

On wing atrophy in carabid beetles (Coleoptera: Carabidae), with special reference to Nearctic *Nebria*

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Abstract. Contributions of Philip J. Darlington, Jr., to our understanding of hindwing atrophy in carabid beetles – including his descriptions of form and structure, analyses of brachyptery in relation to habitat and geographical distribution, discussions of evolutionary mechanisms and selective advantage of brachyptery, and his model for the evolution of montane faunas – are reviewed. Use of brachyptery, especially wing dimorphism, by C.H. Lindroth and others as a tool in biogeographic analysis is discussed. The incidence of brachyptery among Nearctic *Nebria* taxa is described in relation to habitat and geographical distributions and Darlington's views on faunal evolution.

Introduction

Atrophy of hindwings in beetles has long been a phenomenon of interest to coleopterists, biogeographers, and other students of evolution. Wollaston (1854) noted a high incidence of brachyptery (*i.e.* shortwingedness) among beetle species in the fauna of the Madeiran island group and attributed the highly restricted geographical distributions of many species to their limited powers of dispersal resulting from flightlessness. In his *Origin of Species*, Darwin (1859) cited Wollaston's findings in the section entitled 'Effects of Use and Disuse' (pp. 135–136); and wing atrophy *per se* was again addressed in his discussion of 'rudimentary organs' (p. 451). Darwin's classic explanation (known as 'Darwin's factor'; Darlington 1971:170) for hindwing atrophy (brachyptery) among beetles on islands was that it resulted from natural selection augmented by disuse.

'For during thousands of successive generations each individual beetle which flew least, either from its wings having been ever so little perfectly developed or from indolent habit, will have had the best chance of surviving from not being blown out to sea; and on the other hand, those beetles which most readily took to flight will oftenest have been blown to sea and thus have been destroyed' – Darwin (1859:136)

Darwin's interest in this topic stemmed from the need to explain such phenomena as rudimentary or atrophied organs as part of his general theory of evolution by natural selection. It was not intuitively clear why organisms whose ancestors

could fly – presumably a highly advantageous capability – evolved toward flightlessness, a less ‘perfected’ state, nor what mechanism(s) could account for such change. Generations of evolutionary biologists have succeeded Darwin in trying to answer this and related questions. But there are other reasons why hindwing atrophy has continued to receive so much attention.

If we assume, as seems appropriate based on our present knowledge of phylogenetic relationships among insects, that macroptery (*i.e.* presence of fully developed hindwings) represents the ancestral (plesiotypic) condition among beetles, then brachyptery (atrophied hindwings) has evolved independently many times among Coleoptera and other pterygote insects. Although no precise counts have been made of the number of different species worldwide which are known to have some or all members brachypterous, there are probably tens of thousands of such species representing many if not most families of beetles. Phylogenetic relationships are well understood for relatively few beetle species and more inclusive taxa; but it is certain that hindwing atrophy has evolved many thousands of times independently among Coleoptera. Any phenomenon so widespread and recurrent demands explanation, and explanation requires both interest and study.

Biogeographers have traditionally shown keen interest in brachyptery, chiefly because of its implications for the dispersal potential of organisms and the geographical distributions of their respective taxa. As noted briefly above, Wollaston (1854) cited brachyptery as a major factor contributing to restricted ranges of Madeiran beetle species; and appropriate attention has been given to the biogeographic significance of this phenomenon by students of distribution from that time up to and including the present.

Philip J. Darlington, Jr., to whose memory this volume and all included papers are dedicated, maintained an interest in hindwing atrophy among beetles, particularly Carabidae, throughout his professional career. In his taxonomic and faunal studies, he frequently encountered brachypterous carabids. As a taxonomist, he could have simply recorded the occurrence of this and other such features among the organisms he examined and gone on to his next project. But this was not Phil’s way. In each project, he sought to explore the underlying causes for patterns which he discovered, be they structural, distributional, or other evolutionary patterns. In this quest for more general understanding, he found inquiry into the topic of hindwing atrophy to be informative from taxonomic, evolutionary, and biogeographic perspectives. There were patterns he recognized, repeatedly, and could not ignore; and his scholarly contributions in this regard serve as the basis of our present understanding of this phenomenon in carabids.

My own interest in this topic stems from work with Nearctic species of the carabid genus *Nebria* Latreille during the past 15 years. Members of many *Nebria* species and subspecies have hindwings slightly or greatly reduced in size; and I have recognized patterns in the occurrence of this trait with respect to habitat distributions, geography, and phylogenetic relationship.

The aims of this paper are three. The first is to provide a review of Darlington's studies of wing atrophy in carabid beetles and discuss his findings and conclusions. The second is to briefly discuss some ways in which wing atrophy, and particularly dimorphism in wing development, among carabid beetles has been used as a tool in biogeographic studies. The third aim is to describe and analyze the occurrence of this phenomenon among Nearctic *Nebria* taxa in relation to Darlington's conclusions with respect to habitat distributions and geographical and phylogenetic relationships.

Darlington's studies of hindwing atrophy

Philip Darlington was first and foremost a systematic entomologist whose taxonomic interest focused on carabid beetles. Early in his career, he took advantage of opportunities to travel, first widely in North America and then in the West Indies, South America, and the South Pacific, including New Guinea and Australia; and each area provided him with new field experiences and carabid specimens upon which he based his subsequent studies. Through his examination of specimens collected in the mountains of the northwestern (Darlington 1930) and southeastern (Darlington 1931) United States and on West Indian islands (Darlington 1937, 1939, 1941, 1947, 1953a, 1953b), Phil found that many carabid species in such areas have some or all members brachypterous. His first major paper specifically on this topic (Darlington 1936) was based mainly on data from his faunal work in eastern North America, particularly in the Presidential Range, White Mountains, New Hampshire. This was followed by a second important contribution (Darlington 1943) which presented data based on his studies in other areas and clarified and/or extended ideas presented in the 1936 paper. Subsequent papers reported on his work with the faunas of Australia (Darlington 1956, 1961), New Guinea (1971), and tropical islands in general and the West Indies in particular (Darlington 1970). Each of these papers was both descriptive and analytical in nature; but rather than discussing the content of each individually, I will review Darlington's findings and conclusions in an integrated discussion organized by topic.

