JOURNAL OF NATURAL HISTORY, 1986, **20**, 283–297

Geographic patterns of colour variation in North American *Nicrophorus* burying beetles (Coleoptera; Silphidae)

ROBERT S. ANDERSON and STEWART B. PECK*

*Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3 and *Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada*

(Accepted 25 July 1985)

Adult individuals of the burying beetle species *Nicrophorus defodiens* Mannerheim, *N. guttula* Motschulsky, and *N. investigator* Zetterstedt show extensive geographic variation in elytral colour patterns, from an orange and black banded pattern to one where maculations are extremely reduced. Individuals with slightly to extensively reduced maculations are generally confined to Pacific coastal localities but, as variation is continuous and extremes are often sympatric, do not warrant separate specific or subspecific status. Examination of the geographic distribution of the colour of the basal article of the antennal club of *N. guttula* individuals shows the colour of the article to be associated with variation in elytral colour. This confirms that *N. hecate* Bland, previously characterized by a red basal article of the antennal club, is a junior synonym of *N. guttula* Motschulsky, previously characterized by a black basal article. The possible roles of thermoregulation and mimicry accounting for the variation in elytral colour are briefly discussed.

Introduction

Variation in elytral colour pattern is evident in adult individuals of species of the genus *Nicrophorus* (Silphidae). These are the large carrion beetles commonly referred to as sexton or burying beetles because of their habit of interring small vertebrate carcasses, upon which they rear their larvae. Typically, adult individuals possess largely black elytra with two contrasting bright orange or orange-red transverse bands or maculations. Individuals of some Nearctic species have the elytral bands reduced to a series of spots and one Nearctic species, *N. nigrita*, is wholly black. In the 15 species in North America north of Mexico, extensive variation in the extent and form of the colour bands in known in only four species; *N. carolinus*, *N. defodiens*, *N. guttula*, and *N. investigator*. Horn (1880) was the first to note that extensive variation occurred in the elytral colour patterns of *Nicrophorus*. He stated (Horn, 1880: 232) that *N. guttula* 'illustrates the tendency to melanism shown by many other species [of insects in general?] which extend from the Plains to California, and it may be here observed that the fauna of California often replaces the coloured eastern species by one entirely black'. He also noted extensive variation in colour patterns in *N. investigator* [= *N. melsheimeri* of Horn], and *N. defodiens* [= *N. vespilloides* of Horn, in part]. Variation in *N. carolinus* was only noted upon discovery of an immaculate specimen from Tuba City, Arizona, initially described as a separate species, *N. mystacallis* (Angell, 1912), but subsequently synonymized with *N. carolinus* (Arnett, 1944). Further and more detailed studies by Hatch (1927, 1957) resulted in the introduction and use of an abundance of names describing each minutely different colour variant in many species, but in particular those of *N. defodiens*, *N. guttula* and *N. investigator*.

Because the highly variable colour patterns were frequently employed as primary diagnostic characters in early keys and descriptions, many species were misidentified, species distributions were inaccurately mapped, and the classification became confused. We have now resolved these taxonomic and distributional inaccuracies but elsewhere have only presented a brief description of colour variation within each species (Anderson and Peck, in press).

This paper primarily presents the data upon which are based the interpretations of the taxonomic significance of the results of detailed studies of the geographic distribution of colour patterns of elytra in *N. defodiens, N. guttula*, and *N. investigator* and of the basal article of the antennal club in *N. guttula*, the latter used by Arnett (1944) and Miller and Peck (1979) to distinguish *N. hecate* Bland (red basal article) as a distinct species from *N. guttula* (black basal article). Sufficiently large samples were not available to discuss patterns of variation in *N. carolinus*.

Materials and methods

Totals of 1241 specimens of *N. defodiens*, 2684 specimens of *N. guttula*, and 759 specimens of *N. investigator* from various localities in North America, north of Mexico were examined. These were obtained as loans from various institutional collections and from our own field sampling. Institutions and the curators from which specimens were borrowed are as follows.

