed yet, but seem reliable, as adult flies of the first generation in both species are conspicuously larger than those of the second (V.K., personal observations), because the stem galls of *C. grandinata* Rondani on *Solidago* (Rübsamen 1910, Korneyev 1990) look similar to the rosettelike stem galls of *C. argyrocephala* on *Achillea ptarmica* (Wahlgren 1944), and *C. misella*, *C. melaena*, *C. argyrocephala*, and *C. grandinata* are closely related.

From a preliminary analysis of phylogenetic relationships of the *Campiglossa* (*Campiglossa*) and allied groups (V.K., unpublished data), either the bivoltine and mixed or the monovoltine and gallicolous cycle probably is the basic character of the genus. Shifting to host-plant species with later and shorter flowering periods or smaller flower heads (*Artemisia*, *Solidago*, *Achillea*) may lead to oviposition into young shoots and buds and/or loss of the flower-head generation, whereas shifting to host plants with larger flower heads and longer flowering periods leads to the loss of shoot-gall generation. Indeed, most of morphologically ‘advanced’ *Campiglossa* feed in flower heads without inducing galls.

In *Oxyna*, phylogenetic polarities of the rhizome gall induction (*O. flavipes* Loew and *O. nebulosa* Loew) and feeding in stem without inducing galls (*O. paretina* Linnaeus, *O. stackelbergi* Korneyev, *O. superflava* Freidberg, and *O. albiplia* Loew) are unclear. The two biological habits belong to different morphological groups, however, the gallicolous species do not form a monophyletic group, whereas the group of nongallicolous species is monophyletic (V.K., unpublished data); therefore, the secondary loss of gall induction in this group is probable.

**Tephritis–Trupanea Group of Genera** This group, in its widest sense (covering all the genera with white posterior notopleural seta and the radial wing pattern, which are probable synapomorphies of included taxa), is the largest grouping of the *Tephritini* and *Tephritinae*. It contains more than 450 species in more than 40 genera attributed either to the *Dyseuaresta*, *Euarestoides*, *Trupanea* group and a part of the *Spathulina* group, or placed in the *Tephritini incertae sedis* (Norr bom et al. 1999, Korneyev 1999). Merz (1999) recently considered the phylogenetic relationships within a large genus subgroup occurring mostly in the Afrotropical Region and the Mediterranean area of the Palearctic Region. Phylogenetic relationships of most New World genera of this group remain unknown.
Among numerous members of the group that possess rather aberrant genital structures, variously modified wing patterns, head shape, and chaetotaxy, a few representatives retain most plesiomorphic characters which they share with the Eutretini, Tephrellini, and Sphenella and Campiglossa groups. The nonmodified glans of the phallus (with [1] the acrophallus well developed and tubular, [2] the vesica not elongate, [3] the acanthi on the preglands short and small, almost inconspicuous, and [4] the tail-like apico-dorsal process of the glans usually well developed) occurs in predominantly Afrotropical Spathulina and closely related Australian Paraspalathulina, Old World Actinoptera, Palearctic Heringina and apparently in most New World genera related to Euaresta, Neotelephritis, and Dyseuaresta.

The branch represented by Paraspalathulina and Spathulina apparently is a sister group to the remaining majority of the Old World Tephritis-Trupanea group. Apart from the primitive phallus glans, these two genera have uniformly dark setulose oviscapes, two frontal setulae (plesiomorphies) and shining abdomens (synapomorphy). They share bowed L-shaped spermathecae with the other Old World genera of the group (synapomorphy?) (not examined in the New World genera). Larvae of Spathulina species either induce unilocular stem-bud galls on Asteraceae Inuleae (Freidberg 1984) or feed in flower heads of Inuleae or a wider range of hosts (Munro 1938). Oviposition has not been described; aculei are slightly pointed apically and have no specialized features for piercing plant tissues.

Merz (1999) considered oviscape covered by white setulae a synapomorphy of the large cluster of genera he called the Tephritis group. It covers most Afrotropical and Palearctic genera except Spathulina. However, species of Actinoptera and Heringina have only dark setulae on the oviscape, and the glans has either well-developed acrophallus or the apico-dorsal process. Actinoptera rosetta Munro and A. mamulae Rondani induce small, inconspicuous, rosettelike galls on stems; A. contacta Munro induces larger galls on the tips of twigs of Helichrysum. Other species of Actinoptera and Heringina guttata (Meigen) are also associated with Helichrysum or related species of the tribe Inuleae, usually feeding in flower heads without inducing galls.

Tephritis is a large monophyletic aggregation of about 150 species; most Australian species assigned by Hardy and Drew (1996) apparently belong elsewhere. The glans of the phallus is poorly sclerotized at the base, with laterally bowed vesica, but without an acrophallus and modified acanthi at its basal portion (apomorphies), combined with the presence of two frontal and four scutellar setae (plesiomorphies).

Monothalamous 'communal' galls, located just below the flower heads and containing gregarious larvae, were described and figured for T. hurvitzi Freidberg on stems of Scorzonera and Tragopogon (see Fig. 2 in Freidberg 1984). The point of oviposition is unknown. Similar galls sometimes induced by larvae of an undescribed species of Tephritis were observed in Kyrgyzia on Saussurea sordida (V.K., unpublished data). The galls include numerous larvae moving down from overcrowded flower heads into upper portions of the peduncle and inducing growth and swelling of its walls.
T. stigmatica (Coquillett) develop in flower heads of several species of Senecio and Haplopappus or induce spindle-shaped unilocular ‘communal’ galls on Senecio douglasii (Goeden 1988). These species are not closely related.

The stem galls of T. baccharis (Coquillett) and T. arizonaeensis Quisenberry on Baccharis are produced by larvae hatched from eggs inserted into apical or, rarely, axillary buds. These galls are usually monothalamous. The first generation larvae of T. arizonaeensis feed in nongalled, rarely slightly swollen tips, whereas larvae of the second generation develop singly in flower heads (Goeden and Headrick 1991a, Goeden et al. 1993).

T. dilacerata (Loew) induces simple galls in Sonchus flower-head tissue between the base of bracts and the peduncle grows into galls (Shorthouse 1980).

Trupanea, the largest genus of the Tephritinae, includes close to 250 species occurring in all zoogeographical regions. Larvae of Trupanea feed in flower heads, mostly gregariously but sometimes singly. Tr. dumosa Munro is reported to form apical-stem galls on Elytropappus (Munro 1940); such galls resemble those of Tephritis stigmatica, except that the terminal part is permanently open or guarded by hairs. Similar apical shoot galls of Tr. signata on Gnaphalium (Goeden and Teerink 1997b) have the exit closed by a tomentum-covered terminal cap, which is coated inside by liquid feces. Tr. conjuncta (Adams) is a casual gall inducer; it lays clusters of eggs either in flower heads, or in apical buds of Trixus; neonate larvae induce galls when in apical buds (Goeden 1987).

Two species of Euarestella (E. megacephala Hendel and E. pninae Freidberg) and species of Multireticula perspicillata (Bezzi) (= Campiglossa perspicillata Bezzi) develop in the apical portion of stems of Inula, Pulicaria, and Helichrysum (Inuleae) with or without galls.

