

Review of Biogeography, Host Range and Evolution of Acoustic Hunting in Ormiini (Insecta, Diptera, Tachinidae), Parasitoids of Night-calling Bushcrickets and Crickets (Insecta, Orthoptera, Ensifera)

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Abstract. Interest in parasitoids has grown with the recognition that host-parasitoid systems offer opportunities to examine fundamental questions in behavioural and evolutionary ecology. Tachinid flies of the Ormiini possess a conspicuously inflated prosternal region, enabling them to detect the mating songs of their hosts. This speciality makes them a highly suitable group for studies of adaptive radiation. To emphasise further research in this important group of parasitoids, their biogeography and host species are summarised.

The Ormiini are a particularly small group, containing only 68 described species of predominantly tropical, especially neotropical forms. A table of host-parasitoid relations reveals that predominant parasitism is of bushcrickets. The exploitation of cricket songs appears to be a derived pattern that evolved as a host switch some time after the Eocene.

Hypotheses concerning fly-host coevolution and the reasons for the development of hearing are discussed, and include the question of mate finding and avoidance of bats as predators.

Key words. Diptera, Orthoptera, acoustic communication, host-parasitoid relationship.

1. INTRODUCTION

The Tachinidae form the second largest family of Diptera, with over 8000 species described worldwide (CANTRELL & CROSSKEY 1989). Though all are parasitoids, their reproductive strategies are diverse and far less well understood than those of the parasitic Hymenoptera (FEENER & BROWN 1997). Increased interest in parasitoids has coincided with their adoption as theoretical and experimental model systems. This increase in interest has come with the growing recognition that host-parasitoid systems offer unparalleled opportunities to examine fundamental questions in behavioural and evolutionary ecology (GODFRAY 1994).

Most insect parasitoids use chemicals to locate their hosts (EGGLETON & BELSHAW 1993), but tachinid flies of the Ormiini are atypical because they use sound for host-detection (CADE 1975). The acoustic orientation of behaviour is a particularly spectacular example of exploitation of host communication systems. The para-

sitoids exploit the intraspecific acoustic communication, acting as illicit receivers (HAYNES & YEARGAN 1999). Such predation, based on sexual traits, is of central importance to the theory of sexual selection (KOTI-AHO 2001) and should have an intensive impact on host behaviour (BURK 1982a; SAKALUK 1990; ZUK & KOLLURU 1998).

Parasitizing flies rely on acoustic cues (CADE 1975, WALKER 1986). Adult Ormiini possess a conspicuously inflated prosternal region, enabling them to detect the mating songs of their hosts (CADE 1975). The auditory sensitivity of hearing organs is tuned to the dominant frequency of the host's song (LAKES-HARLAN & HELLER 1992; ROBERT et al. 1992). Detection is only the basic part, and accurate directional hearing (MASON et al. 2001) is also necessary for exact localisation of hosts (RAMSAUER & ROBERT 2000). Their biomechanically unique ear (MILES et al. 1995; ROBERT et al. 1996b, 1998; ROBERT 2001) enables flies to exhibit remarkable phonotactic accuracy, even in darkness; *Ormia ochracea* landed at a mean distance of 82 mm

from a loudspeaker repeating the natural host song (MÜLLER & ROBERT 2001).

Once the host is located, the fly deposits first instar larvae (planidia) on or near the host (CADE 1975; ADAMO et al. 1995a; ALLEN et al. 1999), which then penetrate the host's interscleral membranes. After entering the host, the larvae complete development, killing the host when ready to pupate (ADAMO et al. 1995a; ALLEN 1995a; LEHMANN 1998).

The specialities of Ormiini make them a highly suitable group for studies of adaptive radiation. Unfortunately, our knowledge of the majority of Ormiini fly species is poor. One of the goals of this overview is to stimulate further research into the interaction between Ormiini flies and their hosts.

Here, I summarise topics of general interest, in particular biogeography, host usage and the evolution of acoustic hunting.

2. BIOGEOGRAPHY

The tribus Ormiini is currently divided into eight genera containing 67 species worldwide (Tab. 1). This includes two undescribed species mentioned in the catalogues of CROSSKEY (1973) and CANTRELL & CROSKY (1989). The taxonomy is stable for the temperate zones of the Palaearctic (TSCHORSNIG & RICHTER 1998) and Nearctic (O'HARA & WOOD 1999), whereas new species continue to be found in South Africa (BARRACLOUGH 1983, 1996) and Australia (BARRACLOUGH & ALLEN 1996). A number of species probably await discovery in the tropics, as Museum collections contains many not properly determined flies (N. WYATT in litt. 2001; H.-P. TSCHORSNIG in litt. 2000).