Form and structure

Among members of different species sampled, Darlington noted what appeared to be varied stages in the process of hindwing atrophy (Darlington 1936) – from slight to marked brachyptery; and even within single populations of some species, he found variation in size and shape of the hindwing rudiment. These observations suggested to him a particular morphological if not evolutionary sequence in progressive atrophy (Fig. 1a–1f). The first stage (Fig. 1b) involves reduction of the

wing apex, which results in a broad, truncate wing rudiment. The second stage (Fig. 1c) involves narrowing of the rudiment; and subsequent stages (Fig. 1d–f) involve progressive overall reduction in size, with the ultimate stage (not illustrated) represented by a minute scale-like vestige which is firmly attached to the metanotum basally. Reduction in venation pattern also occurs in this sequence, with veins near the base of the anterior wing margin apparently most persistent

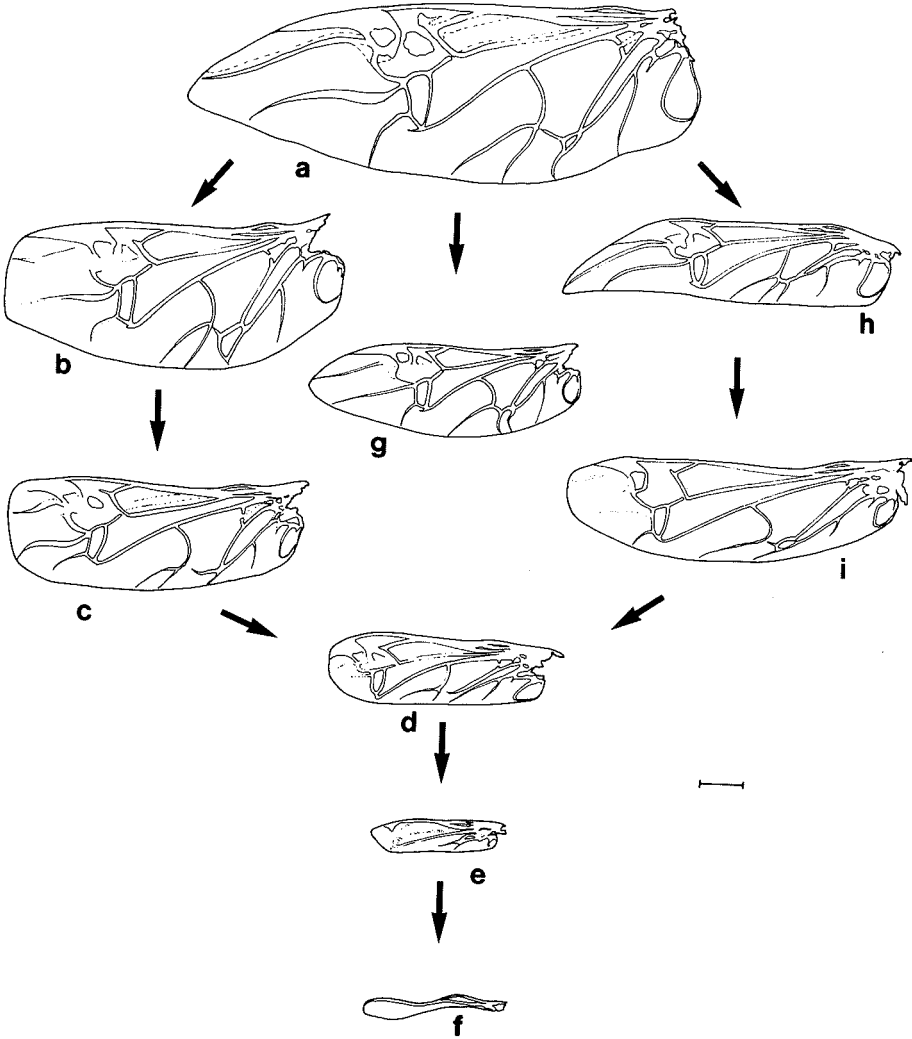


Figure 1. Left hindwing, dorsal aspect: (a) *Nebria meanyi giulianii* Kavanaugh (Milner Creek, California); (b) *N. arkansana arkansana* Casey (White River Mountains, Colorado); (c) *Nebria gregaria* Fischer (Dutch Harbor, Aleutian Islands, Alaska); (d) *Nebria piute utahensis* Kavanaugh (Henry Mountains, Utah); (e) *Nebria lyelli* Van Dyke (Mount Lyell, California); (f) *Nebria turmaduodecima* Kavanaugh (Upper Caribou Lake, California); (g) *Nebria appalachia* Darlington (Soco Gap, North Carolina); (h) *Nebria coloradensis* Van Dyke (Mexican Cut Lake, Colorado); (i) *Nebria purpurata* LeConte (Quandary Peak, Colorado). Arrows denote proposed directions and sequences of evolution of hindwing atrophy. Scale line = 1.0 mm.

(found even in highly atrophied forms; Fig. 1f). However, scale-like vestiges may be without definable veins.

Darlington (1936) suggested that dimorphism and polymorphism in hindwing development might also represent intermediate stages in evolution of a species from one with only macropterous to one with only brachypterous adults, but also that not all species necessarily pass through such a stage.

Another interesting observation, which Darlington (1936) confirmed by extensive dissection of brachypterous representatives of a broad range of carabid (including cicindeline) genera and tribes, was that the evolutionary process of wing atrophy among carabids had apparently never progressed to a point at which the wing rudiment is actually absent. In every instance in which absence of the wing rudiment had been proposed (such as in *Scaphinotus*, *Omus*, *Amblycheila*, and *Tricondyla* species) Darlington was able to find some vestige, however minute, present.

Often, but not always, associated with hindwing atrophy in carabid beetles are characteristic modifications in other structures. Darlington (1936) noted several of these. Elytral humeri tend to be narrowed, rounded, or obliterated in brachypterous forms; and enhancement of medial elytral interlocking mechanisms may also be observed. The metathorax is often shortened, particularly the metanotum, metepisternum, and elytra; and loss or reduction of compound eyes may also accompany wing atrophy. In some species which are dimorphic for wing size (*i.e.* include both macropterous and brachypterous adults), individuals which differ in wing form may also differ rather strikingly in these other traits.

Habitat and hindwing atrophy

It was clear to Darlington (1936, 1943, 1970, 1971) that the habitat distribution of brachypterous forms is not random, but rather that certain patterns are repeated throughout the world. Although a few exceptions are known (Darlington 1937), arboreal and obligate waterside (*i.e.* markedly hydrophilous) carabids are seldom brachypterous. It is among the ranks of geophiles (mesophiles and xerophiles) that a majority of brachypterous carabids are found. According to Darlington (1936, 1943), flight would appear to be highly advantageous in the vertically partitioned forest canopy habitat of most arboreal carabids (see also Erwin 1979); and beetles that occupy waterside habitats could make use of flight to (1) escape flooding; (2) move to other wet areas during dry periods; and (3) migrate seasonally to and from waterside areas. On the other hand, geophilous carabids appear to depend very little, if at all, on flight for survival.

According to Darlington (1936, 1943), a second evident pattern is an altitudinal one. In lowland areas in most parts of the world, even on islands (Darlington, 1947, 1953a), few carabids are brachypterous (Darlington 1936, 1941, 1953b, 1971). In contrast, brachypterous carabids often predominate in montane areas (Dar-

lington 1936, 1939, 1941, 1953b, 1971). Australia, where perhaps 45% of all carabid species have brachypterous members (Darlington 1956, 1961), is perhaps an exceptional area because many lowland forms are brachypterous; but the typical pattern is clearly recognizable in faunas of eastern North America, New Guinea, and the West Indies. In some areas, the relationship between altitude and hindwing form may be exceptionally dramatic. In the West Indies, for example, endemic brachypterous forms appear to have evolved *in situ* from macropterous lowland forms and now predominate at elevations above 5,000 feet (Darlington 1939, 1941) on islands with mountains of that height. On Puerto Rico, however, where the highest peaks are only about 4,000 feet above sea level, brachypterous forms are relatively few, and all apparently descendant from brachypterous ancestors that had evolved atrophied wings before immigrating to Puerto Rico.