An analysis of cecidogeny in the Tephritini, suggests the following conclusions: (1) Except for Oxyna (and possibly also Homoeotricha), females of most genera oviposit into the upper parts of host plants, mostly into preblossom flower heads, or occasionally, into tip or axillary buds; in the latter cases, larvae, which mine plant tissues, usually (but not always) induce galls. (2) In a few examples (Paratephritis, Parafreutreta, Campiglossa sensu strictu), a group of related cecidogenous species exist. (3) In most instances, gall-inducing species occur singly among nongall-inducing relatives.

Certain preferences for host-plant groups by galling Tephritinae are observed in different zoogeographical regions. Astereae (and especially Solidagininae) are favored in the Nearctic Region, Inuleae (mostly Helichrysum and allied genera) in the Paleotropics, including Australia and southeastern Palearctic, and Anthemideae (mainly Artemisia) in the Palearctic Region. From the mosaic distribution of the host-plant characters among taxa in all the major branches of the Tephritinae, it is unlikely that any coevolutionary tendencies between gall-inducing fruit flies and plants occur. The most acceptable assumption will be that the distribution of gall-inducing tephritines among plant tribes depends on the domination of plants of certain tribes in biocenoses inhabited by tephritines, and on the ability of plants to respond to larval feeding.
Non-tephritine Gallers

The only reliable example of galls induced by tephritids other than Tephritinae occurs in Notomma. *N. galbanum* Munro induces unilocular twig galls housing single larvae on Dichrostachys glomerata (Fabaceae: Mimoseae) (Munro 1952). Other Afrotropical species, judging from the sawlike aculeus tip, may have similar habits. The only related taxon is Malica caraganae V. Richter from Kyrgyzia; its larvae feed on seeds in young beans of Caragana (Fabaceae), inducing no galls (V.K., personal observation); the aculeus is comparatively blunt. A previous statement that *M. caraganae* induces galls on Halymodendron (Korneyev 1996) is erroneous; those galls were moth induced and contained remnants of tachinid puparia.

Other Galliculous Tephritidae

Larvae of fruit flies may also feed in the galls induced by other insects. Such organisms are known mostly in genera represented by species associated with fleshy fruits. *Rhacochlaena toxoneura* Loew (Trypetinae: Adramini) feeds in the galls of *Pontania* (Hymenoptera: Tentredinidae) (Kopelke 1984), while the closely related *R. japonica* Ito feeds in fruits of cherries (Ito 1984). In Chetostoma, two species, *C. curvinerve* Rondani and *C. stackelbergi* Rohdendorf, have been recorded as inquilines in the galls of the sawfly *Hoplocampoides* on *Lonicera* (A. Zinoviev, personal observation, V.K., personal observation, Aartsen 1992), while *C. continuans* (Zia) feeds in fruits of *Lonicera* (Kandybina 1977). *Parastenopa elegans* (Blanchard) is possibly an inquiline in galls of *Metaphalara* (Psyllidae) on *Ilex* (Blanchard 1929), and *P. limata* (Coquillett) feeds in fruits of *Ilex* (Benjamin 1934, Phillips 1946). Nearctic *Oxyna palpalis* (Coquillett) is an inquiline in rosette galls of *Rhopalomyia* (Diptera: Cecidomyiidae) on *Artemisia tridentata* (Goeden 2002b), while other species of this genus induce rhizome and stem galls or feed in stems of *Artemisia* without any conspicuous galls.

EVOlUTION OF GALL INDUCTION IN UROPHORA

The evolution of gall-induction behavior in Tephritidae has several questions unanswered. *Urophora* is of particular interest, because it is one of the few gall-inducing tephritids, which offers some insights into major evolutionary steps of gall induction in this group. Therefore, we describe here those steps and discuss the evolutionary innovations, as well as costs and benefits.

Evolutionary Steps

*Urophora* (sensu Freidberg and Norrbom 1999) includes 60 species that are nearly exclusively associated with host plants belonging to Asteraceae (tribe Cardueae: subtribes Echinopsinae, Carduiinae, and Centaureinae) (Korneyev and White 1999, 2000). Several species of *Urophora* have been used in biological weed control projects (Harris 1989a, Harris and Shorthouse 1996). Because species of *Urophora* induce galls of varying complexity, and because several other characters allow distinction between the primitive and
the derived forms, the major steps of the evolutionary history of gall induction within this taxon can be reconstructed with reasonable accuracy. Larvae of *Myopites*, the second large genus of the tribe Myopitini, related to *Urophora*, exploit host plants mainly belonging to the tribe Inuleae in Asteraceae, and induce galls in the capitula. Different structures of galls of *Myopites* and *Urophora* suggest that the cecidogenous habit evolved independently in these two genera (Arnold-Rinehart 1989).

We propose that the larvae of the ancestor (Fig. 6A) of the gall-inducing species of *Urophora* were mining the achenes (seeds) of their host plants (Zwölfer and Arnold-Rinehart 1993). A possible extant model is *Spinicosta agromyzella* (Bezzi), a tephritid species that Clark (1989) (as *Urophora agromyzella*) reared from the achenes of four South African *Berkheya* species (members of the tribe Arctoteae, which structurally resemble thistles of the Cardueae). *S. agromyzella* larva feeds within a single achene, excavating it completely. As the achene is not enlarged or otherwise transformed into a gall, the size of *S. agromyzella* is unusually small. From this supposed origin the following sequence of evolutionary steps can be constructed (Zwölfer and Arnold-Rinehart 1993):

**Step 1 Nonlignified Achene Gall (Ovary Gall)**

The simplest *Urophora* gall is that of *U. quadrifasciata* Meigen, a species well characterized by allozyme and chromosomal data (Pönisch and Brandl 1992) and by its morphology (White and Korneyev 1989). It has retained a number of plesiomorphic traits: its host range is broader than that of the other species of *Urophora* (Zwölfer 1965), its larva feeds within the achene and not in the receptacle, and its gall has no lignified tissues (Shorthouse 1989). Unlike a seed miner, *U. quadrifasciata* stimulates the parenchyma of the vascular bundles and the undifferentiated tissue of the achene to proliferate and to enrich the cells with nutritive substances. Small patches of nutritive tissue differentiate along the base of the larval cavity. Parenchyma cells of the vascular bundles are the principal source of nutrition (Arnold-Rinehart 1989). The galled achene is enlarged considerably and has an opening at its apex. When the larva is mature, only the seed coat remains (Fig. 6B). With an average duration of only 21 d, gall induction occurs much faster than in other more complex galls such as those induced by *U. jaceana* (Hering) or *U. stylata* (Fabricius). Compared with a seed miner such as *S. agromyzella*, the achene gall of *U. quadrifasciata* enables the larva to extract a greater volume of nutrients from the host plant (Harris and Shorthouse 1996).