The pattern of occurrence of this small and highly specialist group of flies is of tropical and subtropical dominance, and only a tiny fraction has reached the temperate climate zones (Fig. 1). The northernmost species are reported from Middle Europe (Switzerland and Hungary; TSCHORSNIG & RICHTER 1998), from Mongolia (RICHTER 1972), and a third one from southern Quebec province in Canada (O'HARA in litt.). The situation is similar in the southern Hemisphere: Ormiini species are lacking in Chile (GUIAMARÃES 1971) and the Argentinean part of Patagonia (GRAMAJO 1998). The greatest diversity, with 29 species, is described from the Neotropics (GUIAMARÃES 1971), accounting for 43 percent of the known world fauna. This pattern holds true for parasitoid Diptera in general (FEENER & BROWN 1997), and more than one-third of all Tachinidae species occur in South America (CANTRELL & CROSSKEY 1996). Comparison on a region-to-region basis shows that the tropical fauna is much more

species rich than the arctic region. The described Neotropical fauna is about double the number of species from Asia and three-times the diversity of the African fauna.

The genera *Opsophasiopteryx* Townsend, 1917 and *Ormiophasia* Townsend, 1919 are practically endemic to South America, whereas the largest genus, *Ormia* Robineau-Desvoidy, 1830, has members in all parts of America, including a few endemic species on Caribbean Islands and in North America. The genus *Therobia* Brauer, 1862 is dominant in the old world, and contains 20 species. The small genera *Phasioormia* Townsend, 1933 and *Homotrixa* Villeneuve, 1914 are confined to Asia, including Australia (CANTRELL & CROSSKEY 1989, 1996, CROSSKEY 1973, 1976), whereas the mono-specific genus *Mediosetiger* Barraclough, 1983 is restricted to South Africa (BARRACLOUGH 1983, 1996). The genus *Aulacephala* Marquart, 1851 has only two representatives, but both species are widely distributed, *A. maculithorax* Marquart, 1851 occurring in southern and central Africa (VAN EMDEN 1944, CROSSKEY 1980) and the Asian species, *A. hervei* (Bequaert, 1922), is widespread (CROSSKEY 1976; RICHTER 1999).

Museum material is sparse probably because Ormiini flies are strictly nocturnal, most active shortly after sunset (FOWLER 1987b; CADE et al. 1996; ALLEN 1998; KOLLURU 1999). Aggregating males of two North American species have been observed around towers in Florida (LEDERHOUSE et al. 1976), suggesting that Ormiini move to hill-tops during mating, like some other tachinid flies. The aggregating period was less than twenty minutes, thus their observation requires search within this period shortly after sunset. Single flies have been taken from light sources at night (UÉDA 1960; TSCHORSNIG in litt.; O'HARA in litt.). Cricket-flies observed during daytime were resting individuals of the North American *Ormia ochracea* (Bigot, 1889) found under leaves of Guava trees (BURK 1982b), and the South African species *Mediosetiger microcephala* Barraclough, 1983 collected at a small sandstone cave (BARRACLOUGH 1996).

A successful approach for fly collection exploited their phonotactic behaviour. Great numbers can be trapped on sound sources (CADE 1975, 1981a; CADE et al. 1996; FOWLER 1987a, c, 1988a, b; FOWLER & GARCIA 1987; FOWLER & KOCHALKA 1985; GRAY & CADE 1999; HUNT & ALLEN 1998; KOLLURU 1999; MANGOLD 1978; WAGNER 1996; WALKER 1986, 1988, 1989, 1993; HENNE & JOHNSON 2001). Despite trap efficiency, only female flies are attracted (WAGNER 1996). Furthermore, sound traps can be used most successfully if the preferred song pattern is known. Even slightly different song types can be partially or totally ignored by the flies (WALKER 1993; WAGNER 1996; GRAY & CADE 1999).

Tab. 1. (Continued).

