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WING POLYMORPHISM, HOST PLANT ECOLOGY, AND BIOGEOGRAPHY
OF *LONGITARSUS* IN ISRAEL
(COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

The phenomenon of Intra-specific wing polymorphism, unusually prevalent in *Longitarsus* (the largest genus of Alticinae), is discussed based on field data and similar polymorphism in other insect groups. In Israel 44% of the species are known to have wing polymorphism, 26% have both flying and flightless morphs within Israel, and 14% have some Israeli populations with varying amounts of both morphs. Aspects of host plant ecology are considered especially relative to the coevolution of the discrete species groups found on each of seven host plant families. Most Israeli *Longitarsus* feed on members of one of two families; i.e. Boraginaceae (33%) or Labiatae (36%). Allotrophy is recorded for 4 species and post-season resting on *Quercus* for 14 species. Based on *Longitarsus* species a detailed percentage analysis of the six zoogeographical components that merge in Israel indicates that the highest affinity is towards the Mediterranean subregion of the Palearctic (52%), especially its East Mediterranean component (23%). A strong affinity is shown to the Euro-Siberian (25%), less for the Irano-Turanian (16%), and least for the Eremian (6%) subregions.

INTRODUCTION

The genus *Longitarsus* apparently contains a relatively large percentage of species with the interesting and little understood phenomenon in insects of intra-specific wing length polymorphism. This polymorphism involves wing reduction (brachyptery) such that flight is not possible for locomotion or dispersal; therefore, flightless morphs. Wing reduction evidently

occurs in a relatively few generations but there are a variety of theories for other polymorphic insect groups as to whether the mechanism is purely genetically selected or only induced by environmental changes or instabilities. Isolation is also potentially an important factor; whereas, wing reduction is not always related to the environment, geography, sex, or season as it is in some insect groups. This wing polymorphism, with some of its principles and probable mechanism is briefly reviewed below as it applies to the special case in *Longitarsus* species, especially relative to the data presented from Israeli *Longitarsus*.

An important aspect of all herbivores is their host plant relationship, and in the case of Israeli *Longitarsus* species, several host plant feeding groups are involved. There is an apparent relationship among at least some of the host plant families of *Longitarsus*, possibly through their secondary defense chemicals, that may have a basis in the coevolution with *Longitarsus* and other herbivores that feed on these plants. The detailed new and known information on host plant ecology (Furth, 1980) indicates major host-family/herbivore species groups of Israeli *Longitarsus* with evidence of rather unusual host switching and/or allotrophy early and late in the season.

Longitarsus also provides a good example of the well known biogeographical crossroads that exists in Israel (Furth, 1975) among 6 biogeographical elements of the Palearctic Region (three Mediterranean, Eremian, Irano-Turanian, and Euro-Siberian). A detailed analysis of Israeli *Longitarsus* species zoogeographical affinities is provided based on a biosystematic study of this group (Furth, 1980). This treatment provides yet another zoogeographical viewpoint to the complexity of the faunal elements and their origins in the Middle East transition zone.

WING POLYMORPHISM

Wing polymorphism is a phenomenon that is widespread throughout the pterygote insect world and has been known for a long time. However, the diversity of types of wing polymorphism in a wide variety of taxa and situations, has led to many different speculations as to its mechanism. The following discussion will concern intra-specific wing length polymorphism in which a single species has flying morphs (full length wings or macropterous) and one or more flightless morphs (short or reduced wings, i.e. brachypterous, micropterous, or apterus (= wingless, *sensu stricto*)).

In many cases there are only two morphs (= dimorphism) involved. Wing polymorphism is known from most insect orders, however, often a species is known from only one of the functional morphs (i.e. flying or flightless) or flightlessness is associated with the sex. Generally in insects the females are more often flightless than the males and this indicates outbreeding (Hamilton, 1978). Interestingly Hamilton found the relatively high number of flightless species that are found in the underbark and dead tree habitat to be male flightlessness. The most numerous and best known examples of wing polymorphism are from the Hemiptera and Coleoptera in which many species are known to have both morphs. I will use examples mostly from these two orders although the principles behind the polymorphic mechanisms may apply to cases in other orders of insects.

Wing polymorphism in general appears to be a rather progressive or advanced (apomorphic) evolutionary phenomenon which, as Mayr (1963) points out, is adaptive because such kinds of diversity increase the efficiency of exploitation of environmental resources. Many of the studies of wing polymorphism in recent years have dealt with trying to explain the causal mechanism in a particular taxon and this has led to some confusion as to the ecological, genetic, and evolutionary principles involved in wing polymorphism.

In a recent thorough treatment of wing polymorphism and diapause determination in water striders (*Gerris*), Vespäläinen (1978) stresses that temporary and permanent habitats necessitate adaptive strategies revolving around wing dimorphism (polymorphism). Vespäläinen further states that the mechanisms of wing length polymorphism determination involve both environmental (= polyphenism) and genetic switches (= genetic polymorphism). This last statement touches on an area of some ambiguity in the subject of polymorphism, because the environmental factors that act as switch mechanisms of wing length must ultimately be acting on the genotype of the individuals. Vespäläinen defines polymorphism as the occurrence in the same population of two (= dimorphism) or more discontinuous phenotypes (morphs) in the same life cycle stage in proportions in which the frequency of the rarest (1% or more) morph cannot be maintained only by recurrent mutation; genetic polymorphs are genetically differentiated and polyphenic morphs arise by environmental switch mechanisms. In his model for *Gerris* Vespäläinen indicates that in most cases polyphenic or environmental factors (temperature and photoperiod) operate in determination of the wing morphs and that only in permanently polymorphic (dimorphic) species, with both

morphs in a population, is the genetic switch mechanism operating. Seasonal polyphenism is polyphenism that is restricted to a part of the year such as in reproductive flying morphs of aphids, seasonal migratory or dispersal morphs in various insect groups.