**Step 2 Unilocular Cup-shaped Ovary-receptacle Gall**

Larvae of *Urophora* spp. belonging to a complex of species (Korneyev and White 2000) (e.g., that of *U. affinis* Frauenfeld) associated with species of *Centaurea* produce simple, lignified, cup-shaped galls (Arnold-Rinehart 1989). The larvae mine through the achene and enter the upper part of the receptacle. Primary nutritive tissue differentiates in small patches along the wall of the larval chamber. Where the main growth phase of the larva occurs, secondary nutritive cells develop from the procambial strands at the
Fig. 6  Types of *Urophora* galls  
A Hypothetical seed-mining ancestor  
B Gall without lignified tissues of *U. quadrifasciata*  
C Unilocular 'cup-shaped' gall of *U. affinis*  
D 'Cup-shaped' galls of *U. jacea*na  
E 'Block-shaped' receptacle gall of *U. stylata*  
F Shoot gall of *U. cardui*  
Key to shading, see (E) dotted (a) = plant tissues, lightly shaded (b) = protective lignified tissues, dark shading (c) = area of secondary nutritive tissue, horizontal stripes (d) = callus tissues closing the exit channel  
Drawings at different scales
base of the gall (Arnold-Rinehart 1989, Shorthouse 1989). Peripheral tissues around the gall parenchyma lignify. They induce a cup-shaped gall, which comprises remnants of the ovary as well as parts of the receptacle (Fig. 6C) U. sirunaseva (Hering) and U. jaculata Rondani induce similar galls in Centaurea solstitialis (Zwolfer 1969, Arnold-Rinehart 1989).

Step 3 Multilocular Cup-shaped Ovary-receptacle Galls

Transitional forms between this gall type and the unilocular cup-shaped ovary receptacle galls exist. The difference is that the originally isolated cup-shaped galls tend to fuse, incorporating a larger part of the inflorescence receptacle (e.g., galls of U. jacea on Centaurea nigra (Varley 1947) (see Fig. 6D) and C. jacea (Arnold-Rinehart 1989)). In U. jacea the completion of the gall requires 28–30 d. The galls induced by U. hispanica (Strobl) in the capitula of Centaurea aspera and Mantisalca salmantica, and by U. cuspidata Meigen in the capitula of Centaurea scabiosa and C. collina also belong to this type (Arnold-Rinehart 1989). The species inducing galls described previously (steps 2 and 3) constitute a separate complex within Urophora (Korneyev and White 2000).

Step 4 Multilocular Block-shaped Receptacle Galls

Galls induced by U. stylata on Cirsium vulgare and C. arvense exemplify multilocular block-shaped receptacle galls (Fig. 6E). Like the species producing cup-shaped galls, the larva of U. stylata enters a floret and feeds its way through the ovary. Thereafter, however, it mines deeply into the receptacle. After about 14 d, small patches of primary nutritive cells appear along the wall of the gall chamber and after 6–7 d, layers of secondary nutritive tissue develop. The channel above the gall chamber, which was formed by the feeding activity of the freshly hatched larva, is filled with spongy callus tissue, as in U. cardui (Lalonde and Shorthouse 1982). After hibernation, this callus tissue partly disintegrates constituting a channel, which serves as the exit route for the adult Urophora. Compared with Urophora species inducing cup-shaped galls, the parenchymatous and lignified gall tissues are more extensive. The lignified tissue may even fill the entire interior of the capitulum. Multilocular block-shaped galls have probably evolved independently in Urophora in several species. They are particularly distinct in a complex (the cardui species group: U. stylata, U. congrua Loew, U. cardui (Korneyev and White 1996)) that has specialized on members of Cirsium. But multilocular block-shaped galls also occur in two members of the solstitialis group (Korneyev and White 1993): U. solstitialis (Linnaeus) on species of Carduus and U. terebrans (Loew) on Cirsium eriophorum. U. mauritanica Macquart, a member of the affinis group (Korneyev and White 1996), induces multilocular block-shaped galls on Carthamus lanatus (Zwolfer and Arnold-Rinehart 1993).

Step 5 Multilocular Shoot Gall

Only shoot (or stem) galls in the Urophora are known in two sister species: (1) U. cardui on Cirsium arvense (Fig. 6F), C. creticum, and C. setosum and (2) U. misakiana on C. setidens (Zwolfer 1965, Han and Kwon 2000). Under
caged conditions, however, *U. cardui* could induce galls and showed successful larval development in the flower heads of *Cirsium arvense* (Shorthouse and Lalonde 1986). This suggests that the ancestors of this species used flower heads (Freidberg 1984) and that the shift to inducing shoot galls was caused by a change in the oviposition behavior of the adult fly. Oviposition into shoot buds by *U. cardui* takes place at an early stage. The gravid female explores the bud thoroughly and if she decides to lay eggs, she will adapt the clutch size (and hence the size of the resulting gall) to the size of the apical meristem of the bud, which may serve as an indicator for the suitability of the host plant (Freese and Zwölfer 1996). Lalonde and Shorthouse (1982, 1983) describe four phases in gall development of *U. cardui*; Sakuth (1996) provides the biochemical details of gall induction by the young larvae of *U. cardui*. Gall induction starts 7–10 d after oviposition, when the larvae mine into the developing stem and transform the pith and procambial tissues into gall parenchyma. During the growth phase (18–32 d after oviposition) cells of this parenchyma proliferate, constituting the primary nutritive cells. In the maturation phase (36–50 d after oviposition) parenchyma near the larva develops into secondary nutritive tissue, and the remaining gall parenchyma turns into lignified elements. Most of the larval growth occurs during this phase. After hibernation, the spongy callus tissues at the top of the gall decompose, thus making an exit channel for the adult fly (Lalonde and Shorthouse 1985). With the exception of the initiation phase, the developmental processes in the remaining three phases correspond with the pattern of development in the ‘block-shaped’ receptacle galls (Arnold-Rinehart 1989).

**Evolutionary Innovations Required in Gall Induction**

Gall induction requires an evolutionary syndrome that integrates processes at the physiological, morphological, behavioral, and ecological levels. We can speculate that oviposition of the hypothetical seed-mining ancestor of *Urophora* species was already specialized and, thus, constituted a preadaptation for the evolution of gall-inducing *Urophora* species. Comparison of the abdominal musculature involved in the oviposition in *U. quadrifasciata* and *U. affinis* with that of two frugivorous tephritids (Berube and Zacharuk 1983) indicates that anatomical adaptations are necessary for the evolution of the galling habit and for the precision in oviposition by *Urophora*, which involves a high degree of control in inserting and maneuvering the ovipositor within the capitulum. Berube and Zacharuk (1983) assume that changes in the ovipositor and the arrangement of the dorsal and ventral muscles of segment 6 may be related to the improved control of the ovipositor during oviposition. Variations in the fine structure of certain sensillar types on the ovipositor of *U. affinis* and two other *Urophora* species (Zacharuk et al. 1986) may be connected with their specialized oviposition behavior.

A key step in the evolution of galls was achieved when *Urophora* larvae developed the ability to influence and alter the growth of meristematic tissue to differentiate into gall parenchyma. The second instars of *Urophora* have larger salivary glands than other tephritids. Some of the substances
these salivary glands produce are cytokinins. Working with second-instar larvae reared in vitro, Sakuth (1996) found that prior to any contact with the host, these instars contained 20,000 pmol cytokinin/g fresh mass of their body. This concentration was much higher than that in tissues of the vegetative or floral buds of Cirsium without galls (18–22 pmol/g fresh mass) or gall tissue in the initial phase (60 pmol/g fresh mass). Eighty percent of the cytokinins and their derivatives in galls in the early growth phase originated from the larvae of U. cardui (Sakuth 1996). The larvae could, thus, create a strong nutritional sink, promote cell division, and delay senescence of the tissues. Exploiting the host plant's hormone mechanisms, they may also have the ability to counteract defensive reactions of the host plant, such as necrosis or abortion.