	N-America	M-America	Caribbean	S-America	Palearctic	Asia	Africa	Australia
<i>Phasioormia</i> Townsend, 1933						(3)		
44 <i>bicornis</i> (Malloch, 1932)						•		
45 <i>pallida</i> Townsend, 1933						•		
46 <i>spec.</i> {Crosskey 1973}						•		
<i>Therobia</i> Brauer, 1862					(3)	(8)	(7)	(3)
47 <i>abdominalis</i> (Wiedemann, 1830)						•		
48 <i>albifacies</i> (Villeneuve, 1914)							•	
49 <i>bicolor</i> (Séguy, 1933)							•	
50 <i>braueri</i> (Kertész, 1899)						•		
51 <i>composita</i> (Séguy, 1925)						•		
52 <i>insularis</i> (Séguy, 1947)						•		
53 <i>japonica</i> (Ueda, 1960)					•			
54 <i>leonidei</i> Mesnil, 1964					•			
55 <i>maculipennis</i> (Villeneuve, 1914)							•	
56 <i>melampodis</i> Seguy, 1969							•	
57 <i>minuta</i> (Séguy, 1926)							•	
58 <i>mongolica</i> (Richter, 1972)					•			
59 <i>papuana</i> (Paramonov, 1955)						•		
60 <i>punctigera</i> (Paramonov, 1955)						•		
61 <i>rieki</i> (Paramonov, 1955)								•
62 <i>secunda</i> (Paramonov, 1955)								•
63 <i>tristis</i> (Séguy, 1926)							•	
64 <i>umbrinervis</i> (Villeneuve, 1925)							•	
65 <i>vesiculifera</i> Bezzi, 1928						•		•
66 <i>vulpes</i> (Séguy, 1948)						•		
<i>Mediosetiger</i> Barraclough, 1983							(1)	
67 <i>microcephala</i> Barraclough, 1983							•	
Sum	8	8	5	29	4	13	9	6

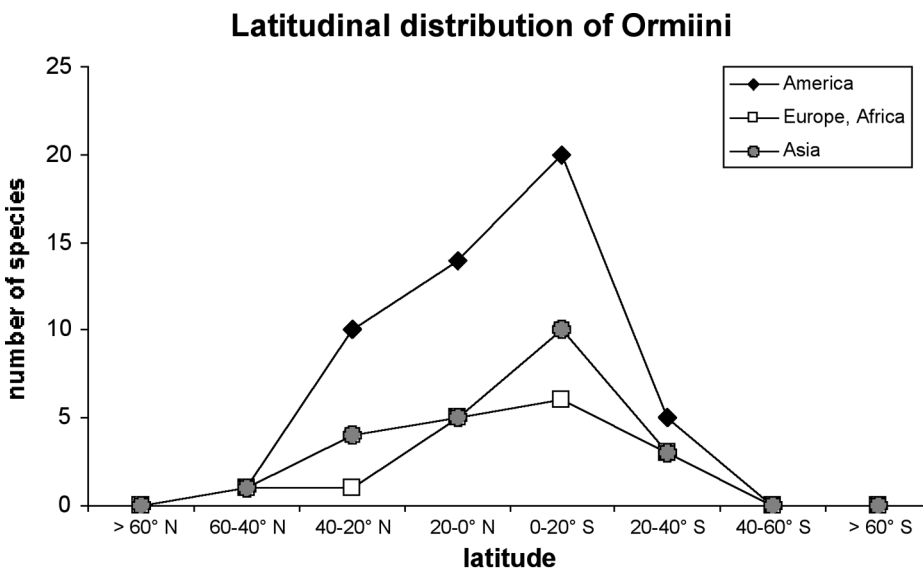


Fig. 1. Number of Ormiini species compared to latitude, treated separately for the American continents, Europe combined with Africa and Asia.

Screening infected host individuals for a parasitoid infection is a highly effective way to sample larvae and consequently flies. Older fly larvae produce a breathing funnel on the host's abdomen, which is visible as a brown dot (LEHMANN & HELLER 1998). Under favourable situations and with parasitism rates over 50 percent at the end of the season (BURK 1982a; ALLEN 1995a; LEHMANN & HELLER 1998), large numbers of flies can be obtained by rearing the parasitized bushcrickets. One advantage of this approach is that both sexes occur in equal numbers (ADAMO et al. 1995b; ALLEN 1995a; LEHMANN unpubl. data).