Darlington's (1936, 1943, 1970, 1971) explanation for both of these patterns – in microhabitat and altitude – relates to habitat stability. Brachypterous carabids have relatively limited powers of dispersal, must live in a single or a series of adjacent habitats, and so can only survive in habitats which are relatively uniform and continuous in distribution and stable on a long-term basis – that is, where environmental catastrophies (Ghiselin 1974) and resulting extinctions of local populations (Van Valen 1971) are unlikely events. Conversely, macropterous carabids have greater dispersal potential and can, at least theoretically, occupy more varied, less stable, temporary habitats. Darlington (1943) used the term 'checkerboard distribution' to describe this kind of patchy distribution of habitat which favors the survival of macropterous forms. In such habitats, where the 'checkerboard' stays about the same size with the same number of 'squares', but the distribution of different kinds of squares keep changing, flight would appear to be of great selective advantage. Brandmayr *et al.* (1983) suggested that habitat stability was the main factor in development of brachypterous elements of the montane carabid fauna in the northern Adriatic region; and Erwin (1979) has discussed the effect of patchy habitat distribution on development of lowland carabid faunas.

What features of mountains contribute to the apparent long-term stability of their habitats? Darlington (1943, 1971) suggested several such features. (1) They provide a limited area of exceptionally uniform and consistent microclimate (*e.g.* cool temperatures and relatively dependable precipitation); (2) They are relatively free from flooding; (3) Certain habitats, including some of the least stable (*e.g.* shores of large, slowflowing streams), are few in montane areas. But perhaps most importantly; (4) they offer residents a built-in buffer against sudden and dramatic climatic change. If climate changes rapidly and dramatically, montane organisms may be able to simply move a short distance up or down in elevation in order to track their required microclimate, whereas organisms in lowlands might have to move hundreds or even thousands of miles north or south to do so. Under such conditions of change, brachypterous organisms might not be able to shift their range horizontally fast enough to keep pace with the shift in

climate, whereas they might be able to do so vertically if they lived in mountains.

It has long been known that brachypterous beetles are frequently encountered on islands (Darlington 1936, 1943; Darwin 1859; Wollaston 1854). Darlington (1943) examined this relationship in detail, using data from his own field work and that of others, and found that mountainous islands do indeed harbor many brachypterous forms, but low, flat islands do not (Darlington 1947, 1953a). Apparently mountains, whether on continents or islands, provide suitable conditions (*e.g.* habitats) for the evolution of brachyptery; but islands *per se* may not unless they are also mountainous.

Geography and hindwing atrophy

Darlington (1936, 1943) also explored the relationship between geography and brachyptery and again recognized some patterns. In general, continental faunas of temperate parts of the world have a higher percentage of species with brachypterous or hindwing dimorphic members than tropical areas. About 24% of the carabid species of the eastern North American fauna are wing dimorphic or include only brachypterous members (Darlington 1936). As noted above, this figure is 45% for the Australian fauna (Darlington 1961); but only 12 to 15% of the South American fauna is brachypterous or hindwing dimorphic. Darlington (1943) suggested that competition with ants in the American tropics may be a factor contributing to the relatively low numbers of geophilous carabids in that area as well as the low incidence of brachyptery.

A second of Darlington's generalizations stated that carabid taxa in which all members are brachypterous tend to occupy smaller geographical ranges (Darlington 1936) than taxa with macropterous members. This contention is supported by Wollaston's data from Madeira.

Why and how does hindwing atrophy evolve?

These of course, are the central questions concerning the phenomenon of wing atrophy. Darwin (1859) suggested that selection was *against* flight; that is, flying beetles are selected against in habitats where brachyptery occurs (see above, and Darlington 1971, for discussion of 'Darwin's factor'). But Darlington (1936, 1943, 1971) has shown that a majority of brachypterous carabids live in habitats on mountains and islands in which they are relatively unexposed to wind. In fact, he found that proportionately fewer montane and islandic carabids occupying exposed habitats are brachypterous than those in more protected habitats.

Darlington suggested (1936, 1943, 1971) that selection was not against flight but rather *in favor of flightlessness*. He cited a study by Jackson (1928) which indicated that brachypterous individuals of a wing dimorphic species of *Sitona* weevil

were more hardy than conspecific macropterous individuals: Darlington (1936) reasoned that brachypterous carabids might be inherently superior to macropterous individuals of the same species because energy normally required for development and maintenance of wings and flight muscles could be redirected to other functions in brachypterous forms. At least in stable habitats where flight is not advantageous, such brachypterous individuals might therefore be more efficiently organized physiologically and/or metabolically than their macropterous conspecifics. Macroptery would still be selected for in unstable, fluctuating habitats (Van Valen 1971); and long-term maintenance of di- or polymorphism in populations could indicate that selection favors flight in certain parts of a species' range and flightlessness in other parts of its range (Darlington 1936).

If selection favors flightlessness except where flight is clearly advantageous, then what is the source of variation upon which this selection can act? Darlington (1936, 1943) believed that mutation provides the initial alternative – flight versus flightlessness; and, subsequently, wing atrophy progresses (as in Fig. 1) through an accumulation of recurrent mutations. He recognized that the first step (*i.e.* the shift from flight to flightlessness) must have great selective significance whereas subsequent steps may not.

Jackson (1928) and Lindroth (1945) demonstrated that brachypterous and macropterous morphs may reflect, at least in *Sitona hispidula* Fabr. and *Pterostichus anthracinus* Ill., respectively, simple Mendelian inheritance, with brachyptery dominant and macroptery recessive. Lindroth's use of wing dimorphic carabid tax in biogeographic inference is discussed below. Whether more advanced stages of hindwing atrophy in carabids represent different alleles of the same gene locus or mutations at one or more other loci is presently unknown.

Darlington's model for the evolution of brachyptery in montane carabid faunas

As an appropriate summary of Darlington's work on hindwing atrophy in carabid beetles, I will briefly review the model which he developed to account for the evolution of brachyptery in such faunas, both on mountains and continental islands and on oceanic islands, which he introduced in his 1943 paper and developed more fully in subsequent papers (Darlington 1956, 1961, 1970).

In full form, his model includes four phases. In the first phase, which Darlington did not name but which I call *constriction*, faunal diversity is reduced or constricted somewhat indiscriminately in relation to the faunas of adjacent lowlands. Limited area is proposed as a major factor restricting this diversity. The second phase, which Darlington called *concentration*, involves further restriction of diversity, but now related to decreased habitat diversity. Habitats most severely limited or lost are those suitable for many hydrophilous and arboreal forms. The result is selection in favor of geophilous carabids, which then appear

to be concentrated in the developing fauna. To the extent that brachyptery is already established among these geophiles, this trait may also be 'concentrated' in this phase. In the third phase, which Darlington called *conversion*, brachyptery evolves *in situ* among taxa descendant from macropterous ancestors. Darlington (1943) suggested that the impetus for 'conversion' is that montane geophiles find flight useless, but not harmful, in small, stable, montane areas. Wing atrophy evolves by selection of brachypterous mutants on the basis of their inherent hardiness and/or physiological efficiency. The fourth and final phase, which I call *proliferation*, involves the geographical differentiation and/or radiation of brachypterous forms in isolated parts of the mountain system, with possible dispersal and subsequent range overlap resulting from climatic fluctuations which affect altitudinal zonation patterns and degree of isolation (Kavanaugh 1979). Readers familiar with Erwin's (1979) 'taxon pulse' model will note how easily these models can be adapted to one another.