The radiation of Urophora and its specialized exploitation of Cardueae hosts with capitula of varying sizes and structures require not only the development of specific host-recognition processes, but also modifications of the structures associated with oviposition. Zwölfer (1983) showed that in nine gall-inducing European Urophora species the length of the oviscape (and hence of the whole ovipositor) closely correlates with the diameter of the bud of the flower head into which oviposition may occur ($r^2 = 0.936$). Concomitant with changes of the ovipositor size, male genital structures had to be adjusted (H.Z., unpublished observations). Another adaptation required by the radiation of Urophora is the modification in the post-hibernation emergence patterns of the adults, which reflect the different phenologies of their host plants (Zwölfer 1983, Burkhardt and Zwölfer 2002).

**Benefits and Costs of the Evolution of Urophora Galls**

Numerous species of Urophora, its broad radiation on Cardueae hosts, and the occurrence of many host races (Zwölfer and Romstöck-Völkl 1991) demonstrate the evolutionary 'success' achieved through induction of galls. Burkhardt (1999) studied the advantages involved in evolution of galls of Urophora by comparing the primitive galler U. quadrifasciata quadrifasciata with the advanced galler U. jaceana; both were studied on Centaurea jacea grown under different nutrient regimes. Burkhardt and Zwölfer (2002) have discussed the trade-offs connected with the evolution of a complex gall. Table 5 summarizes some of the differences. The specialized U. jaceana is able to adjust its clutch size to the quality of the host. Its larvae extract more energy and nutrients via the modified vascular system (Harris and Shorthouse 1996), which leads to a higher body mass and a larger female egg load. The costs of this advantage are the dependence on host populations and a longer developmental period. U. quadrifasciata with its primitive gall profits from a second generation per annum and a broad host range, which provide flexibility and make it a successful colonizer (Harris 1989b). The larvae of Urophora species, which induce block-shaped galls or stem galls, have still higher developmental time costs, but by the extensive lignified tissue of their galls they gain a partial protection against intraguild predation (especially by larvae of Microlepidoptera) and generalist parasitoids (Zwölfer and Arnold-Rinehart 1994).
**Table 5** A comparison of *U. quadrifasciata quadrifasciata* and *U. jacea*

<table>
<thead>
<tr>
<th></th>
<th><em>U. quadrifasciata quadrifasciata</em></th>
<th><em>U. jacea</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Type of gall</td>
<td>Primitive gall, no lignified tissues</td>
<td>Complex gall, lignified tissues</td>
</tr>
<tr>
<td>Adult females, fresh weight</td>
<td>3–4 mg</td>
<td>5–6 mg</td>
</tr>
<tr>
<td>Mean egg load, age 8 days</td>
<td>65.6 eggs/female</td>
<td>170.8 eggs/female</td>
</tr>
<tr>
<td>Acceptable age of bud</td>
<td>1–20 d</td>
<td>1–15 d</td>
</tr>
<tr>
<td>Females recognizes different host quality</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>Mean time spent on bud per deposited egg</td>
<td>6.49 min</td>
<td>1.91 min</td>
</tr>
<tr>
<td>Mean egg number/visited bud</td>
<td>2.0 (0–8.0)</td>
<td>8.0 (2.5–15.3)</td>
</tr>
<tr>
<td>Duration of gall development</td>
<td>20 d</td>
<td>30 d</td>
</tr>
<tr>
<td>Second generation/annum</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Host range</td>
<td>18 Centaurea spp.</td>
<td>2 Centaurea spp.</td>
</tr>
<tr>
<td></td>
<td>1 Serratula sp.</td>
<td></td>
</tr>
<tr>
<td>Long distance dispersal possible</td>
<td>yes</td>
<td>no</td>
</tr>
</tbody>
</table>

**ECOLOGICAL GENETICS OF GALL-INDUCING TEHRITIDS**

Of about 400 existing and 200 described cecidogenous tephritid species (Freidberg 1998) not many have been investigated with respect to their ecological genetics. The research group of Warren G. Abrahamson (Abrahamson et al. 1989, 1994, Abrahamson and Weis 1997, Cronin et al. 2001) and the collaborators of Helmut Zwölfer (Seitz and Komma 1984, Komma 1990, Eber and Brandl 1994, 1996, Romstöck 1987, Romstöck-Völkl 1997) have been studying the population genetics and evolutionary ecology of gall-inducing tephritids. In fact, the ecological genetics of only three gall-inducing tephritid species have been studied in detail. These, however, cover almost all aspects of evolutionary ecology: local adaptation, phylogeography, dispersal, and speciation.

Life history data of gall-inducing species do not differ significantly from those of noncecidogenous species (Freidberg 1984). Such a lack of difference is most probably also true for tephritid behavior (Díaz-Fleischer and Aluja 1999). Except for the capacity to induce galls on diverse plants organs, cecidogenous species share most ecological properties with the noncecidogenous tephritid species. Nevertheless, some characters, listed below, are more often found among the gall-inducing species (Freidberg 1984):  

1. Most are oligophagous, or monophagous.  
2. Males and females meet on their host plants for mating.  
3. Most are univoltine, because availability of appropriate plant parts limits the oviposition period.  
4. Fecundity is lower than in frugivorous tephritids.  
5. Egg survival is high.  
6. Larval and pupal mortality possibly regulate population density. Parasitism of larvae and pupae are the main mortality factors and can reach up to 100 percent.  
7. Dispersal of gall-inducing species may be lower than in frugivorous tephritids.
(8) Combination of these life history traits and behavioral and ecological properties make the gall inducers ideal models for the study of evolutionary and speciation processes (Abrahamson and Weis 1997).

Moreover, the encapsulation in the ‘nutshell’ of the gall is an ecosystem *en miniature* that conserves the history of the tritrophic interactions of plants, gall-inducing flies, and their parasitoids, for several months. These properties ease observation and experimentation in the field, because the individuals can be tracked.

Characters (1), (2), and (3) make the environment of cecidogenous tephritids coarse-grained (Fig. 7): modifications of only a single niche component result in an exchange of a set of environmental conditions. The intimate interaction with plants during oviposition, larval development, pupation, and emergence from the gall require physiological and genetic adaptation of the flies to the hosts, resulting in strong selection pressures. Therefore, if there are more generations per year, then different plant parts are used, for example, change from flower-head galls to stem galls (Huettel and Bush 1972). In some rare cases, even a switch to other host plants occurs in the course of a year, for example, *Myopites cypriacus* Hering (Freidberg 1980).

![Fig. 7 Schematic representation of fine- and coarse-grained environments based on niche structures of three insect species. 1 = habitat of adults, 2 = food of adults, 3 = mating site, 4 = site of oviposition, 5 = habitat of larvae, 6 = food of larvae, 7 = habitat of pupae, 8 = site of over-wintering. From fine- to coarse-grained environment, an increasing number of niche elements coincide. *U. cardui*, with the most coarse-grained niche structure, exists most of its life cycle on or in its host plant. (Adapted from Zwölfer and Bush, 1984)](image)

Host specificity (or even specificity for certain plant parts) makes gall-inducing tephritids suitable model organisms for the study of the evolution of host races, and sympatric and parapatric speciation (Zwölfer and Bush 1984): “host races being partially reproductively isolated populations specializing on different hosts” (Diehl and Bush 1984) and representing “transient stages in sympatric speciation” (Bush 1969, 1994). Disruptive selection, as it occurs if different host plants vary with respect to phenology or spatial distribution, is important in parapatric and sympatric speciation.