3. HOST RANGE

In general, only adult males suffer from parasitism. This is due to the phonotactic host locating tactics of the flies, as mute males are not infected (WALKER & WINERTER 1991; LAKES-HARLAN & HELLER 1992). If females respond acoustically to calling males, they suffer from parasitism as well, as for example in *Ephippiger ephippiger* (Fiebig, 1784). Nonetheless, even in this case significant more males are infected than females (LEONIDE 1969). However, parasitism is not exclusively restricted to calling males, and acoustically responding females. Although deposition of the live fly-planidia (larviposition) is elicited by calling (ALLEN et al. 1999), the fly larvae are found in rare cases in silent males, females and even bushcrickets (Tab. 2). This opportunistic exploitation of hosts might be a direct consequence of Ormiini oviposition pattern. Tachinids – lacking a rigid ovipositor – often deposits mobile planidia larvae rather than eggs (ASKEW 1971; BELSHAW 1994; PRICE 1980). After landing Ormiini female flies deposit planidia either directly on the host, or spread a number of larvae in their vicinity (ADAMO et al. 1995a; CADE 1975), where they are able to survive for up to two hours (ALLEN et al. 1999). More than fifty percent of tested flies had no direct contact with the host individual, but laid a number of planidia in their surrounding area (ALLEN et al. 1999). This might explain the infection of non-calling hosts, who might be located near to a singing male (like larvae), or orientate themselves towards the calling individual (like satellite males: CADE 1981a, or females: FOWLER & GARCIA 1987; PARKMAN et al. 1996). Whether the observed parasitism of non-calling hosts is an incidental by-product or an adaptive strategy enabling the fly to increase the number of potential host individuals remains an open question.

Our current knowledge of the host range of Ormiini flies is restricted (Tab. 2). Out of the 67 known Ormiini species (see Tab. 1), for only 11 species host records are available. This includes three fly species that are

not identified to the species level. Furthermore, for five species only one host has been described. However, a range of host species is the rule for all extensively studied Ormiini species, and ranges from four to thirteen species. This suggests that cricket-flies are opportunistic hunters with a wide spectrum of potential hosts.

The few well-studied species of Ormiini were reared from a great number of hosts, partly due to regional differences in host usage. In *Ormia ochracea* three species of the genus *Gryllus* Linnaeus, 1758 serve as hosts in Florida, two in Texas, whereas a further species is reported from California. A special situation is found on Hawaii, where the fly is introduced and found in the also introduced host *Teleogryllus oceanicus* (Le Guillou, 1841), originally native to Australasia (ZUK 1994). As in Florida, where *Ormia ochracea* infects three different cricket species, alternative hosts are parasitized at the same time and locality. In France seven species of bushcrickets were attacked by *Therobia leonidei* in a single mountainous region (LEONIDE 1969). A similar situation can be observed in *Homotrixa alleni* Barraclough, in Barraclough & Allen, 1996 in Western Australia where, in addition to the main host, three other bushcricket species were parasitized (BARRACLOUGH & ALLEN 1996; LEHMANN unpubl. data, compare Tab. 2). Most of the published data does not provide sufficient information concerning how the different hosts were used and whether the flies exhibited preferences for special species. However, at Mount Spilia in Greece, two alternative bushcricket species were parasitized by *Therobia leonidei* (LEHMANN 1998). The song pattern is remarkably similar in these species (HELLER 1988), and the parasitism rate does not show a significant difference (*Eupholidoptera chabrieri* (Charpentier, 1825): 12%, $n = 17$, *Poecilimon veluchianus* Ramme, 1933: 22%, $n = 23$, $\chi^2 = 0.67$, $P = 0.41$). Obvious differences in the attack rate seem to be inevitably coupled to differences in the song structure of the hosts: species with more repetitive songs are more likely to be infested (LEHMANN & HELLER 1998).

Summarising the available host records, Ormiini flies can be characterised as opportunistic hunters. The taxonomic specificity of these flies is low; they parasitize a wide range of Orthoptera and can easily be reared from alternative hosts. The only features common to all known host species are that they are sexually active at night, produce mating songs and belong to the long-horned suborder Ensifera (Fig. 2).