Clark (1976) more lucidly points out that in genetically determined polymorphism the environment plays little or no part in morph determination and this type is not adaptive in a fluctuating environment; it arises from discontinuous distribution of genetic material in a population (or species). Clark also elucidates environmentally cued polymorphism as environmental stimuli interacting with the genotype to produce a particular morph switching on or off alleles which are common to all members of the population (species).

Southwood (1961) says that in Heteroptera wing reduction is a juvenile character caused by a change in the concentration of juvenile hormone necessary to produce long-winged adults. An excess will produce juvenile traits in adults (short wings) and a deficiency produces adult traits in larvae, in both cases individuals have reduced wings. The indication is that this phenomenon is temperature controlled; therefore, an environmentally determined polymorphism. This would then be particularly important with regard to wing polymorphism at high altitudes and colder temperatures.

Lindroth (1946, 1949) proved that carabid beetle wing polymorphism is genetically determined with the short winged morph being determined by a single dominant allele. He found geographical variation in Scandinavian carabid populations as being either macropterous, brachypterous, or mixed in varying proportions. Lindroth's studies indicate differences in gene frequency for wing polymorphism in geographically different populations; therefore, a genetic determination. The genetic dominance of brachyptery has been demonstrated in several other insect groups (Jackson, 1928; Stein, 1977; Vespäläinen, 1978).

Utida (1972) experimenting with bruchid weevils found the flightless morph to have higher fecundity but less longevity than the flying morph. He also showed that various environmental factors effecting the larvae induced the adult wing length and that over several generations selection favored flightless morphs that had higher fecundity, earlier and shorter development time. Higher fecundity in brachypterous morphs has been shown in various insect groups (Jackson, 1928; see also Dybas, 1978).

Vespäläinen (1978) gives examples of species in which the flightless morph is found in stable isolated habitats. He reasons that in an unstable or temporary habitat there is a higher energy budget needed to produce the fully winged morph which migrates and, thus, delays reproduction until after colonization. Also the cost of producing flight muscles causes a decrease in ovary size and egg production. Therefore, in a stable isolated habitat, migration is selected against because there is a greater risk involved and the conservative short winged morph prevails.

Southwood (1962), reviewing insect migration in relation to habitat, shows that the level of migratory movement is positively correlated with the degree of impermanence of the habitat, and that the prime evolutionary value of migration is in the colonization of changing or temporary habitats. Southwood's data on wing polymorphism in Hemiptera and Coleoptera indicate that the flightless morphs are associated with permanent habitats and the flying morphs with temporary, environmentally changing or unstable (in physical and/or biotic factors) habitats.

Therefore, Vespäläinen (1978) and Southwood (1962) (see also Jackson, 1928 and Darlington, 1943) conclude that winglessness (wing reduction) is selected for in isolated stable habitats. This stability also involves factors of population density and resource availability in addition to acceptable environmental conditions.

Hamilton and May (1977), however, have a rather different outlook on dispersal from stable habitats. Their models show that adaptations for dispersal are important even in uniform and predictable (presumably stable and isolated) environments. They say that it is advantageous for more than one half of the offspring to migrate away from their mother population, even when mortality is very high, so as to avoid inbreeding which would be suboptimal for the population.

The best known situations for the predominance of flightlessness are the isolated and apparently rather stable systems of mountain tops and islands, where similar factors operate to cause this phenomenon. In a broad sense other specialized and isolated situations (ecological or geographical) that may also be stable could produce flightless morphs of a species. Darwin (1859) was impressed by Wollaston's discovery that more than one third of the beetles on Madeira Island were flightless. Darwin speculated that this phenomenon was caused by the flying morphs being blown into the sea or straggling off the island. Darlington (1943) says

that Darwin's explanation of beetle flightlessness on islands is too simple, although he does recognize a minor effect from exposure to wind and straggling as well as from the absence of flooding. He concludes that flightlessness is caused by several factors and one or more may operate in varying intensities, therefore, shifting the proportions of flying and flightless morphs. Carlquist (1966) offers several additional explanations for island flightlessness: entry into the ground feeding habitat and with absence of competitors or predators in that niche; loss of wings is economical because the energy from wing production can go towards other efforts, especially if there is no positive selective pressure for flight. Carlquist, unlike Darlington, considers the Darwin explanation as a prime factor and he offers experimental evidence (from normally flying groups) in support of the idea that flight is unfavorable when a significant proportion of the population can be blown away or straggle away.

It is evident that intra-specific wing length polymorphism is a widespread phenomenon caused by a variety of factors depending on the taxa involved. Its basis is obviously genetic although the final flightless morphs of some species may be produced by environmental pressures (physical and ecological) acting on the genotype. In other cases discontinuity in the gene pool is the sole cause of the production of flying and flightless morphs of a species. It has been shown that wing reduction is a genetically dominant trait probably involving very few alleles. In addition, the loss or reduction of wings and associated musculature permits an increase in fecundity. Therefore, in geographically isolated and ecologically stable situations there is a strong and relatively rapid selection for wing reduction in a population. A significant change in the environmental conditions, invasion from an external gene pool, or even possible mutations could produce flying morphs causing a reversal in the brachypterous tendency of a population. However, there is probably a significant selective advantage in maintaining some winged dispersal morphs in any population (even at a low level) for dispersal/migration and colonization of new habitats, both stable and unstable, and to provide for gene exchange with other populations.

The above general review is necessary for understanding the variety of factors involved in the wing polymorphism of each insect group studied. Certain basic principles of wing polymorphism are widely applicable including in the case of the chrysomelid genus *Longitarsus* considered here. In the literature there are reports of wing reduction and polymorphism in the family Chrysomelidae (Weise, 1882-1893 and Jolivet, 1957), including *Longitarsus*

(Champion, 1910; Kolbe, 1921; Gentner, 1928; Jolivet, 1957, 1967; Mani, 1962; Furth, 1976; and Hamilton, 1979). Champion (1910) reports some populations of *Longitarsus agilis* (Rye) in England have flying females and flightless males, but he says some uncertainty exists as to the sexual connection. Gentner (1928) describes the males of *waterhousei* (Kutschera) (= *ferrugineus* (Foudras)) in Michigan to be flightless and most of the females as fully winged for dispersal purposes. However, he apparently did not actually observe any significant flight by the females.