Agriculture Canada Research Station, Saskatoon, Saskatchewan; M. E. Taylor.
Agriculture Canada Research Station, Lethbridge, Alberta; K. W. Richard.
American Museum of Natural History, New York, New York; L. H. Herman.
Arizona State University, Tempe, Arizona; F. F. Hasbrouck.
British Columbia Provincial Museum, Victoria, British Columbia; R. A. Cannings.
Canadian Forestry Service, Fredericton, New Brunswick; L. P. Magasi.
Cornell University, Ithaca, New York; L. L. Pechuman.
California Academy of Sciences, San Francisco, California; D. H. Kavanaugh.
California Department of Food and Agriculture, Sacramento, California; F. G. Andrews.
Canadian National Collection, Ottawa, Ontario; J. M. Campbell.
Colorado State University, Fort Collins, Colorado; U. N. Lanham.
Field Museum of Natural History, Chicago, Illinois; H. Dybas.
Los Angeles County Museum, Los Angeles, California; C. L. Hogue.
McGill University, Macdonald College, Ste. Anne de Bellevue, Quebec; N. Duffy.
Museum of Comparative Zoology, Cambridge, Massachusetts; A. F. Newton, Jr.
Montana State University, Bozeman, Montana; S. Rose.
Nova Scotia Museum, Halifax, Nova Scotia; B. Wright.
Oregon State University, Corvallis, Oregon; M. D. Schwartz.
Royal Ontario Museum, Toronto, Ontario; G. B. Wiggins.
Saskatchewan Provincial Museum, Regina, Saskatchewan; R. R. Hooper.
United States National Museum, Washington D.C.; T. J. Spilman.
University of Alberta, Edmonton, Alberta; D. Shpeley.
University of British Columbia, Vancouver, British Columbia; R. A. Cannings.
University of California, Berkely, California; J. A. Chemsak.
University of Idaho, Moscow, Idaho; D. E. Foster.
University of Nebraska, Lincoln, Nebraska; B. C. Ratcliffe.
Washington State University, Pullman, Washington; R. Zack.
J. L. Carr Private Collection, Calgary, Alberta; J. L. and B. F. Carr.

The pattern of elytral colouration of specimens of each species was coded and assigned to five or six categories (A, to E or F) with A, and E or F, representing the most and least maculated individuals, respectively. Five categories were erected for *N. defodiens* (fig. 1), and six for each of *N. guttula* (fig. 2) and *N. investigator* (fig. 3).