Two hitherto unknown conclusions can be drawn from this overview:

a) The ancestral state for the occurrence of parasitism is the use of bushcrickets, whereas attacks on gryllids (crickets and mole crickets) are a derived state. Infec-

<i>Poecilimon chopardi</i>					61	
<i>Poecilimon mariannae</i>		T Phaneropterinae		♂ ♂	61, 63–68	
<i>Poecilimon thessalicus</i>		T Phaneropterinae		♂ ♂	61, 63, 70	
<i>Poecilimon zimmeri</i>		T Phaneropterinae		♂	61	
<i>Poecilimon veluchianus</i>		T Phaneropterinae		♂ ♂	61, 63, 66, 69	
<i>Poecilimon</i> nov. spec.		T Phaneropterinae		♂ ♂	61, 63 (sub <i>P. propinquus</i>)	
<i>Therobia vesiculifera</i>		T Conocephalinae			71	Uncertain host
<i>Therobia</i> spec.		T Conocephalinae			57	
1 NUTTING 1953	27 CADE 1981				53 ALLEN 1998	
2 SMYTH IN WOLCOTT 1940	28 CADE 1984				54 ALLEN ET AL. 1999	
3 WOLCOTT 1940	29 WALKER 1993				55 BARRACLOUGH & ALLEN 1996	
4 WOLCOTT 1951	30 ADAMO et al. 1995a				56 HUNT & ALLEN 1998	
5 MANGOLD 1978	31 ADAMO et al. 1995b				57 CANTRELL 1986	
6 FOWLER & KOCHALKA 1985	32 CADE et al. 1996				58 LEHMANN unpubl. data	
7 FOWLER 1987C	33 GRAY & CADE 1999				59 LEONIDE 1963	
8 FOWLER & GARCIA 1987	34 WALKER 1986				60 LEONIDE 1969	
9 FOWLER 1988B	35 WALKER 1989				61 LEHMANN 1998	
10 FOWLER & MARTINI 1993A	36 WALKER 1993				62 HELLER PERS. COMM	
11 FOWLER & MARTINI 1993B	37 WINERITER & WALKER 1990				63 LAKES-HARLAN & HELLER 1992	
12 FRANK et al. 1996	38 WALKER & WINERITER 1991				64 STUMPNER & LAKES-HARLAN 1996	
13 PARKMAN et al. 1996	39 ROBERT et al. 1992				65 LEHMANN & FESTING 1998	
14 WALKER et al. 1996	40 WAGNER 1995				66 LEHMANN & HELLER 1998	
15 FOWLER 1987a	41 REINHARD 1922				67 LEHMANN & LEHMANN 2000a	
16 FOWLER 1987b	42 SABROSKY 1953				68 LEHMANN & LEHMANN 2000b	
17 FOWLER 1988a	43 EDGEComb et al. 1995				69 LAKES-HARLAN 1997	
18 FOWLER & MESA 1987	44 SIMMONS & ZUK 1994				70 LEHMANN et al. 2001	
19 ROBERT et al. 1994	45 ZUK et al. 1993				71 WYATT pers. comm. 2001:accompanying this series (of <i>Therobia vesiculifera</i> from Fiji) there is a specimen of <i>Conocephalus affinis</i> ... I presume this... is the host species, but ...the.. label data does not definitely associate it with any of the flies.	
20 BURK 1982a	46 ZUK 1994				72 HENNE & JOHNSON 2001	
21 WALKER IN SHAPIRO 1995	47 ZUK et al. 1995				73 KOLLURU & ZUK 2001	
22 SHAPIRO 1995	48 ROTENBERRY et al. 1996				74 KOLLURU et al. 2002	
23 FEAVER 1983	49 ZUK et al. 1998					
24 CADE 1975	50 KOLLURU 1999					
25 CADE 1979	51 ALLEN 1995a					
26 CADE 1980	52 ALLEN 1995b					

tion of ground-living gryllids is found only within the New World genus *Ormia*, but nowhere else (Fig. 2). This argument is further strengthened by an outgroup comparison: the Glaurocarini hypothesised to be the sister group of the Ormiini (ZIEGLER 1998), also attacks bushcrickets (CROSSKEY 1965).

b) Most Ormiini species infect members of the subfamily Conocephalinae: seven out of eight Ormiini species infecting bushcrickets were found in at least one member belonging to the Conocephalinae. One reason for this might be the preference of these bushcrickets for open habitats, where they are easy to catch and therefore easy to screen, resulting in an observer bias. Alternatively, species of this subfamily use highly repetitive song patterns, and there is relatively small differentiation between species (BAILEY 1976; HELLER 1988). This might enable the Ormiini to switch easily from one host species to another within this large group, which is found worldwide. Nonethe-

less, we must await further results, to determine if this picture still holds true when more host records become available. In the most intensively researched species (*Homotrixa alleni* and *Therobia leonidei*) there is no clear preference for members of any taxonomic group within the bushcrickets (see Tab. 2).