Kolbe (1921) makes the important observation that 23 Palearctic species of *Longitarsus* are known to have wing polymorphism. He emphasizes geographical and some morphological differences between the flying and flightless morphs of species. He reports that the two morphs usually occur in different populations but occasionally both are found together. He says that in some species the winged form (macropter) is more common, for others the brachypter is most commonly known, whereas many are known from only one morph or the other. Jolivet (1957) treats many aspects of chrysomelid wings and flight including wing polymorphism, especially in *Chrysolina*, with a brief discussion of *Longitarsus*. Jolivet (1967) lists 47 species from Morocco and 14 of these have flying and flightless morphs there. Mani (1962) studied high altitude insects in the Himalayan Mountains and revealed two "apterous" *Longitarsus*, one of which has a winged morph at lower elevations. Hamilton (1979; pers. comm.) observed *rubiginosus* (Foudras) in England with both morphs existing in a single population and with a lesser number of females as flightless morphs. Other records of wing polymorphic *Longitarsus* are scattered throughout the literature, and it is apparent that this polymorphism is relatively more widespread in *Longitarsus* than in other chrysomelid genera.

A potential problem that may effect the accuracy of reports of polymorphic species is sibling species pairs or complexes. In this case a gross morphological examination may indicate that one taxa has different wing morphs but, in fact, two or more species may be involved differing in finer morphological structures (e.g. genitalia) or in biology (biological sibling species) as well as in wing length. Thus, one needs to be very familiar with the taxonomy of the species involved in order not to make erroneous reports of wing length polymorphic species. On the other hand, as Kolbe (1921) points out, there are some minor morphological differences between the fully winged and the reduced winged morphs of a species. The most evident of these is a reduction of prominence of the humeral calli (shoulders) of the

elytra; therefore, macroptera have strongly angled, protruding humeri and brachypters (*sensu lato*) have weaker, rounded or smooth humeri. This trait is very useful for superficial examination of specimens in order to determine their general wing length condition. Kolbe (1921) also mentions differences in sculpturing and coloring of elytra associates with wing length, but I have not observed such differences. Some of these elytral differences associated with wing polymorphism in *Longitarsus* have caused confusion in determination keys when authors separate species based on the winged or "wingless" condition. For example, Blatchley (1921) divided North American *Longitarsus* into two groups (subgenera), those with and without wings. Even some otherwise good modern keys still make the mistake of using presence or absence of wing development for separating *Longitarsus* species (e.g. Mohr, 1966).

In the literature authors have often referred to the wingless or apterous condition of a species. However, as several authors have correctly pointed out (Jolivet, 1957; Leonardi, 1971), besides the fully winged (macropterous) flying morph there are several stages of flightless (wing reduced) morphs. It is difficult to quantify these stages of wing reduction, but I recognize four stages: macropterous = fully winged; brachypterous = wings reduced (at least one half the length of the abdomen) such that flight is not possible; micropterous = rudimentary wing pads or only slightly developed wings (less than one half the abdominal length); and apterous = no vestiges of wings remaining (quite rare).

In my preliminary analysis of Israeli *Longitarsus* (Furth, 1976) I reported 15 of 33 species were known to have wing polymorphism with 8 of these having both flying and flightless morphs within Israel. Since this preliminary treatment, I have had two more years of field work to study this phenomenon more carefully. This additional data has enabled me to make a more comprehensive analysis. Part of Table 1 shows the array of wing polymorphism now known for Israeli populations of *Longitarsus* species as well as those Israeli species known from the literature to be polymorphic outside of Israel. Of the 42 Israeli species 33% (14) of the species are macropterous (flying) and 36% (15) are flightless (brachypterous, micropterous, or apterous). There are 48% (20 species) that have known wing length polymorphism and 29% (12 species) have both flying and flightless morphs within Israel. In almost all of these polymorphic species one morph is more common than the other in the country. Contrary to my previous treatment (1976), this more in-depth analysis has revealed that some populations do contain both flying and flightless morphs (7 species);

however, one morph usually dominates these polymorphic populations. I have found no correlation with sex in these polymorphic populations. Therefore, the idea that all or most winged individuals are female, i.e. for more effective dispersal and new colonization is not the case here, as was indicated by Champion (1910), Gentner (1928) and Hamilton (1979).

To my knowledge there has been no experimental or genetic study of *Longitarsus* wing polymorphism. Therefore, using the known factors in other cases of insect wing polymorphism, the known *Longitarsus* cases, and my own observations and data, I will offer some possible explanations of the mechanism of this phenomenon in *Longitarsus*. It should be noted at the outset that unlike most wing polymorphic insects, flea beetles have an effective jumping habit. Thus, flight in many situations is even less important, especially in stable isolated habitats. Also, as stated elsewhere (Furth, 1976, 1979b), dispersal by wind may play a significant part in the movement of some flea beetle species in certain geographical situations. In this case the flying morphs would be more likely to be transported large distances by the wind, but even flightless morphs may be passively dispersed by strong winds. Rainey (1976) records large numbers of a *Longitarsus* species along with other insects at up to 950 m above in the African Rift Convergence Zone (a region over the East African Rift Valley of wind convergence where westerlies meet easterlies from across North Africa and from the Indian Ocean, respectively). It is evidently unknown whether this *Longitarsus* population that Rainey found was a flying and/or flightless morph. In such a situation the prevailing winds may carry the insects in either direction for great distances and may greatly effect their population ecology.