This type of speciation assumes reinforcement among existing variants. Sympatric speciation has long been controversial because the genetic models explaining it required genes linked for fitness and assortative mating
(Maynard-Smith 1966, Felsenstein 1981). Meeting and mating on the host is a variant of assortative mating that does not require mate recognition. Zwölfer (1974) could demonstrate that this 'rendezvous-behavior' is a strong reproductive isolation mechanism for tephritids. He could show in laboratory experiments, that individuals of different species exchanged courtship signals (e.g., wing movement and presentation). In Petri dishes, without host plants, interspecific crossings could be achieved easily, but only between individuals of the same genus (this was demonstrated for species of Urophora and Chaetorellia). Such crossings did not occur under natural conditions.

If, subsequently, host plants funnel differential fitness, then selection may promote linkage of the host attraction gene and fitness gene (Futuyma 1998). Thus, there is no need for prior linked loci to facilitate sympatric speciation. Moreover, models assuming pleiotropic effects also reduce the strict need for linkage between loci for mate choice and fitness traits (Kondrashov 1986, Kondrashov and Kondrashov 1999). It will be shown later how this scenario can result in host-specific genetic differentiation in Tephritis conura.

Characters (4) to (6) enable the shift to a new host where parasitoid load may be low and this shift possibly compensates initial higher mortality caused by maladaptation to the novel host. Brown et al. (1995) found hostplant-dependent mortalities of Eurosta solidaginis due to differential parasitization rates. The overall mortality due to different parasitoids and predators was about 16 percent lower on the derived than on the ancestral host plant.

Character (7) is important for the genetic population structure of species. Low dispersal capabilities and short flight distances should result in a stepping-stone model rather than an island model (Fig. 8). The only instar during the life cycle of a fly that can disperse over long distances is the adult fly, and the dispersal capability must be related in some way with the duration of this stage.

**DISPERAL, GENETIC POPULATION STRUCTURE, AND PHYLOGEOGRAPHY**

Dispersal and colonization capabilities are important on two different temporal and spatial scales: (1) for the stabilization of a patchy population structure which is the result of a metapopulation dynamic, and (2) for the colonization of new habitats which become available after climatic changes either in the past (e.g., after the ice ages) or presently as a result of global environmental changes.

Spatial genetic structures in cecidogenous tephritids were first studied by Seitz and Komma (1984) when they investigated small- and large-scale genetic variation of Urophora cardui. They observed a high local and regional genetic differentiation of populations. The observed patterns of small scale (0.1–10 km) variation were interpreted as the result of a metapopulation dynamic caused by repeated extinctions of small subpopulations by Eurytoma parasitoids. These results have been corroborated by Zwölfer et al. (1970) and Zwölfer (1979, 1982), who observed extreme local population dynamics
a patchy distribution of *U. cardui* in spite of the availability of host plants. Large-scale (> 100 km) variation was interpreted as the result of recolonization and range expansion after the last Pleistocene glaciation. Obviously, the distribution pattern of *U. cardui* is highly dynamic with immense fluctuations in the population density over time. Eber and Brandl (1996) observed 18.4 to 32.6 percent (average 25.5 percent) extinctions of existing local populations and 19.4 to 44.1 percent (average 28.3 percent) colonizations of empty patches. According to Levins (1970), a metapopulation can exist under these conditions because, on an average, colonization exceeds extinction probability. However, the size (e.g., number of occupied patches) can vary strongly, as extinction is much higher than colonization in some years. This might explain the discrepancy between the estimated dispersal capabilities of *U. cardui* of up to 10 km per yr, observed dispersal distance of about 20 km within 10 yr (Eber and Brandl 1996), and the gaps in the distribution of *U. cardui* in central Europe.

The amount of genetic differentiation in the subdivisions of a population can be estimated by the fixation index $F_{ST}$ (Wright 1951, Nei 1977). From data above we can expect no genetic diversity among regional populations because repeated population bottlenecks, extinctions and recolonizations result in a patch coalescence with an $F_{ST}$ that does not significantly differ from 0 (Gilpin 1991). Significant $F_{ST}$-values exist, supported by cytogenetic studies in southern Germany (Pönisch and Brandl 1992), in spite of (1) different amounts and different rating of the importance (Seitz and Komma

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**Fig. 8** Various types of metapopulations depending on size, direction and mode of dispersal.  
A. Mainland-island model, dominated by the gene flow from the mainland to the islands.  
B. Island model with gene flow between all subpopulations.  
C. One-dimensional linear stepping-stone model.  
D. Two-dimensional stepping-stone model. (Combined after various authors)
1984, Eber and Brandl 1997), and (2) the assumption of limited gene flow among regional populations of *U. cardui*. Because population genetic data integrate over space and time, it is likely that the short-term observations of actual dispersal reflect the long-term scenario only poorly.

Eber and Brandl (1997) could not verify the decline of genetic variation from south to north, which was observed by Seitz and Komma (1984). Eber and Brandl (1997) found only a weak longitudinal component in a principal component analysis of genetic variation. Therefore, we repeated our study in 1999 (Johannesen and Seitz 2003) and 2001 (A.S., unpublished data), and could confirm the strong small-scale genetic differentiation (*F*<sub>ST</sub> up to 0.21 in southern Denmark). We observed a pronounced clinal variation (60 percent change in allele frequency) from the Danish peninsula of Jutland to northern Germany, which was stable over the 2 yr (1999 and 2001). A highly significant correlation between pair-wise genetic and geographic distances among populations of *U. cardui* over a range of 400 km suggests a pronounced isolation by distance and low gene flow (Johannesen and Seitz 2003). Repetition and extension of the large-scale analysis, ranging from southern Finland to France, are still in process. Our findings are in striking contradiction to those of Eber and Brandl (1997) and confirm our 1984 observations. Reasonable explanations for this are different sampling designs, differences in electrophoretic analysis, or misinterpretation of electrophoretic data. Most probably the discrepancies between the studies of Eber and Brandl (1997) and our findings have been caused by a combination of sampling design and different electrophoretic conditions. The patchy distribution of *U. cardui* requires a nested hierarchical sampling that allows for small-scale and large-scale variations, and some of the studied enzyme systems are not easy to analyze. The latter is the case for the locus GOT (=AAT), whose electropherograms are difficult to read. It plays an important role in the genetic structure of *U. cardui*.

Monophagy, as in *U. cardui*, imposes strong constraints on the phytophage with respect to physiology, behavior, and spatial distribution. The expected coupled phylogeography of host plants and their phytophages has not yet been investigated. However, the same phenomenon is expected on the next higher level between tephritids and their specialized parasitoids. Johannesen and Seitz (2003) compared the genetic population structure of *U. cardui* and the ectoparasitoid *Eurytoma robusta* on the Danish peninsula of Jutland and northern Germany. They found a highly significant correlation between the genetic differentiation estimates (*F*<sub>ST</sub>) of the same population pairs of *U. cardui* and *E. robusta*. These results suggest that local dispersal dynamics of the two species are similar, and as the regression coefficient deviates significantly from 1, that the parasitoid is less mobile than its host.