In comparing carabid faunas of different areas with the model, Darlington (1943, 1956, 1961, 1970, 1971) made the following observations. (1) The fauna of Presidential Range, New Hampshire, evolved mainly through restriction and concentration, with no evidence of conversion or proliferation; (2) The montane faunas of at least the larger, more mountainous islands of the West Indies and of New Guinea evolved through all four phases; but because the faunas of respective adjacent lowlands are essentially devoid of brachypterous forms, conversion from macropterous ancestry and subsequent proliferation were extremely important phases in faunal development in each of these areas; (3) The montane faunas of Australia evolved mainly through restriction and concentration. Brachypterous montane forms represent descendants of brachypterous lowland forms rather than products of conversion. It will be interesting to make similar comparisons among montane faunas from other areas in the future using this model.

Use of hindwing atrophy as a tool in biogeographic studies

If the occurrence of brachypterous forms in particular habitats reflects long-term stability of such habitats, then might not the occurrence of such forms in particular geographical areas indicate regions of relatively long-term stability as well, especially if this pattern is repeated among several or many taxa? In fact, this generalization, which is founded chiefly on ecological evidence, has been widely applied in biogeography, but mainly as a tool for inference in reconstruction of Quaternary and post-glacial biotic distribution and history.

Carl H. Lindroth, renowned Swedish biogeographer, specialist in carabid systematics and ecology, and Darlington's long-time friend and colleague, was particularly successful in using the distributions of brachypterous forms to recognize areas of long-term occupation, such as glacial refugia (Lindroth 1979b), ancient routes of faunal dispersal (Lindroth 1963), and centers of primary intro-

duction (Lindroth 1957) of foreign species. I will briefly review some of Lindroth's findings using this tool.

As noted above, Lindroth (1945) conducted breeding experiments using adults of *Pterostichus anthracinus* Ill., a wing dimorphic northern European species, and was able to determine (1) that state of hindwing development is inherited in simple Mendelian fashion; (2) that the brachypterous form is dominant; and (3) that this dimorphism is asexual (*i.e.* proportions of brachypterous and macropterous individuals in each population are equal for both sexes) (Lindroth 1979b). Lindroth assumed that this represented a typical rather than aberrant mode of inheritance. Because macropterous individuals are homozygous for this trait, such individuals, and populations thereof, cannot give rise to brachypterous individuals, except by recurrent mutation (which Lindroth assumed occurs relatively infrequently). However, brachypterous individuals can produce macropterous offspring. It follows that, in general, populations with a preponderance of the brachypterous individuals represent older populations than those with only or a majority of macropterous individuals. Therefore, Lindroth often focused his attention on wing dimorphic species and carefully plotted the geographical distributions of the different morphs (Lindroth 1979b).

Using this technique, he was able to infer from a preponderance of brachypterous individuals in populations in northwestern Scandinavia that glacial refugia had existed in that area at least during the last major Pleistocene glaciation (Lindroth 1970) (although duration of occupation of this region has recently been questioned by some workers; see Coope 1979). He also proposed such a refugial area for coastal parts of the northeastern United States and southeastern Canada, based on similar evidence (Lindroth 1971). And, by plotting the distributions of different wing morphs among dimorphic European carabid species which had been inadvertently introduced into North America, he was able to propose sites of primary introduction, on both east and west coasts, based on the high incidence of brachyptery among populations of such species in these port areas (Lindroth 1957). More recently, however, Spence and Spence (*in press*) have shown that brachypterous individuals are capable of much more rapid spread from proposed centers of introduction than Lindroth appreciated. Such spread is no doubt assisted by human transport; and so Lindroth's conclusions may be appropriate only to the extent that intrinsic means of spread have been the dominant mode.

Dimorphic species are not the only ones he found useful. By reference to the high incidence of brachyptery found among carabids in Beringian Alaska as opposed to the Aleutian arc, Lindroth (1963 and 1979a) concluded that Beringia had served as an important glacial refugium and route for faunal exchange between eastern Asia and northwestern North America whereas the Aleutian/Commander Islands arc had not played such a role.

In his analysis of the extant carabid fauna of an area in southwestern Kodiak Island, which geologists concluded had remained at least partially icefree during the last glacial maximum, Lindroth (1969) again cited the high incidence of the

brachyptery (88%) in the high altitude fauna of that area as evidence in support of survival of a fauna there in a 'closed refugium' (Lindroth 1970) (*i.e.* in a *nunatak* refugium). Unfortunately, he included among his 'brachypterous' taxa those whose members lacked evident flight muscles at the time of capture, even if they were macropterous. These data are therefore more difficult to interpret and compare with those of other workers in other areas, where only true brachyptery was recorded as such; and conclusions reached may require re-examination (see also further comment below). Nonetheless, the contention that areas rich in taxa with brachypterous members may represent old centers of distribution and/or survival remains a generalization worth testing.

Hindwing atrophy in the nearctic *Nebria* fauna

Genus *Nebria* Latreille is Holarctic in distribution, with several hundred species described from the Palaearctic Region. At present, 55 species are known to occur in North America, including three Holarctic species (one of which is strictly trans-Beringian in distribution). One European species has been introduced at least twice into North America but has not become established and is not considered further here.

Of the 55 native species, 37 (67.3%) are monotypic and 18 (32.7%) are polytypic. Eleven species are represented by two subspecies, four by three subspecies, two by four subspecies, and one by six subspecies. The relatively high incidence of taxonomically significant geographical variation is no doubt related to the fact that all Nearctic members of the genus are adapted to cool or cold habitats. Most taxa are restricted to montane areas, which are characteristically isolated from other such areas by intervening lowlands. Such gap areas are evidently significant barriers to the free intermontane dispersal of individuals and serve to limit the geographical ranges of taxa as well.

Nearctic *Nebria* diversity is mainly western, where North American topographic diversity is also greatest. Only six species are represented east of the Mississippi River, of which only three are restricted to that region. A list of known Nearctic *Nebria* species and subspecies is provided in Table 1.

Incidence of hindwing atrophy

The incidence of hindwing atrophy among Nearctic *Nebria* taxa is quite high (see Table 1). Twenty-eight species (50.9% of the fauna) are known only from brachypterous members; and 34 species (61.8% of the fauna) have at least some members with hindwings atrophied. However, no Nearctic *Nebria* taxon is presently known to have populations in which both brachypterous and macropterous forms co-exist. There is considerable variation among different taxa in the form of

wing rudiments (Fig. 1); and interpopulational variation may also be found; but, again, intrapopulational variation in the size and form of hindwing vestiges is generally very slight.

All the hindwing forms illustrated in Figure 1 are represented among Nearctic *Nebria* taxa, as are the variations in form of elytral silhouette illustrated in Figure 2 (except for form 'g', which is found only among members of certain Palaearctic taxa). Other structural changes described by Darlington (1936), such as relative reduction in size of the metathoracic sclerites, elytral length, and size of the compound eyes, are associated with hindwing atrophy in members of several *Nebria* taxa. However, these changes may also occur without associated wing atrophy. Adults of *Nebria eschscholtzii* Menetries, for example, have elytra distinctly narrowed basally, with humeri markedly rounded, yet hindwings are macropterous in all individuals studied to date.