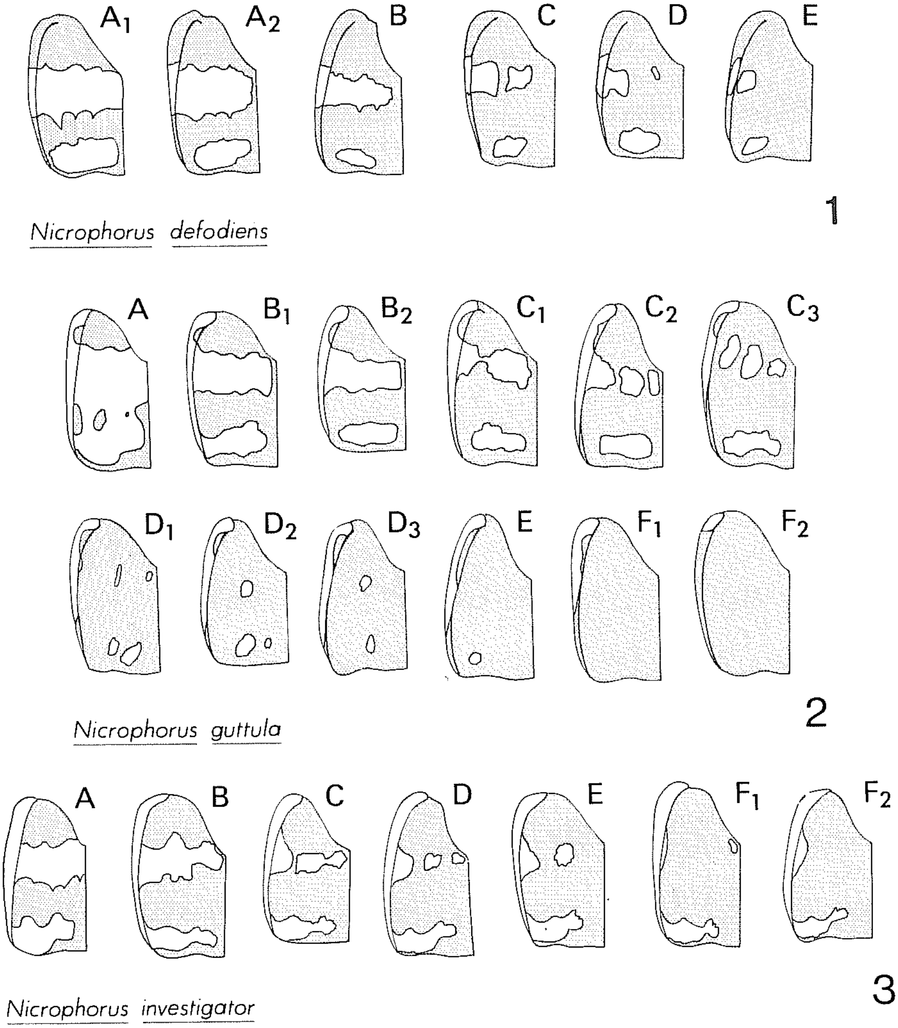

FIG. 1–3. Variation in elytral colour pattern in adult individuals of *Nicrophorus* species. Fig. 1. *Nicrophorus defodiens*. Fig. 2. *Nicrophorus guttula*. Fig. 3. *Nicrophorus investigator*.

Choice of these groupings of patterns was based largely on the work of Hatch (1927, 1957). They are arbitrarily defined, but each share some common feature of the pattern, represent the range of variation in a manageable number of groups, and represent successive stages in reduction of the colour pattern from the banded state to one in which the spots are reduced and the elytra largely black. Subscripts have been used in the figures to indicate slightly different patterns but which do not warrant separate group status.

We had to assume that no collecting biases were involved in collection of specimens borrowed from museums. As noted by Goulet and Baum (1981) this may be an unfounded assumption in some instances because knowledgeable local collectors soon learn to recognize rarer forms and concentrate on the selection of these individuals. Samples we collected using baited pitfall traps were not subject to such biases as all specimens collected were retained.

Relative abundance data of colour variants for each state or province throughout the Nearctic range of each of the three species are presented in tables 2, 4 and 6. Where each species occurs in western coastal states of provinces, details of colour variation within large samples from a particular geographic locality or group of localities, are given in tables 1, 3 and 5 and additionally are presented in the form of pie diagrams on maps (figs 4–6). Remaining localities within these coastal states or provinces from which specimens were examined, are plotted on these same maps and the relative abundance of colour variants from these remaining localities lumped and presented in tables 1, 3, and 5. Lists of localities of all specimens examined of each species from coastal states and provinces are presented in Appendices 1–3.

Also presented for *N. guttula* are data on the geographic distribution of individuals differing in the colour of the basal article of the antennal club (either red or black (table 7), and a histogram showing the association of antennal and elytral colour patterns (fig. 7).

Results

Geographic distribution of colour variants for *N. defodiens*, *N. guttula*, and *N. investigator* are shown on figs 4–6 and tables 1–6. Individuals with reduced maculations in all three species are more prevalent in Pacific coastal states and provinces than they are in inland states and provinces (tables 1–6).

No individuals of *N. defodiens* with extensively reduced maculations (groups E and F) were found at inland localities. Only a single specimen of group C (Mount Robson; BC) and scattered individuals of group B (Salmon Arm, Lilloet, Terrace, Mission City; all BC) were found inland. Most specimens from coastal sites showed at least some degree of reduction in maculation. All coastal sites for which large samples were available, except the northernmost (Wrangel and Ketchikan; AK) show a preponderance of individuals with moderately reduced maculations (groups C and D). All individuals examined from inland states and provinces were fully maculated.