4. EVOLUTION OF ACOUSTIC HUNTING

Ormiini flies are unique within the Tachinidae in having a sound receptive organ able to detect and localise their hosts' phonotactically. Some Sarcophagidae flies of the tribus Emblematomini have independently evolved an ear with similar anatomy (LAKES-HARLAN et al. 1999; KOHLER & LAKES-HARLAN 2001), but with a different tympanal mechanical response to sound (ROBERT et al. 1999). Both groups are parasitoids of sound-producing insects and the acoustic sense is used

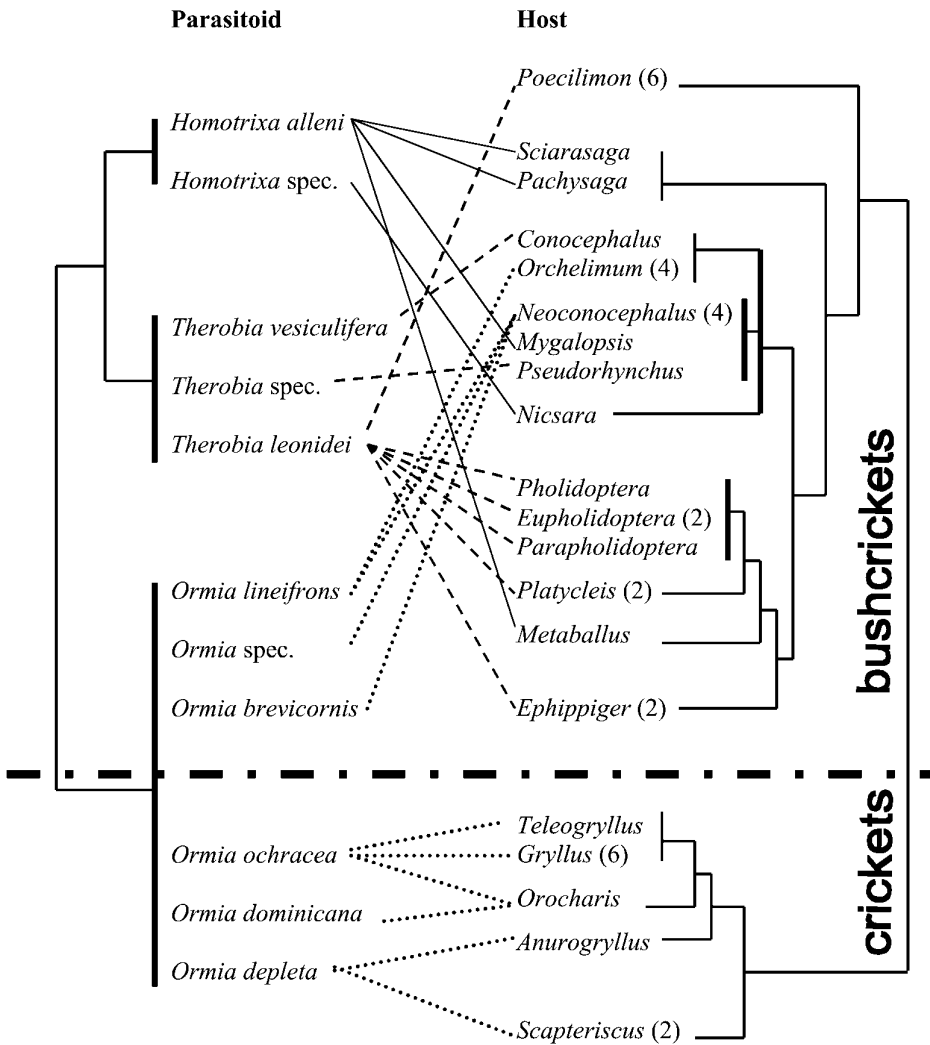


Fig. 2. Host phylogeny compared to a preliminary tree of 11 Ormiini flies with known host species (compare Tab. 2). Thick lines indicate unresolved branches. The orthopteran phylogeny follows the overview in GWYNNE (2001). Within the Ormiini BARRACLOUGH & ALLEN (1996) proposed a closer relationship between *Homotrixa* and *Therobia*; in the genus *Ormia* the species *depleta*, *ochracea* and *dominicana* possess a similar hearing organ (ROBERT et al. 1996a).