Table 1. Condition of hindwings and geographical range size in Nearctic *Nebria* taxa

	Character state ¹										Range size ^{2,3}	
	a	b	c	d	e	f	g	h	i	MLER-ss	MLER-s	
<i>N. virescens</i> Horn	a										960	960
<i>N. altisierrae</i> Kavanaugh	a										240	240
<i>N. campbelli</i> Kavanaugh	a										70	70
<i>N. paradisi</i> Darlington						f					320	320
<i>N. turmaduodecima</i> Kavanaugh						f					10	10
<i>N. gouleti</i> Kavanaugh	a										685	685
<i>N. hudsonica</i> LeConte	a										3350	3350
<i>N. lacustris lacustris</i> Casey	a										2160	2160
<i>N. lacustris bellorum</i> Kavanaugh											60	
<i>N. nivalis nivalis</i> Paykull	a										15891	17100
<i>N. nivalis gaspesiana</i> Kavanaugh											1585	
<i>N. crassicornis crassicornis</i> Van Dyke											350	2830
<i>N. crassicornis intermedia</i> Van Dyke											2830	
<i>N. frigida</i> Sahlberg	a										4870	4870
<i>N. gyllenhali castanipes</i> Kirby	a										6900	22550
<i>N. gyllenhali lassenensis</i> Kavanaugh											720	
<i>N. gyllenhali lindrothi</i> Kavanaugh				d							685	
<i>N. suturalis</i> LeConte				d							4030	4030
<i>N. obliqua obliqua</i> LeConte	a										4440	4440
<i>N. obliqua chuskae</i> Kavanaugh		b									10	
<i>N. appalachia</i> Darlington							g				150	150
<i>N. pallipes</i> Say							g				2240	2240
<i>N. darlingtoni</i> Kavanaugh	a										95	95
<i>N. mannerheimii</i> Fischer	a										2870	2870
<i>N. diversa</i> LeConte			c								1740	1740

Table 1. Continued.

	Character state ¹									Range size ^{2,3}	
	a	b	c	d	e	f	g	h	i	MLER-ss	MLER-s
<i>N. desolata</i> Kavanaugh				d						110	110
<i>N. navajo</i> Kavanaugh			c							10	10
<i>N. eschscholtzii</i> Menetries	a									1800	1800
<i>N. lyelli</i> Van Dyke					e					10	10
<i>N. danmanni</i> Kavanaugh					e					10	10
<i>N. wallowae</i> Kavanaugh	a									10	10
<i>N. acuta acuta</i> Lindroth	a									3330	3420
<i>N. acuta quileute</i>											
Kavanaugh	a									60	
<i>N. acuta sonora</i>											
Kavanaugh	a									50	
<i>N. jeffreyi</i> Kavanaugh	a									10	10
<i>N. sahlbergii sahlbergii</i> Fischer	a	b								4090	4160
<i>N. sahlbergii modoc</i>											
Kavanaugh	a									60	
<i>N. sahlbergii triad</i>											
Kavanaugh	a									30	
<i>N. arkansana arkansana</i> Casey	a	b	c							650	3390
<i>N. arkansana edwardsi</i>											
Kavanaugh	a									2500	
<i>N. arkansana fragilis</i> Casey			c	d						550	
<i>N. arkansana oowah</i>											
Kavanaugh	a									10	
<i>N. zioni zioni</i> Van Dyke				d						160	185
<i>N. zioni oasis</i> Kavanaugh				d						10	
<i>N. charlottae</i> Lindroth			c							80	80
<i>N. gregaria</i> Fischer			c							1540	1540
<i>N. haida</i> Kavanaugh			c							60	60
<i>N. lituyae</i> Kavanaugh			c							180	180
<i>N. louiseae</i> Kavanaugh			c							60	60
<i>N. gebleri gebleri</i> Dejean	a									2400	3100
<i>N. gebleri albimontis</i>											
Kavanaugh	a									10	
<i>N. gebleri cascadenis</i>											
Kavanaugh	a									800	
<i>N. gebleri fragariae</i>											
Kavanaugh	a									10	
<i>N. gebleri rathvoni</i>											
LeConte	a									650	
<i>N. gebleri siskiyouensis</i>											
Kavanaugh	a									80	
<i>N. carri</i> Kavanaugh						f				240	240
<i>N. kincaidi kincaidi</i> Schwarz						f				1280	1570
<i>N. kincaidi balli</i>											
Kavanaugh						f				170	
<i>N. spatulata spatulata</i> Van Dyke						f				50	280
<i>N. spatulata sierrae</i>											
Kavanaugh						f				200	
<i>N. ovipennis</i> LeConte						f				480	480
<i>N. manyi manyi</i> Van Dyke	a									2390	3000

Table 1. Continued.

	Character state ¹										Range size ^{2,3}	
	a	b	c	d	e	f	g	h	i	MLER-ss	MLER-s	
<i>N. meanyi giulianii</i> Kavanaugh	a										30	
<i>N. meanyi lamarckensis</i> Kavanaugh	a										20	
<i>N. meanyi sylvatica</i> Kavanaugh	a										185	
<i>N. metallica</i> Fischer	a										5160	5160
<i>N. labonteii</i> Kavanaugh	a										10	10
<i>N. piperi</i> Van Dyke	a										2060	2060
<i>N. schwarzi schwarzi</i> Van Dyke	a										370	1330
<i>N. schwarzi beverlianna</i> Kavanaugh	a										10	
<i>N. ingens ingens</i> Horn				d							90	200
<i>N. ingens riversi</i> Van Dyke				d							30	
<i>N. vandykei vandykei</i> Bänninger				d							315	550
<i>N. vandykei wyeast</i> Kavanaugh				d							130	
<i>N. purpurata</i> LeConte									i		530	530
<i>N. calva</i> Kavanaugh					e						10	10
<i>N. sierrablancae</i> Kavanaugh				d							20	20
<i>N. catenata</i> Casey								h			660	660
<i>N. coloradensis</i> Van Dyke								h			200	200
<i>N. piute piute</i> Erwin & Ball								h			20	210
<i>N. piute sevieri</i> Kavanaugh				d							170	
<i>N. piute utahensis</i> Kavanaugh				d							10	
<i>N. steensensis</i> Kavanaugh								h			10	10
<i>N. trifaria trifaria</i> LeConte									i		700	950
<i>N. trifaria pasquineli</i> Kavanaugh								h			400	

¹ Character states a to i are illustrated in Figure 1 and discussed in the text.

² MLER: = maximum linear extent of range, measured as a straightline distance between the two most distant known localities for the taxon; MLER-ss = for monotypic species and subspecies of polytypic species taken individually; MLER-s = for all species, with subspecies of polytypic species taken collectively.

³ All range sizes measured in kilometers.