**HOST RACE FORMATION AND SPECIATION**

*Urophora cardui* is monophagous on *Cirsium arvense* in Central Europe. In Eastern Europe, it infests the closely related *Cirsium setosum* and in the
eastern Mediterranean region *C. creticum* (White and Korneyev 1989). Frenzel et al. (2000) studied populations in the Ural Mountains and observed greater numbers of chambers in each gall, and larger galls. Given the high variation of gall sizes within Central Europe, this does not necessarily indicate essential differences between *U. cardui* populations infesting these different hosts.

The best-documented example of the complex relationship among geographic distribution, host-plant association, and ecological and genetic interactions is that of *Eurosta solidaginis* (Abrahamson and Weis 1997). *E. solidaginis* induces stem galls on several goldenrod species; of these, *Solidago altissima* and *S. gigantea* are the primary hosts. Population genetic studies carried out by two different methods give contrasting results with respect to geographic variation and host-plant association. Enzyme electrophoretic studies (Waring et al. 1990) demonstrate a clear association between genetic traits of fly populations and host plants. *E. solidaginis* populations reared from *S. altissima* and *S. gigantea* had higher genetic distances between than within the two hosts. In an analysis of mtDNA variation, however, the dominating effect was geographic location of the populations (Brown et al. 1996). Five different haplotypes have been observed that showed a clear split into western (two haplotypes) and eastern (three haplotypes) clades. Four haplotypes have been observed in flies from *S. altissima* and two haplotypes in *S. gigantea*, one of which was unique to these populations. From these data it could be assumed that *S. altissima* is the ancestral host of *E. solidaginis*. Because of the low genetic variation and low number of individuals studied in this analysis no further conclusions are possible.

Another gall-inducing tephritid, *Tephritis conura*, may at present be on the way from formation of host races to formation of sibling species. *T. conura* appears to have diverged genetically on several species of thistle (*Cirsium*) that today are largely allopatrically distributed, but which also exhibit contact zones and areas of true sympatry (Seitz and Komma 1984, Komma 1990, Romstöck 1987, Romstöck-Völkl 1997). Compared with *E. solidaginis*, *T. conura* attacks at least eight species of *Cirsium* (*C. heterophyllum*, *C. oleraceum*, *C. erisilthales*, *C. palustre*, *C. spinosissimum*, *C. canum*, *C. filipendulum*, and *C. tuberosum*). However, *T. conura* does not attack all species of *Cirsium* over their entire distribution range in Central Europe. In spite of the availability of mixed stands of different, potential host species, only one is attacked (Romstöck-Völkl 1997).

In such a context of combination of geographical distributions and host potential plants, *T. conura* appears as a promising model to evaluate processes of speciation and incipient radiation. The diversification and processes promoting reproductive isolation of *T. conura* can be studied by testing the importance of mate versus host recognition in allopatry as well as in areas of sympatry. Work on *T. conura* has shown that biotypes which diverge at one enzyme locus (hexokinase) have homogeneous allele frequencies at other loci and even a common altitudinal cline at the locus GOT (=AAT) (Seitz and Komma 1984, Komma 1990). Such a divergence might be expected under sympatric or parapatric speciation where disruptive selection only
influences a few loci (Sezer and Butlin 1998). A complication in *T. conura*, however, is that differences in temporal flowering between host-plant species might isolate fly populations and have caused divergence by genetic drift. The *T. conura* system provides an opportunity to test whether allele frequency differences at a 'diagnostic' locus are involved in diversification of new biotypes, or are a passive consequence of temporal allopatry.

The genetic differentiation of *T. conura* in relation to its host-plant species has been described in an area where two host-plant species, *Cirsium oleraceum* and *C. heterophyllum*, are sympatric, parapatric, and allopatric (Seitz and Komma 1984). This work has been continued by population-genetic (Komma 1990) and population-ecological (Romstöck 1987, Romstöck-Völkl 1997) analyses as well as simulation modeling (Seitz 1992).

In summary, the key findings from these studies (Romstöck Völkl, 1997) are:

- Based on enzyme electrophoretic studies, *T. conura* shows a significant host-plant related genetic structure, which is the consequence of the variation of only a few marker enzymes. Most of these data refer to the relation between *T. conura* and its host plants *C. heterophyllum* and *C. oleraceum*. Limited information is available from localities with mixed stands of two or more host-plant species.

- Mating of *T. conura* is influenced by the presence and species of host plant. But there is no strict correlation between host-plant species and biotype of the fly. These observations are available only with respect to *C. heterophyllum* and *C. oleraceum*. Laboratory experiments and information from localities with other host-plant species, especially mixed stands of two or more host-plant species, are unavailable.

- *T. conura* preferentially oviposit in the host-plant species from which they emerged. These observations are limited with respect to flies from *C. heterophyllum* and *C. oleraceum* and four to five host species as alternative hosts.

- Survival of *T. conura* larvae in flower heads varies depending on the origin of the flies and plant species (observations limited as explained above).

- Numerical simulations (Seitz 1992) show that a genetic determination of host-plant selection and host-related survival is sufficient for the establishment of a stable genetic differentiation of populations that can lead to a separation of the gene pool. Neither linkage of genes nor a genetic determination of mate recognition is required.

An UPGMA phenogram of Nei's genetic distances (based on allele frequencies) (Fig. 9) demonstrates that the degree of genetic divergence of host-associated populations of *T. conura* vary with respect to host plant. The amount of variation in *T. conura* between populations originating from different hosts is between that of local populations and the described species of tephritids.
CONCLUSIONS

Cecidogeny evolved several times within the Tephritidae, also within the subfamily Tephritinae. This suggests that the gall-inducing trait was the result of an evolutionary process related to the life history of exploiting plants, especially flower heads. As was demonstrated for Urophora, induction of galls requires ‘special’ interactions with the host plants and adaptations, which most probably resulted in a narrower host range if more elaborate galls evolved. It can be expected from the resulting strong link between physiology and ecology of host plants and their phytophages that, as a consequence, the spatial distributions of plants and flies change the mode of gene flow and lead to a coupled phylogeography.

Unfortunately, a molecular phylogeny of most of the gall-inducing tephritids is unavailable. Together with the phylogeography of host plants and parasitoids, molecular phylogeny could offer greater insights into processes and phylogenetic pathways as well as into the ecological forces that control spatial distribution patterns of species.