for host location (see this review and LAKES-HARLAN et al. 2000; SOPER et al. 1976 for *Emblemasomatini*). The hearing organs in Diptera have evolved from a chordotonal precursor organ (EDGECOMB et al. 1995; LAKES-HARLAN et al. 1999) as most tympanal ears of insects (FULLARD & YACK 1993; HOY & ROBERT 1996; STUMPNER & VON HELVERSEN 2001). How can we explain the evolutionary selective pressures for non-hearing flies to evolve a sound-detecting organ?

The ancestral tachinids were probably active during the day and unable to detect sound, like the majority of extant tachinids (BELSHAW 1993, 1994). Therefore it could be assumed that Ormiini ancestors behaved similar. The first specialisation in their evolution could have been the parasitism of bushcrickets using visual stimuli. During this period it might have been advantageous for the flies to attack adult bushcrickets. Larger body-size could have been one reason for parasitizing adult hosts, instead of larvae, as more parasitoids might develop successfully within one individual, leading to larger parasitoid offspring with a higher fecundity (KOLLURU & ZUK 2001). Probably a second reason for utilising adults is their longer life span, because larvae moult into the successive stage within a few days. Both factors, bigger host size and longer stable conditions inside a host, may favour adult bushcrickets as hosts. However, adult bushcrickets are mostly hidden in the vegetation (especially during the day) making them more difficult to detect. Therefore, the reception of vibration might provide additional information to detect a hidden prey. Vibrations are produced during body movements and in a very intense way during courtship singing in bushcrickets (KALMRING 1985). In woody plants, vibrational signals can spread over large distances and can be detected by many insect species (MARKL 1983). All flies have a clear preadaptation for this detection in that they possess a chordotonal organ in their thorax (EDGECOMB et al. 1995). The blowfly *Sarcophaga bullata*, although without a hearing device, can detect vibrations from 100 to 10000 Hz (LAKES-HARLAN et al. 1999). This chordotonal precursor seems to be a preadaptive structure in the sequence of evolution leading to tympanal ears in Diptera (EDGECOMB et al. 1995; LAKES-HARLAN & HELLER 1992; LAKES-HARLAN et al. 1999). Predators that are not specialised in their prey, take advantage of the calling songs of male bushcrickets and use already existing information to localise their hosts (illicit receivers of intraspecific communication: HAYNES & YEARGAN 1999; ZUK & KOLLURU 1998). The detection of host signals has led to extreme adaptations in the hearing abilities of flies, that are tuned towards the frequency content of host songs (LAKES-HARLAN & HELLER 1992; ROBERT et al. 1992). However, as predicted for airborne communication (HAYNES & YEAR-

GAN 1999), song recognition in parasitoids is less specific (STUMPNER & VON HELVERSEN 2001) and includes the song patterns of several species. Where a choice is available, species with more repetitive songs are more likely to be infested (LEHMANN & HELLER 1998; WALKER 1993).

Parallel to the transformation of the chordotonal organ into a detector of airborne sound, flies presumably also became active at night, when most of their bushcricket hosts call (HELLER & VON HELVERSEN 1993; WALKER 1983). Acoustic communication during the night is advantageous for bushcrickets permitting the avoidance of predators that hunt visually (compare HELLER 1992; HELLER & VON HELVERSEN 1990; WALKER 1983) and possibilities of better sound propagation after sunset (RÖMER 1993; RÖMER & LEWALD 1992; VAN STAADEN & RÖMER 1997). The nightly activity pattern of the flies might have evolved earlier than the hearing of airborne sound. The African *Glaurocara flava* (Thompson, 1868) is a night-active parasitoid of bushcrickets, but without the conspicuously inflated prosternal region for sound detection (CROSSKEY 1965). Species of Glaurocarini share a number of similarities with species of Ormiini, which make these taxa possible sister groups (TSCHORSNIG 1985; ZIEGLER 1998), and the Glaurocarini might thus represent a transitional evolutionary step in the evolution towards the highly adapted Ormiini.