A dendrogram which illustrates proposed phylogenetic relationships among Nearctic *Nebria* taxa is presented in Figure 3. Extant and hypothetical ancestral taxa which are thought to have (or have had) all members with hindwings atrophied are represented by thickened line segments. Character states for all taxa are listed in Table 1 and described below. Examination of the dendrogram suggests that hindwing atrophy has evolved from the macropterous condition at least 17 times independently. Continued progressive atrophy has apparently occurred independently in at least eight additional taxa. Based on proposed phylogenetic relationships of *Nebria* taxa and the distribution of character states

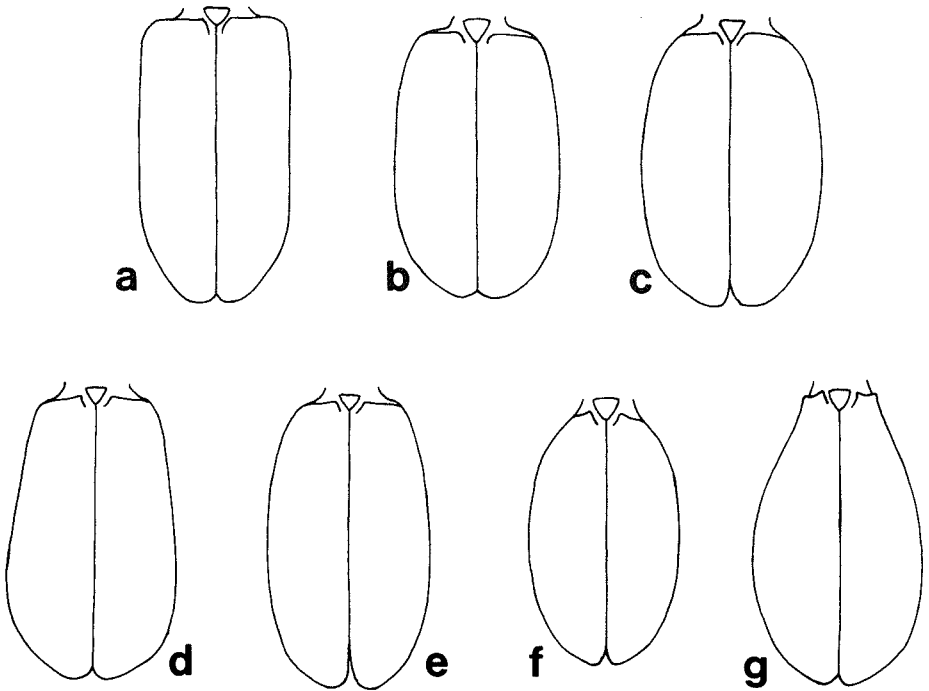
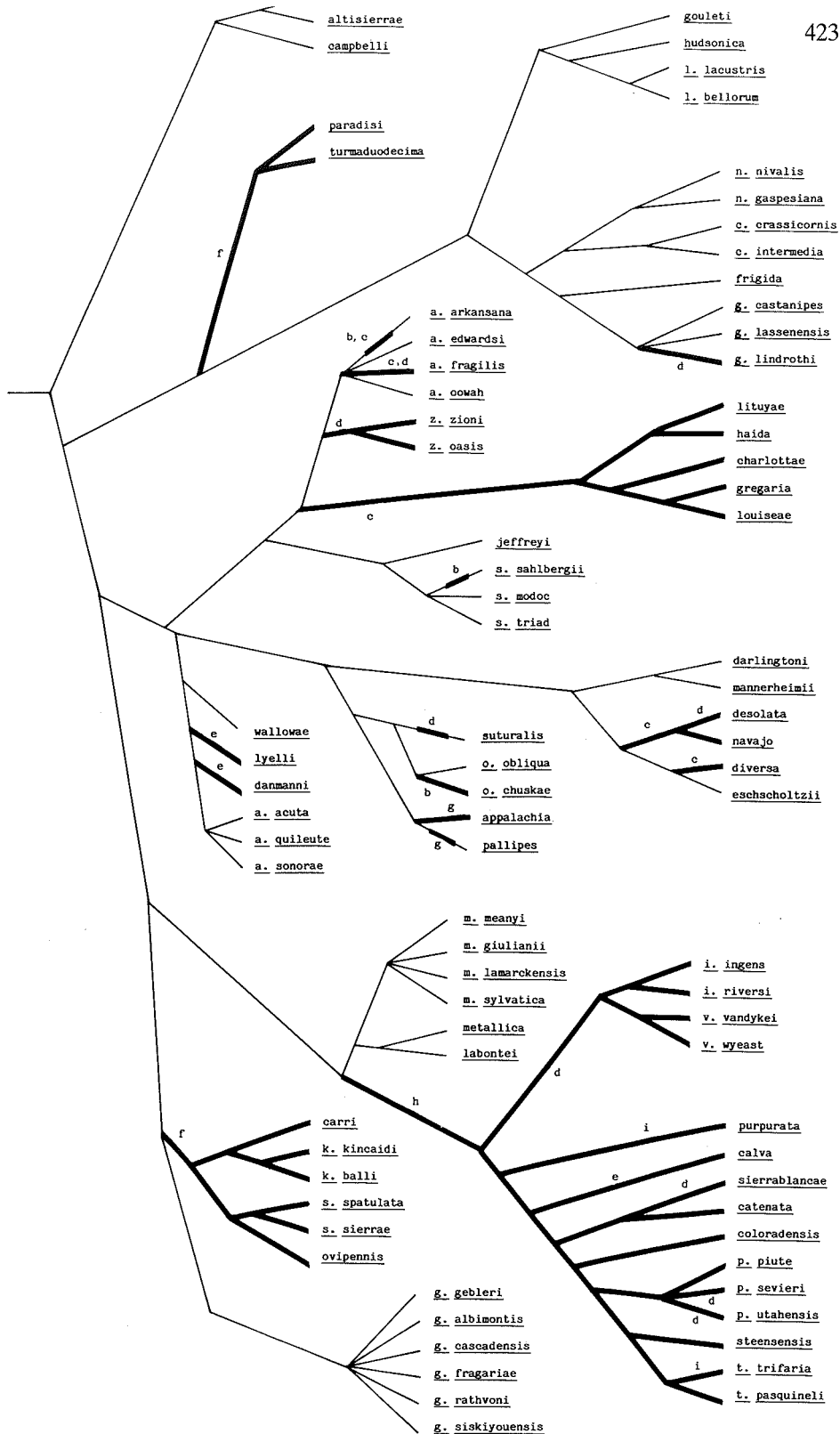


Figure 2. Examples of variation in form of elytral silhouette among *Nebria* taxa, dorsal aspect: (a) 'rectangular' form; (b) 'subrectangular' form; (c) 'subovoid' form; (d) 'subovoid-narrowed' form; (e) 'subovoid-elongate' form; (f) 'ovoid' form; (g) 'teardrop' form.

among their members, directions of evolutionary change in progressive wing atrophy can be suggested (Fig. 1). Darlington (1936) proposed a typical sequence of change in wing form which is very similar to that found among most Nearctic *Nebria*. This sequence can be described as follows. The macropterous condition (Fig. 1a) is taken as the starting point. Atrophy begins with reduction of wing apex area (Fig. 1b). The rudiment is next narrowed through loss of posterior wing area (Fig. 1c). Subsequent atrophy involves overall reduction in size and venation, from a distinctly wing-like vestige (Fig. 1d) to a lightly-veined, spatulate lobe (Fig. 1e), and finally to a strap-like vestige which is barely recognizable as a wing. The evolution of wing atrophy in most Nearctic *Nebria* lineages follows this sequence; but there are evidently at least two exceptions which apparently represent two additional sequences. The first is a change from macropterous (Fig. 1a) to what appears to be just a miniature of the full-sized wing (Fig. 1g). This character state is found only in *Nebria appalachia* Darlington adults and in some members of one population of its sister species, *Nebria pallipes* Say. In the third sequence, the change appears to be from the macropterous form (Fig. 1a) to a narrowed rather than truncate form (Fig. 1h). In the next step in the sequence, the wing apex is reduced, but not distinctly truncate (Fig. 1i). Because some taxa



closely related to taxa with character states 'h' and 'i' have wing vestiges indistinguishable from those for states 'd' and 'e', I suggest that the first and third sequences converge, resulting in wing vestiges with the form of states 'd' and 'e' derived from two separate (and probably genetically distinct) processes of hindwing atrophy. This convergence can only be recognized in relation to a hypothesis of phylogenetic relationship based on analysis of other characters.