A similar pattern can also be seen for *N. investigator*. No individuals of this species with even slightly reduced maculations (groups B–F) were found in inland states and provinces or at inland localities in coastal states and provinces. Unlike *N. defodiens*, no individuals with reduced maculations were found at southern coastal localities (fig. 6, localities 4, 5). All individuals at these localities were fully maculated. Individuals of *N. investigator* with reduced maculations were only found at northern coastal localities (fig. 6, localities 2, 3; other coastal Alaskan localities; Queen Charlotte Islands; BC). At these localities, only a few individuals show a moderate degree of reduction in maculation (groups C–E) as was so for *N. defodiens* at coastal localities. Most individuals of *N. investigator* have either only slightly reduced (if at all) or markedly reduced maculations.

Unlike the previous two species, individuals of *N. guttula* with reduced maculations are known from inland states and provinces (table 4). Most of these have only slightly reduced maculations but two specimens from Arizona (groups D, E) and 26 from south-western Nevada (groups D–F) possess markedly reduced maculations. Within coastal states and provinces, fully maculated individuals (groups A, B) predominate in the north in British Columbia (99%), Washington (99%) and to a lesser extent in Oregon (56%) (fig. 5, table 3). Individuals with reduced maculations (groups D–F) predominate in California (87·5%) (fig. 5, table 3). Within Oregon and California, predominance of less maculated individuals (groups D–F) decreases northward. Coastal localities in southern California are all represented almost wholly by