Infection has severe consequences for parasitized hosts, and this could have influenced signalling within these hosts. One possible way to escape the selective pressure of parasitism could be the evolution of low frequency signals, which do not match the frequency tuning of the flies. However, the production of lower frequency songs is more expensive in energetic terms for bushcrickets (PRESTWICH 1994). Furthermore, the usage of lower song frequencies by the hosts will also drive the flies to adapt their hearing abilities towards these frequencies. It is likely that such developments took place in the West-Australian bushcricket *Sciarasaga quadrata*, which calls at a lowered peak frequency around six kHz (ALLEN 2000). The local parasitoid *Homotrixa alleni* possesses one interneuron, which is also tuned to six kHz (LAKES-HARLAN et al. 1995), but with a low sensitivity. Even if the bushcricket host is not fully protected, its low song frequency might have reduced the success of the fly. Such a battle between a host and its fly enemy might be the starting point for flies to evolve the ability to detect low sound frequencies (LAKES-HARLAN 1997). Within the North-American genus *Ormia* such a transition has taken place, with a change from the usage of bushcricket hosts with high song frequencies towards gryllids, which call at low frequencies (see Fig. 2). Lower song frequencies with their longer sound waves

tender directional hearing problematic for a tiny insect. Flies have overcome this problem by using special neuronal coding strategies, leading to accurate directionality in hearing even at low sound frequencies (MASON et al. 2001; MÜLLER & ROBERT 2001; OSHINSKY & HOY 2002).

5. TIME SCALE

Hearing and sound production in insects has evolved independently several times and has led to an enormous diversity of auditory systems (FULLARD & YACK 1993; HOY & ROBERT 1996). For the Ensifera it is likely that acoustic signalling and hearing developed from vibratory communication in a coevolutionary process adapted for mate finding (STUMPNER & VON HELVERSEN 2001). In any case, hearing seems to be a very ancient invention in Orthoptera, and developed at least 200 million years ago (GOROCHOV 1996). Bushcricket fossils from Denmark (55 million years old) have very modern tympanic structures (RUST et al. 1999). Thus, hearing and male calling must have been well established and widespread within the bushcrickets and crickets before higher flies (Brachycera) radiated after the Cretaceous-Tertiary crisis (HENNIG 1969). The fossil record of Tachinidae includes 10 species in 8 genera of either Tertiary or Quaternary origin. The earliest records being the genera *Electrotachina* Townsend, 1938 and *Palaeotachina* Townsend, 1921 found in Eocene/Oligocene Baltic amber, of about 45 million years in age (EVENHUIS 1994). Tachinids might be older than the known fossil records, but nonetheless the evolution of exploitation of singing hosts by Ormiini must undoubtedly be younger than the evolution of singing in bushcrickets. Even so, the parasitism of gryllids cannot be the result of a coevolutionary process, but rather reflect a host switch from bushcrickets to crickets long after both groups had separated. The reasons for such a host switch in some species of the genus *Ormia* are unclear, but the advantages must exceed the costs of tuning the hearing organ towards lower frequencies and the development of a new method of directional hearing in the cricket parasitizing species (MASON et al. 2001).

The evolution of insect-feeding bats antedates the evolution of Tachinidae. *Icaronycteris* Jepsen, 1966, from the lower Eocene of North America, is the oldest known bat (BENTON 1993). Around 50 million years, during the middle Eocene, bats with fully developed echo orientation (HABERSETZER & STORCH 1988, 1989) were already part of the acoustic environment. Ultrasound hearing in the Ormiini is sometimes assumed to have been maintained to avoid predation by bats during nocturnal activity (ROBERT et al. 1994, 1996a).

Even extant male flies of *Ormia ochracea* show a broad hearing spectrum including frequencies in the ultrasonic (ROBERT et al. 1992) that might be used to detect bat biosonar. Nonetheless, the evolution of this hearing-ability is certainly coupled to the exploitation of calling hosts. However, this hearing ability would only be necessary for females, which attack the hosts. Why male flies hear is still puzzling, but one alternative explanation to bat avoidance, might be to enable them to home towards singing hosts in the search for conspecific females for matings.

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