There have been indications that within a polymorphic species the flying morph prefers host plants of different but related genera than the flightless morph (Peyerimhoff, 1911 and Furth, 1976, 1979b). However, with more thorough field work and closer examination it is apparent that both morphs can often be found on different host genera but one morph may be in very low percentage. Peyerimhoff (1911) reported consistently finding flightless morphs of *candidulus* (Foudras) in France and North Africa on *Daphne* (Thymelaceae) and in North Africa a flying morph only on *Thymelaea*. However, Normand (1937) disagreed reporting both morphs on both plant genera, but one usually in very low percentage. Heikertinger (1926) records the wingless morph of *lateripunctatus* on *Symphytum* and *Pulmonaria* and the winged morph on *Borago*; however, this case must now be studied in more detail. Probably the more mobile flying morph can colonize hosts of related genera (or species) that are widely dispersed having a

different population ecology. All initial colonizers will be flyers, but after several generations flightless individuals may appear. If there is a somewhat stable stand of this more dispersed plant, then a relatively large proportion of flightless individuals may develop. On the contrary, those hosts that tend to grow in large concentrated stands and that exist in a seasonally stable and isolated situation will tend to produce flightless morphs.

Thus, this herbivore/host plant situation with environmentally isolated and stable conditions favors the genetic dominance of wing reduction, enabling higher fecundity and more rapid reproduction. However, in some cases fully winged individuals will be maintained, even if only at a very low percentage, in order to disperse and colonize other stands of the same or related host plants as well as to interbreed with other populations. Very stable, possibly old, populations may be entirely without flying morphs, and thus inbred.

In the case of Israeli populations of *Longitarsus* species there is no evidence that intra-specific wing length polymorphism is caused by changes in environmental conditions, especially because the various combinations of this polymorphism occur in all parts of this environmentally diverse country. There is no tendency in Israeli *Longitarsus* for more flightless species or morphs of a species to be found on mountain tops or isolated island-like situations; although geographical and ecological (especially host plant) isolation are certainly important factors in this polymorphism. In conclusion, all evidence indicates that intra-specific wing length polymorphism in *Longitarsus* is genetically controlled.

HOST PLANT ECOLOGY

Phenology

Few species of *Longitarsus* are agricultural pests and this in addition to their tiny size and root feeding larval habits (therefore difficult to rear) have created a void of information regarding their bio-ecology and life cycle. The following are general comments from extensive field work on Israeli *Longitarsus*. Adults pass the harsh season (usually the summer in Israel) in the soil or debris probably not very far from the previous year's host plant populations and emerge apparently with a combination of environmental cues (temperature, humidity, and photoperiodism)

TABLE 1: Wing Polymorphism and Host Plant Relationships of Israeli *Longitarsus*

Boraginaceae	Labiatae	Compositae	Plantaginaceae	Scrophulariaceae	Convolvulaceae	Linaceae
<i>aeneus</i> -(b&m) / "±" K	<i>alfierii</i> Q ±	<i>albus</i> +	<i>bytinskii</i> - (b)	<i>hermonensis</i> -	<i>pellucidus</i> Q + / "±" J	<i>parvulus</i> ? (M) Q ± (b) *
<i>albineus</i> +	<i>allotrophus</i> ² Q -	<i>gracilis</i> ? (M) Q +	<i>luridus</i> ⁵ ? (M&H) Q ± *	<i>nigrofasciatus</i> Q ±		
<i>anchusae</i> - / "±" K	<i>ballotae</i> ± *	<i>stragulatus</i> ? (J) + / "±" J	<i>melanocephalus</i> +	<i>tabidus</i> + / "±" K		
<i>dimidiatus</i> ± *	<i>bertii</i> ± (m&b)	<i>succineus</i> ⁴ ? (M) - / "±" K	<i>pratensis</i> +			
<i>emarginatus</i> ¹ - (a)	<i>eminatus</i> Q -					
<i>fuscoaeneus</i> ± (b&m) *	<i>eminus</i> -					
<i>lateripunctatus</i> Q ± *	<i>karlheinzii</i> -					
<i>linnaei</i> +	<i>lycopi</i> + / "±" K					
<i>mirei</i> -	<i>membranaceus</i> +					
<i>nigrilividus</i> ± (b)	<i>nanus</i> Q ± *					
<i>nimrodi</i> -	<i>obliteratus</i> Q ± (b)					
<i>punctiger</i> -	<i>rectilineatus</i> Q +					
<i>suturalis</i> ? (M) Q + / "±" J	<i>tunetanus</i> ? (P) -					
<i>truncatellus</i> -	undescribed A ³ +					
	undescribed B Q +					

EXPLANATION OF TABLE 1:

- ? = host family unknown in Israel; from literature as follows (in parenthesis after species name): M = Mohr, 1966; P = Peyerimhoff, 1925; J = Jolivet, 1967; H = Heikertinger, 1926.
- 1-5 = allotrophy with secondary host of: 1 - Geraniaceae; 2 - Dipsacaceae; 3 - Plantaginaceae; 4 - Boraginaceae, Labiatae, Plantaginaceae, and Convolvulaceae (Heikertinger, 1926); 5 - Boraginaceae, Compositae, and Dipsacaceae (Peyerimhoff, 1919; Furth, 1980), and Ranunculaceae (Heikertinger, 1926).
- Q = post-season resting on *Quercus*.
- + = macropterous (flying morph).
- = micropterous (flightless morph).
- (b) = brachypterous (flightless morph).
- (a) = apterous (flightless morph).
- (b&m) = both brachypterous and micropterous forms found in Israel.
- ± = polymorphic species within Israel.
- ±* = polymorphic species within Israel, at least some populations containing both morphs.
- "±" K = recorded in literature as polymorphic (K = Kolbe, 1921; J = Jolivet, 1967).

and chemical cues from very young host plants; at least chemical cues probably enable host plant finding. They begin feeding on the very young rosettes (annuals) or first small leaves (perennials) on either leaf surface, but many species seem to prefer the underside of the leaf. This may be due to the physical nature of the leaves, for protection, or just inter-specific feeding patterns; it does make collecting them quite difficult. After some period of feeding (probably 1-2 weeks), they begin to mate and lay single or clumps of small elongate, yellow or orange eggs on or in the soil near the base of the plant. Presumably the larvae hatch and burrow into the roots where they may cause considerable damage. I have not yet been successful at rearing the larvae under lab conditions. Pupation evidently takes place in dirt cells beneath the surface. The generation time and number of generations are unknown for Israeli *Longitarsus*; however, it seems apparent that most species have only one generation per year. It may be possible that a few species manage to complete a second generation, but this is only speculative at present.