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REFERENCES

Aartsen, van, B 1992 Nieuwe en zeldzame boorvliegen voor de Nederlandse en Belgische fauna (Diptera Tephritidae) Entomologische Berichten (Amsterdam), 52 73–76


Arnold-Rinehart, J 1989 Histologie und Morphogene se von Urophora- und Myopites-Blutenkopfgallen (Diptera Tephritidae) in Asteraceae Ph D thesis, University of Bayreuth, Germany

Basov, V M, and V A Korneyev 1987 Exit of tephritid flies (Diptera Tephritidae) from their larval chambers [in Russian] Problems of general and molecular biology (Kiev), 6 47–51

Benjanun, F H 1934 Descriptions of some nativetrypted flies with notes on their habits United States Department of Agriculture Technical Bulletin, 401 1–95

Berube, D E, and R Y Zacharuk 1983 The abdominal musculature associated with the oviposition in two gall-forming tephritid fruit flies in the genus Urophora The Canadian Journal of Zoology, 61 805–814


Blanchard, E E 1929 Descriptions of Argentine Diptera Physis (Buenos Aires), 9 458–465


Burkhardt, B 1999 Eiablageverhalten, Gallentyp und Fitness von Urophora-Arten (Diptera Tephritidae) bei unterschiedlicher Wirtsqualitat Ph D thesis, University of Bayreuth, Germany

Burkhardt, B, and H Zwolfer 2002 Macro-evolutionary trade-offs in the tephritid genus Urophora benefits and costs of an improved plant gall Evolutionary Ecology Research, 4 61–77


Clark, M M 1989 Insect herbivore communities colonising the flower heads of *Berkheya* in South Africa and Carduaceae in Europe and California Ph D thesis, University of Cape Town, South Africa

Cronin, J T, K Hyland and W G Abrahamson 2001 The pattern, rate, and range of within-patch movement of a stem-galling fly Ecological Entomology, 26 16–24


Eber, S, and R Brandl 1997 Genetic differentiation of the tephritid fly *Urophora cardui* in Europe as evidence for its biogeographical history Molecular Ecology, 6 651–660

Farris, J S 1988 HENNIG86, version 1.5 © Program and reference Available from J S Farris, 41 Admiral Street, Port Jefferson Station, New York 11776, USA

Felsenstein, J 1981 Skepticism towards Santa Rosalia, or why are there so few kinds of animals Evolution, 35 124–138

Foote, B A 1967 Biology and immature stages of fruit flies the genus *Icterica* (Diptera Tephritidae) Annals of the Entomological Society of America, 60 1295–1305


Foote, R H, F L Blanc, and A L Norrbom 1993 Handbook of the fruit flies (Diptera Tephritidae) of America north of Mexico Comstock Publishing Associates, Ithaca, USA


Freidberg, A 2002 Systematics of *Schuspterini* (Diptera Tephritidae Tephritinae), with description of new genera and species Systematic Entomology, 27 1–29


Freidberg, A, and F Kaplan 1993 A study of *Afretreta Bezz* and related genera (Diptera Tephritidae Tephritinae) African Entomology, 1 207–228

Freidberg, A, and J Kugler 1989 Fauna Palaestina: Insecta IV Diptera Tephritidae Israel Academy of Sciences & Humanities, Jerusalem, Israel

Frenzel, M., S. Eber, S. Klotz, and R. Brandl 2000 Ecological comparison across geographical distributions The thistle gall fly *Urophora cardui* (Diptera Tephritidae) on two different *Cirsium* hosts. European Journal of Entomology, 97 183–189


Gilpin, M 1991 The genetic effective size of a metapopulation. Biological Journal of the Linnean Society, 42 165–175


Goeden, R D 1990a Life history of *Eutreta diana* (Osten Sacken) on *Artemisia tridentata* Nuttall in southern California Pan-Pacific Entomologist, 66 24–32

Goeden, R D 1990b Life history of *Eutreta simplex* Thomas on *Artemisia ludoviciana* Nuttall in southern California (Diptera Tephritidae) Pan-Pacific Entomologist, 66 33–38


Goeden, R D 2002b Life history and description of immature stages of *Oxyna palpalis* (Coquillett) (Diptera Tephritidae) on *Artemisia tridentata* Nuttall (Asteraceae) in southern California Proceedings of the Entomological Society of Washington 104 537–553


Goeden, R D 2002e Life history and description of adults and immature stages of *Goedenia stenoparia* (Steynskali) (Diptera Tephritidae), on *Gutierrezia californica* (De Candolle) Torrey and A Gray and *Solidago californica* Nuttall (Asteraceae) in southern California Proceedings of the Entomological Society of Washington, 104 702–715

Goeden, R D 2002f Life history and description of adults and immature stages of *Goedenia steyskali*, n sp (Diptera Tephritidae), on *Grindelia hurutula* Hooker and Arnott var *hurutula* (Steyermark) M A Lane (Asteraceae) in southern California Proceedings of the Entomological Society of Washington, 104 785–800


Goeden, R D, and D H Headrick 1991a Life history and descriptions of immature stages of *Tephritis baccharis* (Coquillett) on *Baccharis salicifolia* (Ruzin and Pavon) Person in southern California (Diptera Tephritidae) Pan-Pacific Entomologist, 67 86–98


Goeden, R D, and D H Headrick 1992 Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera Tephritidae) on native Asteraceae in southern California Proceedings of the Entomological Society of Washington, 94 59–77

Goeden, R D, and D H Headrick 1999 Life history and description of immature stages of *Neaspilota wilsom* Blanc and Foote (Diptera Tephritidae) on *Hazardia squarrosa* (Hooker and Arnott) E Greene (Asteraceae) in southern California Proceedings of the Entomological Society of Washington, 101 59–77

Goeden, R D, and A L Norrbom 2001 Life history and description of adults and immature stages of *Procedochares blae*, n sp (Diptera Tephritidae), on *Isocoma ardena* (E Greene)


Hancock, D L. 1986 New genera and species of African Tephritinae (Diptera: Tephritidae), with comments on some currently unplaced or misplaced taxa and on classification. Transactions of the Zimbabwe Scientific Association, 63: 16-34.


Hancock, D L. 2000 Taxonomic affinities of Deroparia Munro, Euryphalaena Munro and Xenodorea Munro (Diptera: Tephritidae: Tephritinae) African Entomology, 8: 261-264.


Hardy, D E. 1973 The fruit flies (Tephritidae-Diptera) of Thailand and bordering countries. Pacific Insects Monograph, 31: 1-353.


Harris, P. 1989a The use of Tephritidae for the biological control of weeds. Biocontrol News and Information, 10: 7-16.