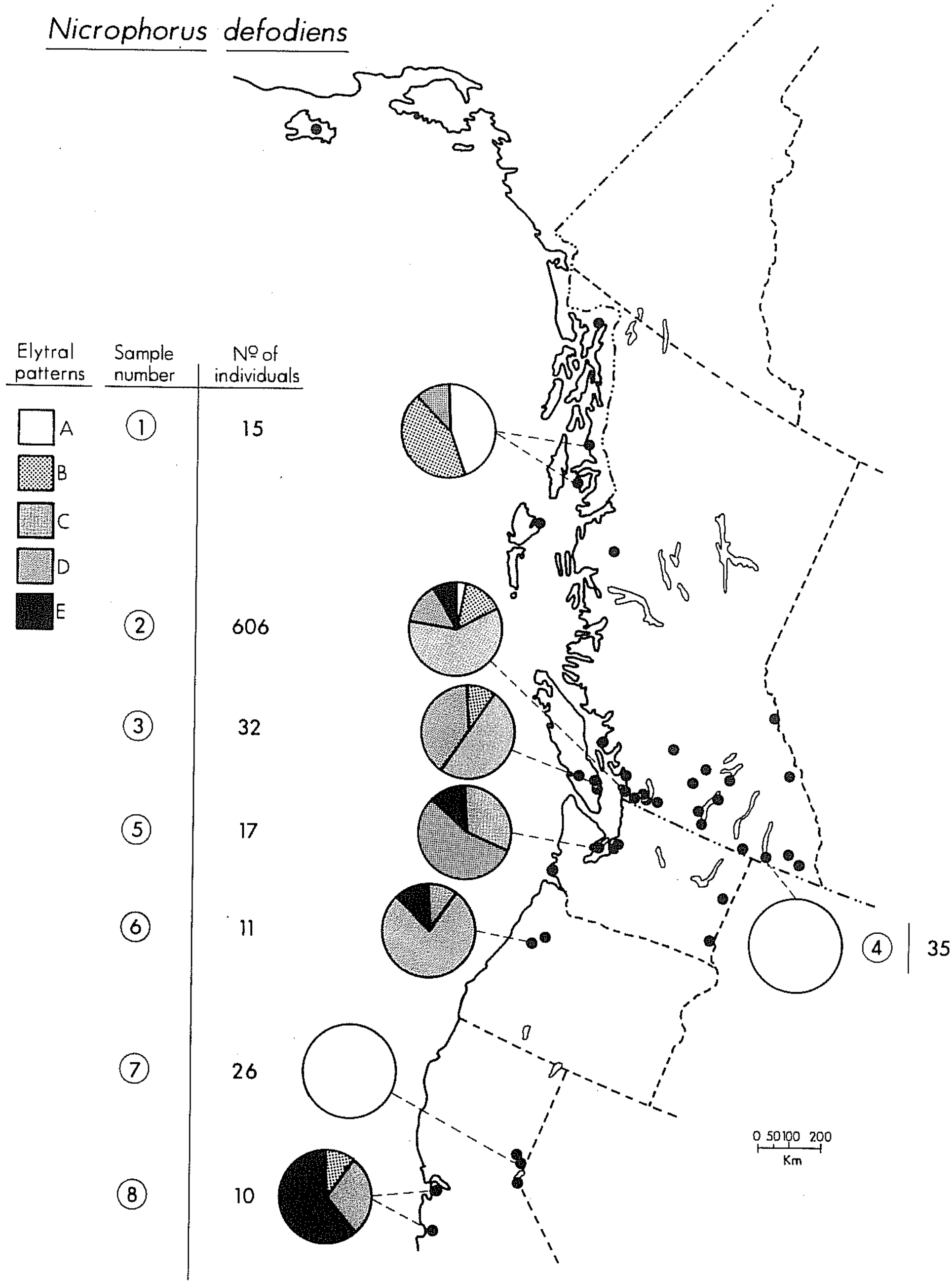

FIG. 4. Distribution and relative abundances of adult individuals of *Nicrophorus defodiens* with different elytral colour patterns in western coastal USA and Canada. Elytral patterns refer to those illustrated in fig. 1. Sample numbers refer to those listed in table 1. Details of relative abundance of each pattern for each sample are found in table 1. Dots indicate collection localities as listed in Appendix 1.