In many Israeli species, especially the Boraginaceae feeders, the adults emerge, feed, copulate and lay eggs in the winter months (November till February); after which they probably randomly disperse and/or die, while the larvae are feeding underground on the roots. Other species emerge and begin reproduction later in the spring (March-April). The emergence and reproductive season is evidently correlated with the host plant ecology (see the range of collection dates for the seasonality of various species of Israeli *Longitarsus*, Furth, 1980). It is interesting to note, especially from a species competition standpoint, that in most species groups on a host family (see Table 1) I have observed two or more species feeding simultaneously on a single host plant. This is especially prominent among the winter borage-rosette feeding species in which I have collected up to seven different species on one or two adjacent members of a host plant species.

A rather unusual phenomenon in several alticine genera is the post-season resting and/or limited feeding on oaks (*Quercus*); typified by *Longitarsus*. At least 14 species of *Longitarsus* (Table 1) have been taken repeatedly (along with other alticines) and usually in significant series on a few species of *Quercus*, after their normally preferred hosts have dried out. This was observed in the summer and fall months (July-October) and especially in mountain oak forests, e.g. Mt. Meron and Mt. Hermon. It appears that at least some species are doing a limited amount of feeding on the oak leaves (personal data). The reason for this is

not yet apparent, however, it is possible that they are simply seeking shaded areas and feeding to maintain a minimum water balance during the xeric climatic conditions at those seasons; rather than adopting a true summer diapause in the soil or debris, where they probably eventually do spend some time. Feeding on *Quercus* leaves at this season seems quite unusual because of the established unpalatability to most herbivores of their leaves late in the season due to accumulation of tannins (Feeny, 1970). There are indications of this phenomenon in past host records in Europe (Heikertinger, 1925, 1926), on various deciduous trees including oaks, and even on *Cedrus* in Cyprus (personal data); however, in Israel only on oaks. This phenomenon needs further investigation to discover the role of this post-season host refugium.

Coevolution

Similar to the widespread distribution and species diversity of *Longitarsus*, there is a wider range of host plant families than for most alticine genera. Table 1 shows the range of Israeli *Longitarsus* host plant families taken from field data. In the few cases where Israeli hosts are unknown, the recorded host family (with reference) is given. This array of host families in Israel is representative of the known *Longitarsus* hosts from Europe. Mohr (1966) lists over 60 species of *Longitarsus* from Middle Europe with known hosts in the same families (with the addition of Ranunculaceae) and in a similar proportion. In most cases the beetle species in these host plant feeding groups are restricted to hosts in that family. These beetle species groups are often morphologically related to varying degrees indicating (along with their ecological similarity) a similar phylogeny or at least coevolutionary lineage. Table 1 shows the seven *Longitarsus* species groups present in Israel according to their host plants.

There is no obvious phytochemical relationship known among all of the seven host plant families of *Longitarsus* as is evident for the three mustard oil (thioglucoside = secondary defensive chemical) containing families that serve as the only hosts for *Phyllotreta* (Furth, 1979). Five of the seven host families in Table 1 (excepting Compositae, Linaceae) belong to the order Tubiflorae (Gibbs, 1974). *Longitarsus* evidently consists of species groups that have evolved with the secondary plant chemistry of particular host families. It is possible that phytochemical similarities exist among some *Longitarsus* host families especially with the secondary defensive chemicals presumably used by the beetles to find their hosts; however, only limited phytochemical

information of this kind exists. Certain kinds of alkaloids and essential oils (fragrance in the Labiatae), and caffeic acid derivatives exist in several of these host families (Hegnauer, 1964, 1966; Gibbs, 1974). Hegnauer (1964) suggests many phytochemical relationships between Boraginaceae and Labiatae; he recommends further investigation of these. Hegnauer (1966) also notes chemical similarities between Boraginaceae and Compositae: the toxic pyrolizidine alkaloids common in *Senecio*; inulin (also in *Cephalaria*, Dipsacaceae - see Table 1); and caffeic acid derivatives. Although these phytochemical features of *Longitarsus* host families are somewhat confusing, there are some indications of relationships between and among some families. It is possible that some essential oils (also found in Geraniaceae, *Erodium* (Gibbs, 1974); see Table 1) are responsible for host selection in *Longitarsus*; however, further phytochemical/biochemical investigations are necessary to establish this.

Jolivet (1953, 1967, and in litt., 1976) has used the term allotrophy for the cases where a beetle is found to feed on a completely unrelated host from its normally preferred (primary) host plant. There are several apparent cases of allotrophy in Israeli *Longitarsus* (Table 1). However, the populations are often not geographically separated from those on the preferred hosts. For example, the truly apterous *emarginatus* normally prefers Boraginaceae but I have found it early in the season in several localities on several species of *Erodium* (Geraniaceae). The undescribed species near *minusculus* normally feeds on Labiatae (*Molucella*) but has been found early in the season on *Plantago* (Plantaginaceae). The new species *allotrophus* normally prefers Labiatae (*Prasium* and *Stachys*) but has been taken in series at several locations on *Cephalaria* (Dipsacaceae). This phenomenon of allotrophy seems rather unusual for the normal alticine feeding pattern. It is possible that at a young age these secondary host plants (allotrophs) have a similar chemistry to that of the primary hosts that is also attractant and palatable for the beetles. It is also possible that the allotrophs are actually phytochemically related to the preferred hosts. However, allotrophy may indicate a trend towards host plant switching which is certainly an important aspect of herbivore/host plant relationships and one of the alternatives in their coevolutionary struggle. Allotrophy is probably more common than previously thought. *Longitarsus luridus* and *succineus* provide still other examples of species with a host plant spectrum broader than most *Longitarsus* (Table 1). Instead of the possibility of host switching,

these two widespread species may have achieved their ubiquity through their biochemical flexibility to feed on a variety of host families. Their host plants, however, are mainly in the same families used by other species groups of *Longitarsus*. This fact too may indicate a relationship in the secondary phytochemistry of these primary *Longitarsus* host plant families. Such phenomena as allotrophy and host plant switching offer "food for thought" in flea beetle/host plant coevolution; they need to be investigated further in the field and in the laboratory.