Harris, P., and J D Shorthouse 1996 Effectiveness of gall inducers in weed biological control The Canadian Entomologist, 128 1021–1055
Hendel, F 1927 49 Tryptetidae, pp 1–221, pls 1–17 In E Lindner [ed] Die Fliegen der palaearktischen Region Volume 5 Stuttgart, Germany
Hering, E M 1938 Neue Bohrfliegen aus Brasilien (32 Beitrage zur Kenntnis der Tryptetidae) Revista de Entomologia (Rio de Janeiro), 8 187–196
Houard, C 1909 Les Zoococcides des Plantes d’Europe et du Bassin de la Mediterranee Volume 2 A Hermann et Cie, Paris, France
Huettel, M D., and G L Bush 1972 The genetics of host selection and its bearing on sympatric speciation in Procedochares (Diptera Tephritidae) Entomologia Experimentalis et Applicata, 15 465–480
Ito, S 1984 Die japanischen Bohrfliegen, Lfg 2–6, pp 49–288 Maruzen, Osaka
Johannesen J., and A Setz 2003 Comparative population structures of the fruit fly Urophora cardui and its primary predator, the ectoparasitic wasp Eurytoma robusta Entomologia Experimentalis et Applicata (in press)
Kaltenbach, J H 1874 Pflanzenfeinde aus der Klasse der Insekten Stuttgart, Germany
Kandybura, M N 1977 Luchnki plodovykh mukh-pestrokrilok (Diptera, Tephritidae) [Larvae of fruit-infesting fruit flies (Diptera, Tephritidae)] [in Russian] Opredelitel po Faune SSSR, izdavaemye Zoologicheskim institutom AN SSSR, 114 1–210
Kieffer, J-J., and P Jorgensen 1910 Gallen und Gallentiere aus Argentinien Zentralblatt fur Bakteriologie, Parasitenkunde und Infektionskrankheiten, Abt II 27
Komma, M 1990 Der Pflanzenparasit Tephritis conura und die Wirtsgattung Cirside Wissenschafts-Verlag Dr Wibert Maraun, Frankfurt/M, Germany
Kondrashov, A S 1986 Sympatric speciation when is it possible? Biological Journal of the Linnean Society, 27 201–223
Kondrashov, A S., and F A Kondrashov 1999 Interactions among quantitative traits in the course of sympatric speciation Nature, 400 351–354
Kopelke, J-P 1984 Der erste Nachweis eines Brutparasiten unter den Bohrfliegen Natur und Museum (Frankfurt-am-Main), 114 1–28
Korneyev, V A 2002 New and little known Eurasian Dithyrcini (Diptera, Tephritidae) Vestnik zoologii, 36 3–13
Korneyev [Korneev], V A, and I M White 1993 Fruit flies of the Eastern Paleartic species of Urophora R. D (Diptera Tephritidae) II Review of species of the subgenus Urophora s str
Phylogenetic Relationships, Ecology and Ecological Genetics of Tephritidae


Korneyev, V A, and I M White 1999 Tephritids of the genus Urophora R-D (Diptera, Tephritidae) of East Paleartic III Key to Paleartic species Entomological Review (Washington), 79: 296–309


Lalonde, R G, and J D Shorthouse 1982 Exit strategy of Urophora cardui (Diptera Tephritidae) from its gall on Canada thistle The Canadian Entomologist, 114: 873–878


Maynard-Smith, J 1966 Sympatric speciation American Naturalist, 100: 637–650


Mihalyi, F 1960 Furolegyek Trypetidae Magyarorszag Allatvilaga, 15: 1–76

Munro, H K 1925 Biological notes on South African Trypaneidae (fruit-flies) I Memoirs Union of South Africa Department of Agriculture, 1: 3: 39–67

Munro, H K 1926 Biological notes on the South African Trypaneidae (Tephritidae fruit-flies) II Memoirs Union of South Africa Department of Agriculture, 1: 5: 17–40


Munro, H K 1947 African Tephritidae (Diptera) A review of the transition genera between Tephritinae and Trypetinae, with a preliminary study of the male terminalia Memoirs of the Entomological Society of Southern Africa, 1 [i–vii], 1–284

Munro, H K 1949 A new gall-inducing trypetid from South Africa Journal of the Entomological Society of Southern Africa, 12: 130–133


Munro, H K 1952 A remarkable new gall-inducing trypetid (Diptera) from southern Africa, and its allies Entomology Memoirs Union of South Africa Department of Agriculture and Forestry, 2: 329–341


Munro, H K 1957 Sphenella and some allied genera (Trypetidae, Diptera) Journal of the Entomological Society of Southern Africa, 20 14–57

Nei, M 1977 F-statistics and analysis of gene diversity in subdivided populations Annals of Human Genetics, 41 225–233


Novak, J A, and B A Foote 1975 Biology and immature stages of fruit flies the genus Stenopa (Diptera, Tephritidae) Journal of the Kansas Entomological Society, 48 42–52


Ponsch, S, and R Brandl 1992 Cytogenetics and diversification of the phytophagous fly genus Urophora (Tephridae) Zoologischer Anzeiger, 228 12–25

Radhakrishnan, C 1984 A new Tephrela (Diptera Tephridae) from Meghalaya, India Bulletin of the Zoological Survey of India, 5 (2–3) 41–44

Ramos, T C 1997 TreeGardener 2 2 Program and manual Museu de Zoologia, Universidade de Sao Paulo, Brazil

Romstock, M 1987 Tephritis conura Loew (Diptera Tephritidae) und Cirsium heterophyllum (L.) Hill (Cardueae) Struktur- und Funktionsanalyse eines ökologischen Kleinhyrren Ph D thesis, University of Bayreuth, Germany


Rubsaamen, E H 1910 Uber deutsche Gallmucken und Gallen Zeitschrift fur Wissenschaftlichen Insektenbiologie, 6 125–132

Sakuth, T 1996 Die Bedeutung der Cytokinine fur Entstehung und Wachstum von Urophora cardu-Gallen im Stengel der Ackerdistel (Cirsium arvense) Ph D thesis, University of Bayreuth, Germany


Shorthouse, J D 1980 Modification of the flower heads of Sonchus arvensis (family Compositae) by the gall former Tephritis dilacerata (Order Diptera, Family Tephritidae) Canadian Journal of Botany, 58 1534–1540


Shorthouse, J D, and R G Lalonde 1986 Formation of flowerhead galls by the Canadian thistle gall-fly, Urophora cardu (Diptera Tephritidae), under cage conditions The Canadian Entomologist, 118 1199–1203

Wahlgren, E 1944 Cecidologiska antechungar V Entomologisk Tidskrift, 65 50–121
Wangberg, J K 1980 Biology and immature stages of fruit flies the genus Eurosta (Diptera Tephritidae) Journal of the Kansas Entomological Society, 53 205–219
Wangberg, J K 1981 Gall-inducing habits of Acturina species (Diptera Tephritidae) on rabbitbrush (Compositae Chrysothamnus spp) in Idaho Journal of the Kansas Entomological Society, 54 711–732
Waring G L, W G Abrahamson, and D J Howard 1990 Genetic differentiation among host-associated populations of the gallmaker Eurosta solidaginis (Diptera Tephritidae) Evolution, 44 1648–1655
Wasbauer, M S 1972 An annotated host catalog of the fruit flies of America north of Mexico (Diptera Tephritidae) Occasional Papers of the Californian Department of Agriculture, Bureau of Entomology, 19 1–172
Wright, S 1931 The genetical structure of populations Annals of Eugenics, 15 323–354
Zwolfer, H 1965 Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe Technical Bulletin Commonwealth Institute of Biological Control, 6 81–154
Zwolfer, H 1969 Urophora sirunaseva (Hig) (Dipter Tephritidae), a potential insect for the biological control of Centaurea solstitialis L in California Technical Bulletin Commonwealth Institute of Biological Control, 11 105–155
Zwolfer, H 1979 Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls Fortschritte der Zoologie, 25 2/3 331–333
Zwolfer, H 1982 Das Verbreitungsgebiet der Bohrfliege Urophora cardui L (Diptera Tephritidae) als Hinweis auf die ursprünglichen Habitate der Ackerdistel (Cirsium arvense (L) Scop) Verhandlungen der Deutschen Zoologischen Gesellschaft, 1982 298
Zwolfer, H W Englert, and W Pattullo 1970 Investigations on the biology, population ecology and the distribution of Urophora cardui L Weed projects for Canada Progress report XXVII Commonwealth Institute of Biological Control, Delemont, Switzerland