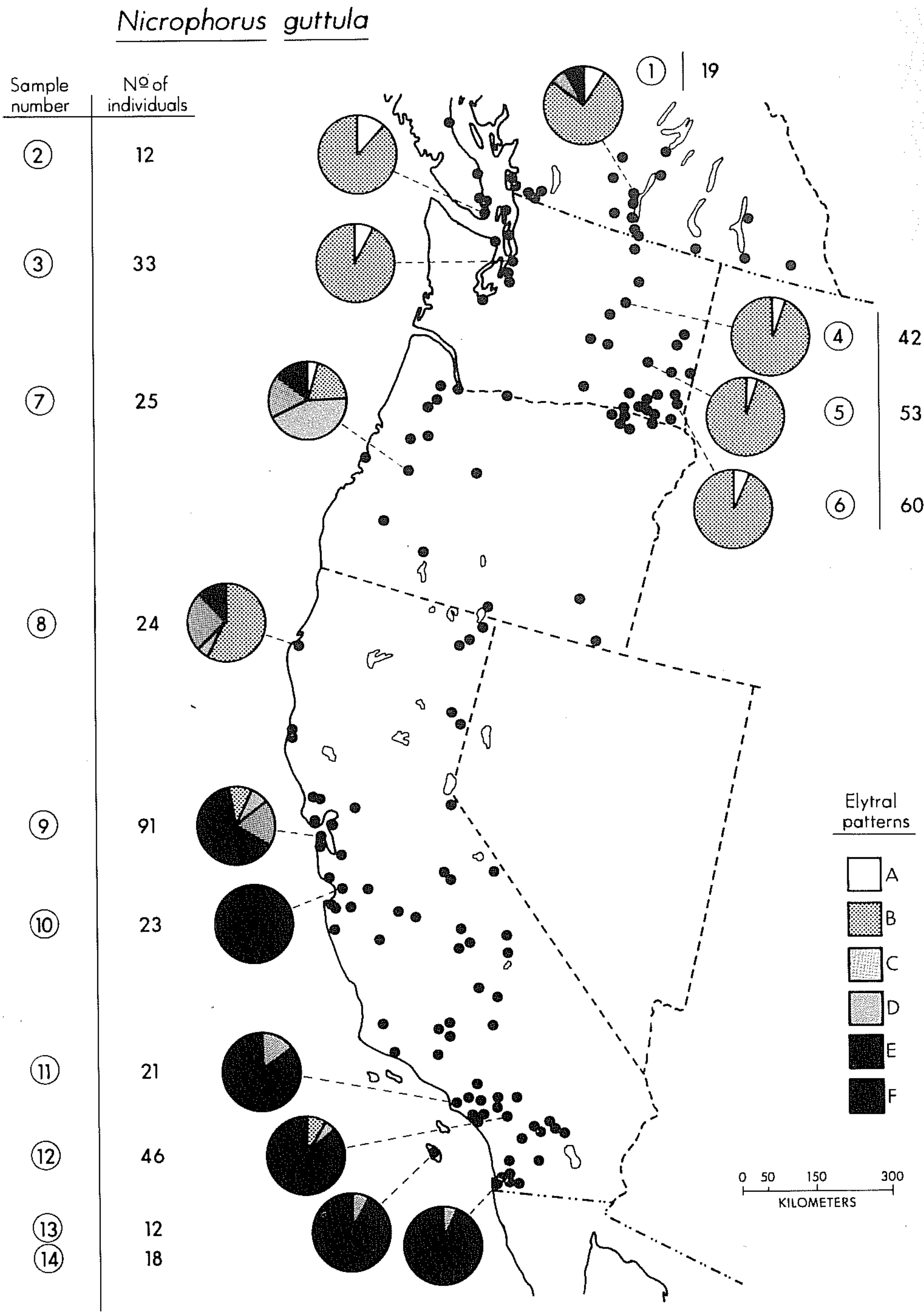

FIG. 5. Distribution and relative abundances of adult individuals of *Nicrophorus guttula* with different elytral colour patterns in western coastal USA and Canada. Elytral patterns refer to those illustrated in fig. 2. Sample numbers refer to those listed in table 3. Details of relative abundance of each pattern for each sample are found in table 3. Dots indicate collection localities as listed in Appendix 2.