BIOGEOGRAPHY

Despite the relatively low species diversity in the vast desert regions of southern Israel and the Sinai Peninsula the overall diversity in the Middle East, especially Israel, is high compared to similar sized regions. This is because Israel is situated at a biogeographical crossroads or transitional zone of the tropical Ethiopian (Sudanian) Region and three or four major subregions (subtropical and temperate) of the Palearctic Region. The Palearctic subregions used here are as follows: Mediterranean (Méd.) subregion predominates in areas adjacent to the Mediterranean Sea and associated with its climate and ecology. In this subregion it is practical to refer to Circum-Mediterranean (Circ-Med.) for species distributed around most of the Mediterranean area. Also, because there are significant differences in species distribution patterns between the east and west sections of the Med., it is appropriate to differentiate between them (E. Med. and W. Med.). These differences within the Med. subregion are probably due to Pleistocene sea level fluctuations that created barriers and isolated some species. The Med. elements are the dominant zoogeographic affinity in Israel especially in the north and central parts of the country. The Eremian (Er.) subregion has been referred to in the past as Saharo-Sindian or more accurately Saharo-Arabian. It comprises the desert elements in the area extending from NW Africa across the Sahara to the Arabian Peninsula and Israel. This xeric subtropical element is prevalent in the Dead Sea, Negev and Judean Deserts of southern Israel and in the Sinai Peninsula. The Irano-Turanian (IT) subregion exists primarily in high plateau and steppe areas from central Asia to Iran, Turkey, Syria, and Jordan. This is a major element in northern Israel, especially on Mt. Hermon and the Golan Heights. The Euro-Siberian (ES) subregion includes much of middle and northern Europe and USSR (especially Siberia), southeast to northern Iran and Turkey, east to Japan. In Israel this element is apparently

an extension from its defined region, possibly along mountain chains or possibly a relictual disjunction from glacial times. In Israel it exists in the north, i.e. Upper Galilee, Mt. Hermon, and Golan Heights. In the case of species known from these Israeli provinces it may be difficult to distinguish between ES and IT affinity. The Ethiopian Region is not represented by any Israeli *Longitarsus*. Evidently the arid southern and western deserts are effective barriers to tropical and subtropical elements of *Longitarsus* because also the Eremian affinity is relatively low (Table 2). The boundaries of the Palearctic subregions are primarily based on Zohary (1966) and other details of these subregions relative to Israeli Alticinae have previously been discussed (Furth, 1979). The following information and analysis of Israeli *Longitarsus* zoogeographical affinities will contribute to a more general understanding of the historical biogeography of the Middle East as well as to *Longitarsus* phylogeny.

Since the preliminary analysis of this genus (Furth, 1976, 1979) considerably more field data has enabled a more lucid analysis of Israeli *Longitarsus* biogeographical affinities and trends. However, as in the preliminary analysis there is a distinct difference in the biogeographical affinities of *Phyllotreta* and *Longitarsus*. *Phyllotreta* shows a distinct affinity towards the Eremian subregion (30% in the most restricted sense) and significantly less affinity with each of the three Med. elements (Circ-Med.=5%; E. Med. = 15%; W. Med. = 5%), although totally they are only slightly less important. The ES and IT (5% each) play relatively minor roles in zoogeographical affinity of *Phyllotreta* (Furth, 1979). However, in general for Israeli *Longitarsus* the Er. affinities (5.95%) are the least important of all Palearctic subregions, although the Med. elements totally (especially Circ-Med and E. Med.) are primary. The ES and to a lesser degree, the IT affinities are relatively more significant than for *Phyllotreta* (Table 2, line 5). Part of the change in the analysis from the preliminary study (Furth, 1976, 1979) is due to the fact that a few species that were previously considered as known species, with known affinities, were subsequently discovered to be new to science and hence with very restricted known distributions. In such cases, because of the paucity of data from surrounding regions, they are considered to be of uni-regional biogeographic affinity or even endemic when actually they may be more widespread. Such pseudo-endemics (Furth, 1979) must not be emphasized too heavily because future collecting will reveal their true affinity. However, with good ecological data concerning even these locally known populations (e.g. new species), some reliable predictions can be made as to their primary

affinity, even though they may not be a truly restricted endemic. Of course, part of the reason for the changes in the present analysis is because of considerably more ecological and geographical data that has been collected since the preliminary research. For some of the above reasons I have seen fit in Table 2 to analyze the zoogeographic affinities separately including and excluding the 8 new species. The multi-regional (Palearctic or Holarctic) species are much less valuable in this type of biogeographical analysis than those with restricted distribution; thus, it is also useful to analyze the affinities eliminating such widespread species. Consequently, the method used in Table 2 allows the reader to see various aspects of the analysis combined. This table shows each biogeographic component as a part of the whole Israeli *Longitarsus* fauna as well as the various significant levels of combination, including exclusion of the widespread species.

Because I know of no truly objective method for analysis of biogeographic affinity when bi- or multi-regional species are involved, there is an element of subjectivity. The percentages given in Table 2 are based on recorded distribution and on my own field data with special emphasis on the ecological as well as geographical parameters of each species distribution. Therefore, each species receives a value of 1.0; i.e. *aeneus* = Circ-Med. = 1.0, *anchusae* = Circ-Med./ES = 0.6/0.4, *luridus* = ES/Circ-Med./IT = 0.4/0.3/0.3 (=Palearctic and widespread), etc. This detailed percentage analysis gets rather complicated; however, careful examination of the various combinations in Table 2 reveals the zoogeographical affinities of Israeli *Longitarsus*. In Table 2, lines 1-4 show the separate affinities of each component: uni-regionals (U); new species (N); bi-regionals (B); and widespread (W) species, respectively. A review of the totals (line 5) reveals that, as might be expected, the combined Med. elements (52%) are dominant; strongest being Circ-Med. and E.-Med., with little affinity to W. Med. However, unlike *Phyllostreta*, there is a strong affinity towards the ES subregion (26%), a significant connection to IT subregion (16%); but quite weak influence from the Er. subregion (6%). Because the new species distributions are probably not yet fully known, it may be first useful to examine the affinities excluding new species (line 6). This level of analysis again shows that the combined Med. elements are dominant, especially Circ-Med. with 29%, as is affinity to ES (27%); but significantly less E. Med. (14%) influence. A more general overview, by adding the widespread species (line 7), does not reflect any significant changes in this pattern. However, because 6 of 8 new species are assumed