That three different sequences of progressive wing atrophy are evident, that intrapopulational variation in wing form is slight or undetectable, and that other structural changes typically associated with wing atrophy are seemingly 'uncoupled' (*i.e.* may occur associated with macroptery rather than brachyptery) all suggest that the evolution of wing atrophy among Nearctic *Nebria* has been more complex than, or otherwise different from, that in other groups studied to date.

Habitat distribution and hindwing atrophy

As noted above, Darlington (1936, 1943) found a close relationship between habitat and the occurrence of brachyptery. Data presented in Table 2. indicate a clear relationship between macrohabitat (or 'life zone'; Merriam 1894, 1898) and brachyptery among Nearctic *Nebria* taxa. There is a distinct trend for increased incidence of brachyptery with increased altitude. Members of more than 70% of *Nebria* taxa living in the 'alpine' zone (*i.e.* above treeline) in North American mountains are brachypterous. Perhaps surprisingly, a similar high incidence is found in the 'upper sea beach' zone. This finding suggests that these two habitats offer relatively long-term stability to their respective inhabitants. They have no doubt survived as temporally continuous, climatically stable habitats in western North America for millions of years. During glacial periods, alpine zone areas no doubt expanded in size, as such zones were depressed downward on mountains. Similarly the extent of upper sea beach areas may have been greater in glacial periods, when worldwide sea levels were much lower than at the present.

There does not appear to be any clear relationship evident between islands as habitats and brachyptery among Nearctic *Nebria* taxa. Of six species occurring in the Queen Charlotte Islands, British Columbia, four (66.7%) have brachypterous members; and adults of two of three *Nebria* taxa present in the Aleutian Islands (66.7%) are also brachypterous. However, brachypterous forms in these

←

Figure 3. Dendrogram representing proposed phylogenetic relationships among Nearctic *Nebria* taxa. Uniformly thickened line segments denote extant taxa and/or hypothetical ancestral taxa in which all members are presumed to have atrophied hindwings; line segments only partly thickened denote extant taxa in which some, but not all, members have atrophied hindwings. Scientific names of taxa are listed in Table 1. Lower case letter beside a thickened line segment denotes character state of hindwing at that point in dendrogram and in all descendant lines unless otherwise noted. Character states are illustrated in Figure 1, listed for all taxa in Table 1, and discussed in text.

two areas are closely related and, with one exception, represent descendants of brachypterous ancestral stocks which are also represented by brachypterous members on the mainland. Residence on islands is clearly incidental to this brachyptery. Also, only two of eight *Nebria* species occurring on Vancouver Island have brachypterous members and none of the three species inhabiting Kodiak Island is structurally brachypterous (but see Lindroth 1969).

Geographical range and hindwing atrophy

There are several aspects of geographical range upon which the incidence of brachyptery might be assumed to have an effect. One of these is range size. Both Wollaston (1854) and Darlington (1936, 1943) suggested that taxa with brachypterous members tend to occupy more restricted ranges than those with macropterous members. In order to test this hypothesis among Nearctic *Nebria*, I calculated the 'maximum linear extent of range' (MLER) (*i.e.* the straightline distance between the two most distant known localities) as a measure of range size for each taxon (Table 1). In one test, only species (with the ranges of included subspecies taken together) were compared; and in a second test, all subspecies and monotypic species were compared with each other. Results of these tests are presented in Table 3. As expected, the mean range sizes (*i.e.* mean values for MLER) for taxa with brachypterous and macropterous individuals differ significantly ($P < 0.01$). Mean range size for brachypterous forms is only 14% of that for macropterous forms in the comparison among species and 17.7% of the latter in the comparison among all taxa.

Another aspect of geographical range is the distance between isolated conspecific populations and the effect of brachyptery on gene flow among these. In a previous paper (Kavanaugh 1979), I used data from my study of Nearctic *Nebria* to test aspects of the 'allopatric speciation' model. For example, to test the

Table 2. Hindwing atrophy and habitat among Nearctic *Nebria* taxa

Macrohabitat ¹	Total taxa	Brachypterous taxa ²	% Brachypterous taxa
Arctic	2	0	0.0
Alpine	37	27	73.0
Hudsonian	57	23	40.4
Canadian	43	12	27.9
Upper Sonoran	9	2	22.2
Upper Sea Beach	7	5	71.4

¹ Macrohabitats listed, except for 'Upper Sea Beach', are equivalent to 'life zone' concepts of Merriam, 1894 and 1898.

² Taxa in which all members apparently have atrophied hindwings.

assumption that rate of taxonomically significant differentiation (*i.e.* speciation or subspeciation) is proportional to the degree of isolation of populations or groups of same, I compared the gap distances measured between most proximate populations of geographically isolated conspecific subspecies and tried to relate gap size to flight capability. I expected to find that mean gap distances between subspecies with brachypterous members would be less than between subspecies with macropterous individuals, but no such relationship could be found. Similarly, a proposed relationship between reduced flight capability (*i.e.* brachyptery) and tendency toward geographical differentiation (*i.e.* subspeciation) could not be demonstrated. One interpretation of these results is that flight is of little, if any, importance in present long-range dispersal between and maintenance of gene flow among isolated, conspecific populations of *Nebria*. However, a more realistic interpretation is that present gap sizes are mainly a function of topography and simply do not reflect a dynamic relationship between allopatric populations, and, further, that gap sizes are at present larger than necessary to effectively isolate populations of macropterous as well as brachypterous individuals.

As noted above, Lindroth (1963, 1969, 1979a) was interested in the geographical distribution of brachyptery as an indicator of geographical areas which may have served as centers for long-term survival, for example, during Pleistocene glaciations. By plotting the geographical ranges of all Nearctic *Nebria* taxa with brachypterous members on a single map (Fig. 4), coincident occurrence of such taxa is apparent. The pattern which emerges is one in which five areas stand out as major centers of nebrine brachyptery (in which three or more taxa are represented), with perhaps four other minor centers (each with two taxa represented), and a number of other areas in which single taxa with brachypterous members occur. Major centers include (1) the Southern Rocky Mountains of Colorado, where as many as five taxa with brachypterous members occur sympatrically; (2) the Sierra Nevada of California, where as many as four such species co-occur; (3)

Table 3. Size of geographical range and wing atrophy among nearctic *Nebria* taxa

	Species		Species and subspecies	
	Macropterous ¹	Brachypterous ²	Macropterous	Brachypterous
Number of taxa ³	21	28	42	38
Mean range size ⁴	2,625.2	370.5	1,669.5	295.0
S.D. of mean	13,558,928.7	246,296.9	7,985,849.6	178,178.4
S.E. of mean	803.5	93.8	436.0	68.5
t values	9.21		8.65	
F values	55.05		44.82	

¹ Taxa in which all members apparently have fully-developed hindwings.