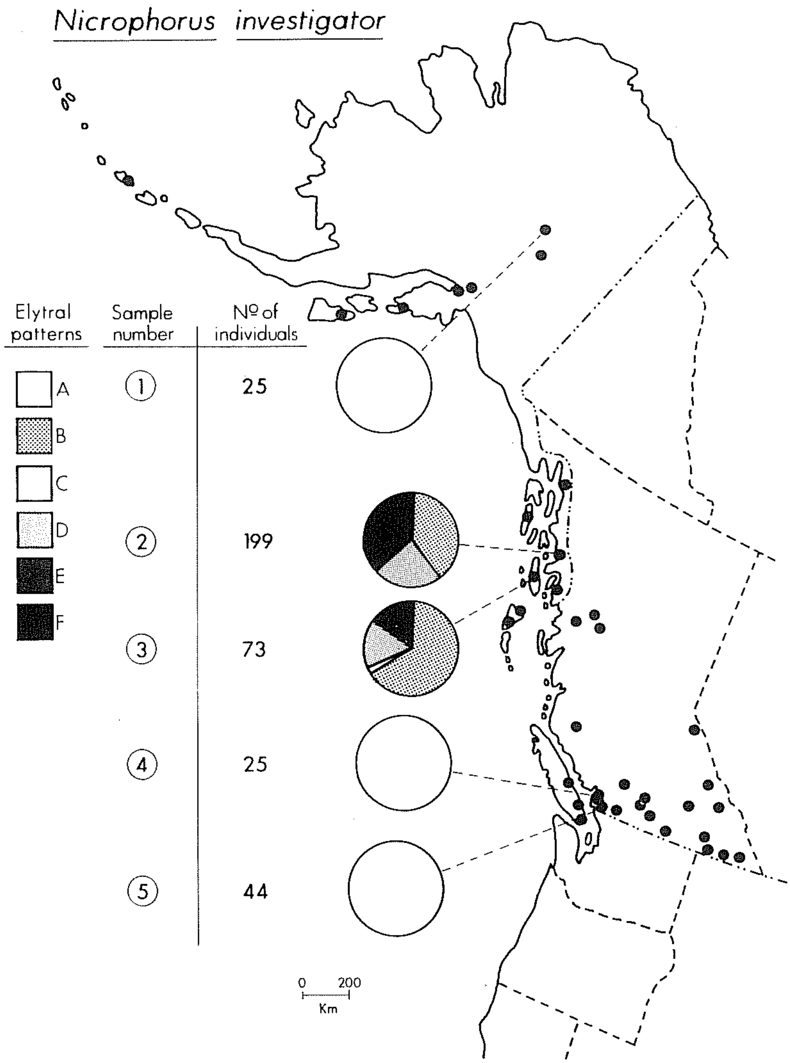

FIG. 6. Distribution and relative abundances of adult individuals of *Nicrophorus investigator* with different elytral colour patterns in western coastal USA and Canada. Elytral patterns refer to those illustrated in fig. 3. Sample numbers refer to those listed in table 5. Details of relative abundance of each pattern for each sample are found in table 5. Dots indicate collection localities as listed in Appendix 3.

individuals with extensively reduced maculations (group F). Further north, individuals with reduced maculations (groups D–F) decrease in predominance in San Francisco (85%), but especially Eureka (33%) and Eugene, Oregon (32%). Coastal Oregon localities are represented by at least some less extensively maculated individuals. Inland Oregon localities are represented only by fully maculated individuals (groups A, B). On the other hand, virtually all Californian localities, whether inland or coastal, are represented by at least some individuals with markedly reduced maculations (groups D–F but especially F). Only to the north and east are there localities with significant numbers of more fully maculated individuals (groups A–C). As in

N. investigator, most individuals of *N. guttula* examined have either only slightly reduced (if at all) or almost completely reduced maculations.

Also in *N. guttula*, the anterior and posterior transverse bands of a large number of specimens are joined longitudinally resulting in an almost entirely orange elytral pattern (group A). This pattern is widespread throughout prairie states and provinces and throughout the desert states of the south-western USA. It is the predominant colour pattern in New Mexico (59.5%) and is also very frequent in Arizona (43%). A similar pattern also occurs, although rarely, in specimens of *N. investigator*, *N. tomentosus* Weber and *N. marginatus* Fabricius.

Table 1. Relative abundances of adult individuals of *Nicrophorus defodiens* with different elytral colour patterns in western coastal USA and Canada.

Locality no.	No. of individuals	Locality	Elytral pattern				
			A	B	C	D	E
1	15	AK: Ketchikan, Wrangel	7	7	—	1	—
2	606	BC: Aldergrove, Hope, Lions Bay, Squamish, White Rock, Vancouver	12	101	355	95	43
3	32	BC: Duncan, Genoa Bay	—	2	16	12	—
4	35	BC: Creston	35	—	—	—	—
5	15	WA: Bremerton, Monroe, Seattle	—	—	5	10	2
6	11	OR: Corvallis, Turner	—	—	1	9	1
7	26	CA: Hobart Mills, Lake Tahoe, Quincy	26	—	—	—	—
8	10	CA: Marin Co., San Mateo Co.	—	1	3	—	6
	4	Other Alaskan localities	—	4	—	—	—
	122	Other British Columbia localities	72	19	28	2	1
	6	Other Washington localities	6	—	—	—	—

Elytral patterns refer to those illustrated in fig. 1. Sample numbers refer to those listed in fig. 4. 'Other localities' are those indicated by dots in fig. 4 but not represented by pie diagrams.