TABLE 2. Percentage of Biogeographical Affinity for Israeli *Longitarsus*

Distribution*	Circ-Med.	E.Med.	W.Med.	ES	IT	Er.	Total
1. Uni-regional (13)	4.76	7.14	4.76	4.76	4.76	4.76	30.94
2. New Species (8)	0.0	14.29	0.0	2.38	2.38	0.0	19.05
3. Bi-regional (12)	12.38	1.43	0.0	11.19	2.86	0.72	28.58
4. Widespread (9)	7.62	0.0	0.0	7.62	5.71	0.48	21.43
5. U+N+B+W (42)	24.76	22.86	4.76	25.95	15.71	5.95	100.00
6. U+B/U+B (25)	28.80	14.40	8.00	26.80	12.80	9.20	100.00
7. U+B+W/U+B+W (34)	30.59	10.59	5.88	29.12	16.47	7.35	100.00
8. U+B+N/U+B+N (33)	21.81	29.09	6.06	23.33	12.73	6.98	100.00
9. U/U+B	8.00	12.00	8.00	8.00	8.00	8.00	52.00
10. U/U+B+W	5.88	8.82	5.88	5.88	5.88	5.88	38.22
11. U+N/U+N+B	6.06	27.27	6.06	9.09	9.09	6.06	63.63
12. U+N/U+N+B+W	4.76	21.43	4.76	7.14	7.14	4.76	49.71

*Lines 1-4 are percentages of the total number of species (42); their sum total is line 5.

Lines 6-12: the distributional elements on the right of the slash mark are the divisors.

U = Uni-regional species; B = Bi-regional (or Tri-) species;

N = New species; W = Widespread species.

to be of E. Med. affinity with one each from ES and IT, their addition (line 8) changes the pattern completely by elevating the E. Med. affinity (29%). Before considering the full effect of the new species, it is useful to examine the other restricted components, i.e. the uni-regionals and endemics (lines 9 and 10). These are presumably better known distributionally than the new species, interestingly they have an almost equal affinity to all biogeographical elements E. Med. with one more than the others (the two endemic species are both E. Med. affinity); ca. 8-12%, 6-9%, and 5-7% in decreasing order of restricted analysis (= lines 9, 10, and 1, respectively). Notwithstanding the probable lack of distributional knowledge for the 8 new species, they are still validly considered as uni-regional and, therefore, quite useful in a restricted analysis (lines 11 and 12). At the most restrictive level of analysis (line 11), as indicated in line 8, the addition of the new species has greatly increased the affinity to E. Med. (27%) as well as ES and IT (9% each) relative to the Circ-Med. affinity (6%).

All considered the total of the individual components (Table 2, line 5) seems to be representative as to the zoogeographical trend of Israeli *Longitarsus*. It shows less affinity for the southern arid Eremian habitats and more towards the northern ES and IT than does *Phyllotreta*. In the strictest sense of biogeography (combined herbivore and host plant distributions), there is no apparent explanation for this difference because the crucifer-related host families of *Phyllotreta* are not necessarily bound to arid climates nor are the major host families of *Longitarsus* (Boraginaceae, Labiatae, Compositae, Scrophulariaceae) especially linked to northern habitats (Good, 1974). However, this seems to indicate that the truly xeric environments of the Eremian subregion act to some degree as an effective barrier to *Longitarsus* species and/or their host plants. *Longitarsus* also differs by having a large number (9) of widespread species (Table 2, line 4) as compared to *Phyllotreta* (3). This may indicate the much broader general distribution of *Longitarsus* species. In Israel both of these largest alticine genera show strongest affinity to the Mediterranean subregion of the Palearctic, especially the E. Med. element.

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REFERENCES

- Blatchley, W.S. 1921. Notes on Indiana Halticini with characterization of a new genus and descriptions of new species. *Journal of the New York Entomological Society*, 39(1): 16-21.
- Carlquist, S. 1966. The biota of long distance dispersal. *The Quarterly Review of Biology*, 41: 247-270.
- Champion, G. 1910. Note on the sexual characters of *Longitarsus agilis* Rye. *Entomologist's Monthly Magazine*, 46: 261.
- Clark, W. 1976. The environment and the genotype in polymorphism. *Zoological Journal of the Linnean Society*, 58: 255-262.
- Darlington, P. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs*, 13: 37-61.
- Darwin, C. 1859. On the origin of species by means of natural selection... John Murray, London.
- Dybas, H. 1978. Polymorphism in Featherwing Beetles, with a revision of the genus *Ptinellodes* (Coleoptera: Ptiliidae). *Annals of the Entomological Society of America*, 71(5): 695-714.
- Feeny, P. 1970. Seasonal changes in oak leaf tanins and nutrients as a case of spring feeding by winter moth caterpillars. *Ecology*, 51: 565-581.