² Taxa in which all members apparently have atrophied hindwings.

³ Taxa in which some, but not all, members are brachypterous not included in this analysis.

⁴ Based on data presented in Table 1; all values in kilometers.

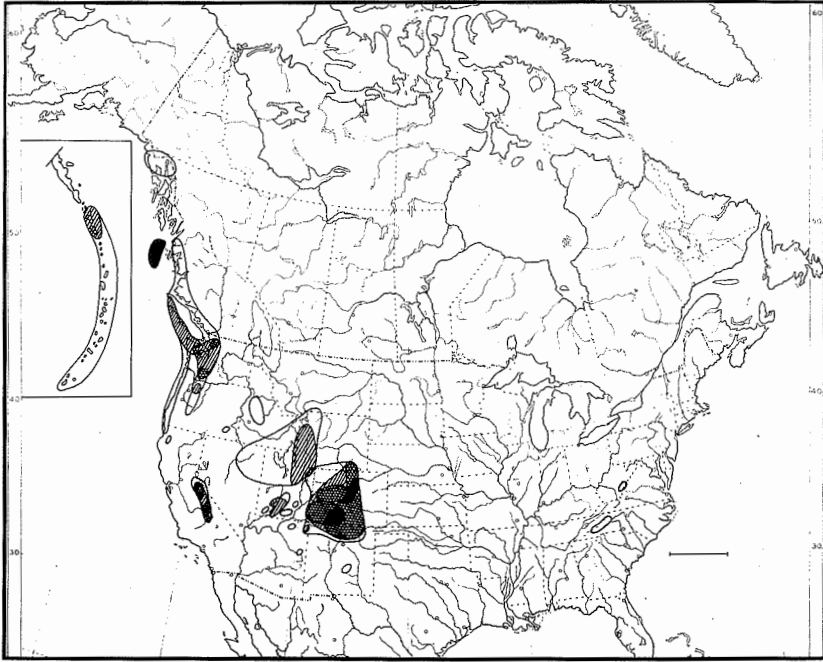


Figure 4. Map illustrating coincidence of geographical ranges of Nearctic *Nebria* taxa in which members have atrophied hindwings. Area enclosed by solid line = one species; obliquely-hatched area = two species; cross-hatched area = three species; solid black area = four or more species. Scale line = 500 km.

the Cascade Range in Washington, where as many as three such species co-occur; (4) the Olympic Mountains of western Washington, where as many as three such species occur sympatrically; and (5) the Queen Charlotte Islands of British Columbia, where four such species occur, but where no more than two are found sympatrically. Minor centers include (1) the Sevier Plateau and adjacent ranges and plateaus in southcentral Utah; (2) the Wasatch Mountain system of southwestern Wyoming, southeastern Idaho, and northern Utah; (3) the west coast of Vancouver Island, British Columbia; and the inner Aleutian Islands. These data and present knowledge of the co-occurrence of non-nebriine carabids with brachypterous members in these areas suggest that they have served as centers for both long-term survival and differentiation.

Darlington's model for the evolution of brachyptery in montane faunas and Nearctic Nebria

A hypothesis of phylogenetic relationships among extant *Nebria* taxa (Fig. 3) permits us to attempt to interpret the evolution of particular montane faunas (see Table 4) with respect to Darlington's model (1943). For example, the nebriine

fauna of the Cascade Range in Washington includes only four of 16 taxa (25% of the fauna) with brachypterous members. Each of these, however, is related to other taxa with brachypterous members. Therefore, coincidence of brachyptery in this montane fauna appears to have resulted from 'concentration' and not 'conversion' or 'proliferation'. In contrast, five of seven taxa (71.4% of the fauna) represented in the Front Range of the Southern Rocky Mountains, Colorado, have brachypterous members. Only two of these are related to other taxa with brachypterous members; the remainder are related to taxa with macropterous members. Hence, this fauna appears to have evolved through both 'concentration' and 'conversion', but not 'proliferation', phases. Finally, the fauna of the Sierra Nevada includes 13 taxa, six of which (46.2% of the fauna) have brachypterous members. Of these, only one taxon, *Nebria lyelli* Van Dyke, is a descendant of macropterous ancestors. However, two pairs of subspecies, each with only brachypterous members, occupy restricted, vicariant portions of the mountain range. This suggests that 'concentration', 'conversion', and 'proliferation' phases have each played a role in the evolution of this fauna. The next step toward understanding the development of each of these faunas is to study other carabid groups represented, using the same approach, to see if these other groups reflect the same evolutionary sequence.

Functional flightlessness without brachyptery: atrophy or absence of flight muscles

As noted above, Lindroth (1969) combined taxa with macropterous members and those found to be structurally flightless (*i.e.* brachypterous) in compiling his list of

Table 4. Nearctic *Nebria* taxa with brachypterous members, in selected montane areas

Taxon	Montane areas		
	Front range Rocky Mts.	Cascades	Sierra Nevada
<i>N. g. lindrothi</i>	X		
<i>N. suturalis</i>	X		
<i>N. a. arkansana</i>	X		
<i>N. purpurata</i>	X		
<i>N. t. pasquineli</i>	X		
<i>N. paradisi</i>		X	
<i>N. k. kincaidi</i>		X	
<i>N. k. balli</i>		X	
<i>N. v. vandykei</i>		X	
<i>N. lyelli</i>			X
<i>N. s. spatulata</i>			X
<i>N. s. sierrae</i>			X
<i>N. ovipennis</i>			X
<i>N. i. ingens</i>			X
<i>N. i. riversi</i>			X

'flightless' carabids in the Kodiak Refugium fauna. He did so because examination of specimens at his disposal revealed that flight muscles were absent or atrophied. He considered such individuals to be functionally flightless and felt justified in adding their numbers to his list of structurally flightless taxa.

This raises several questions which I have not yet begun to address among Nearctic *Nebria*. For example, how many taxa have members which are macropterous yet functionally flightless? Is there any seasonal or other variation in flight muscle development and/or atrophy? Is there intrapopulation variation in the development of these muscles, perhaps even dimorphism such that flying and flightless morphs do co-exist, with variation in muscle development rather than wing development? Van Schaick Zillesen and Brunsting (1984) found that laboratory exposure of larvae and pupae of *Pterostichus oblongopunctatus* (Fab.) to limited food supply and extreme photoperiod resulted in some adults with fully developed flight muscles, whereas such adults (*i.e.*, with fully developed flight muscles) are unknown among samples from the field. To what extent, if any, may environmental conditions affect development of flight muscles in *Nebria*?

Lindroth (1969) listed *Nebria sahlbergii* Fischer and *Nebria metallica* Fischer as flightless, whereas I have always (and in this paper) included them among the macropterous rather than brachypterous (flightless) forms. Clearly, additional study is required; but it would seem appropriate, nonetheless, to distinguish between a stage in the evolution of flightlessness which involves only atrophy or loss of flight muscle from one which also involves hindwing atrophy. Recognition of this additional stage is a modest extension of the useful general hypothesis of evolution of flightlessness developed by Darlington and Lindroth.

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