- Furth, D.G. 1975. Israel, a great biogeographic crossroads. *Discovery*, 11(1): 2-13.
- Furth, D.G. 1976. Alticinae of Israel, with special reference to the systematic, zoogeographic, and host plant relationships of *Phyllotreta* and *Longitarsus* (Coleoptera: Chrysomelidae). Copyrighted, unpublished Ph.D. dissertation from Cornell University.
- Furth, D.G. 1979. Zoogeography and host plant ecology of the Alticinae of Israel, especially *Phyllotreta*; with descriptions of three new species (Coleoptera: Chrysomelidae). *Israel Journal of Zoology*, 28(1): 1-37.
- Furth, D.G. 1980. Zoogeography and host plants of *Longitarsus* in Israel, with descriptions of six new species (Coleoptera: Chrysomelidae). *Israel Journal of Entomology*, 13(1979): 79-124.
- Furth, D.G. 1980. Inter-generic differences in the metafemoral apodeme of flea beetles (Coleoptera: Chrysomelidae). *Systematic Entomology*, 5 (in press).
- Gentner, L.G. 1928. The Mint Flea Beetle (*Longitarsus waterhousei* Kutsch.). *Canadian Entomologist*, 60: 264-266.
- Gibbs, R.D. 1974. Chemotaxonomy of flowering plants. McGill-Queen's University Press, Montreal.
- Good, R. 1974. The geography of the flowering plants. Edition 4. Longman Group Ltd., London.
- Hamilton, W.D. 1978. Evolution and diversity under bark. In: Diversity of insect faunas. L.A. Mound and N. Waloff (eds.). *Symposia of the Royal Entomological Society of London*, 9: 154-175.
- Hamilton, W.D. 1979. Wingless and fighting males in fig wasps and other insects. In: Reproductive competition and selection in insects. M.S. Blum and N.A. Blum (Eds.). Academic Press, New York.
- Hamilton, W.D. and R.M. May. 1977. Dispersal in stable habitats. *Nature*, 269: 575-581.
- Hegnauer, R. 1964. Chemotaxonomie der Pflanzen. Birnhauser, Basel. Vol. 3: Dicotyledoneae Acanthaceae-Cyrillaceae.

- Hegnauer, R. 1966. Ibid. Vol. 4: Daphniphyllaceae-Lythraceae.
- Heikertinger, F. 1925. Resultate fünfzehnjähriger Untersuchungen über die Nahrungsflanzen einheimischen Halticinen. *Entomologische Blätter*, 21(4): 155-163.
- Heikertinger, F. 1926. Ibid, 22(1): 1-9.
- Jackson, D. 1928. The inheritance of long and short wings in the weevil *Sitona hispidula*, with a discussion of wing reduction among beetles. *Transactions of the Royal Entomological Society of Edinburgh*, 55: 665-735.
- Jolivet, P. 1953. Les Chrysomeloidea des Isles Baleares. *Memoires, Institut Royal des Sciences Naturelle de Belgique*, Ser. 2. 50: 1-88.
- Jolivet, P. 1959. Recherches sur l'aile des Chrysomeloidea (Coleoptera). *Memoires, Institut Royal des Sciences Naturelle de Belgique*, Ser. 2. 51: 1-180, 58:1-52.
- Jolivet, P. 1967. Notes systematiques et ecologiques sur les Chrysomelides Marocains (Coleoptera). *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc*, Trimestres 3/4(1966): 305-393.
- Kolbe, H. 1921. Über Mutationen und Aberrationen deutscher und auswärtiger Coleopteren und anderer Insekten. *Deutsche Entomologische Zeitschrift*, 3/4: 386-408.
- Leonardi, C. 1971. Considerazioni sulle *Psylliodes* del gruppo *napi* e descrizione di una nuova specie (Coleoptera, Chrysomelidae). *Atti della Societa Italiana per il Scienze Naturali del Museo Civico di Storia Naturale Milano*, 112(4): 485-533.
- Lindroth, C.H. 1946. Inheritance of wing dimorphism in *Pterostichus anthracinus* Ill. *Hereditas*, 32: 37-40.
- Lindroth, C.H. 1949. Die fennoskandischen Carabidae. III. *Goteborgs Vetenskapsoch Vitterhetssamhalles Handlingar* 6, foljd Ser. B. Vol. 4, pp. 911.
- Mani, M.S. 1962. Introduction to high altitude entomology. Methuen, London.

- Mayr, E. 1963. *Animal species and evolution*. Belknap Press, Harvard, Cambridge, Massachusetts.
- Mohr, K-H. 1966. Chrysomelidae. In: *Die Käfer Mitteleuropas*. H. Freude, K. Harde, und G. Lohse (Eds.). Boeckle and Evers, Krefeld. Vol. 9: 701-729.
- Normand, H. 1937. Contribution au Catalogue des Coléoptères de la Tunisie. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 28(2): 129-137.
- Peyerimhoff, P. 1911. Description et discussion de deux nouvelles races de *Thyamis* (Coleoptera, Chrysomelidae). *Bulletin de la Société Entomologique de France*, 80: 211-212.
- Peyerimhoff, P. 1925. Coleopteres du Nord-Africain. *Annales de la Société Entomologique de France*, 94: 15-17.
- Rainey, R.C. 1976. Flight behaviour and features of the atmospheric environment. In: *Insect flight*. R.C. Rainey (Ed.). Symposia of the *Royal Entomological Society of London*, Vol. 7: 75-101.
- Southwood, T.R.E. 1961. A hormonal theory of the mechanism of wing polymorphism in Heteroptera. *Proceedings of the Royal Entomological Society of London*, (A) 36 (4-6): 63-66.
- Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Review*, 37: 171-214.
- Stein, W. 1977. Die Beziehung zwischen Biotop-Alter und Auftreten der Kurzflügeligkeit bei Populationen dimorpher Russelkäfer-Arten (Coleoptera, Curculionidae). *Zeitschrift für Angewandte Entomologie*, 83: 37-39.
- Utida, S. 1972. Density dependent polymorphism in the adult of *Callosobruchus maculatus* (Coleoptera, Bruchidae). *Journal of Stored Product Research*, 8: 111-126.
- Vespäläinen, K. 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In: *Evolution of insect migration and diapause*. H. Dingle (Ed.). Springer-Verlag, New York.

Weise, J. 1882-1893. Naturgeschichte der Insecten Deutschlands.
W. Erichson (Ed.). Nicolaische, Berlin. Vol. 6.

Zohary, M. 1966. Flora Palaestina. Part 1. Equisetaceae to
Moringaceae. Israel Academy of Sciences and Humanities.
Goldberg Press, Jerusalem.