Table 2. Relative abundance of adult individuals of *Nicrophorus defodiens* with different elytral colour patterns throughout the known Nearctic range.

Province or State	Total no. of individuals	Elytral pattern				
		A	B	C	D	E
Alberta	53	53	—	—	—	—
British Columbia	793	119	122	399	109	44
Manitoba	28	28	—	—	—	—
New Brunswick	14	14	—	—	—	—
Northwest Territories	4	4	—	—	—	—
Nova Scotia	33	33	—	—	—	—
Ontario	167	167	—	—	—	—
Quebec	53	53	—	—	—	—
Saskatchewan	7	7	—	—	—	—
Alaska	19	7	11	—	—	—
California	26	26	—	1	3	6
Oregon	11	—	—	1	9	1
Washington	23	6	—	5	10	2
Total	1241	517	133	406	132	53

Elytral patterns refer to those illustrated in fig. 1.

Table 3. Relative abundances of adult individuals of *Nicrophorus guttula* with different elytral colour patterns in western coastal USA and Canada.

Locality no.	No. of individuals	Locality	Elytral pattern					
			A	B	C	D	E	F
1	19	BC: Vernon	1	16	1	—	1	—
2	12	BC: Victoria	1	11	—	—	—	—
3	33	WA: Seattle	1	32	—	—	—	—
4	42	WA: Grand Coulee	1	41	—	—	—	—
5	53	WA: Ritzville	1	52	—	—	—	—
6	60	WA: Pulman	2	58	—	—	—	—
7	25	OR: Eugene	1	5	11	4	—	4
8	24	CA: Eureka	—	15	1	6	2	—
9	91	CA: San Francisco	—	7	6	17	1	60
10	23	CA: Carmel, Monterrey, Pacific Grove, Santa Cruz, Watsonville	—	—	—	—	1	22
11	21	CA: Anaheim, Claremont, Glendora, Los Angeles, Pasadena, Santa Monica, Yorba Linda	—	—	—	3	—	18
12	46	CA: Idyllwild, Palm Springs, Riverside	—	2	1	—	—	43
13	12	CA: San Clemente Island	—	—	—	1	—	11
14	18	CA: San Diego	—	—	—	1	—	17
	160	Other British Columbia localities	6	154	—	—	—	—
	87	Other Washington localities	1	84	—	1	—	1
	50	Other Oregon localities	1	35	6	3	—	5
	254	Other California localities	—	25	4	18	4	203

Elytral patterns refer to those illustrated in fig. 2. Sample numbers refer to those listed in fig 5. 'Other localities' are those indicated by dots in fig. 5 but not represented by pie diagrams.

Table 4. Relative abundance of adult individuals of *Nicrophorus guttula* with different elytral colour patterns throughout the known Nearctic range.

Province or State	Total no. of individuals	Elytral pattern					
		A	B	C	D	E	F
Alberta	19	3	15	1	—	—	—
British Columbia	191	8	181	1	—	1	—
Saskatchewan	4	—	4	—	—	—	—
Arizona	214	92	117	3	1	1	—
California	489	—	49	12	46	6	376
Colorado	100	46	54	—	—	—	—
Idaho	275	15	232	27	1	—	—
Montana	31	—	31	—	—	—	—
Nebraska	70	26	43	1	—	—	—
Nevada	124	1	91	6	9	11	6
New Mexico	272	162	110	—	—	—	—
North Dakota	1	1	—	—	—	—	—
Oregon	75	2	40	17	7	-	9
South Dakota	127	39	87	1	—	—	—
Utah	125	27	96	2	—	—	—
Washington	275	6	267	—	1	—	1
Wyoming	303	21	282	—	—	—	—
Total	2684	449	1699	71	54	19	392

Elytral patterns refer to those illustrated in fig. 2.

Table 5. Relative abundances of adult individuals of *Nicrophorus investigator* with different elytral colour patterns in western coastal USA and Canada.

Locality no.	No. of individuals	Locality	Elytral pattern					
			A	B	C	D	E	F
1	25	AK: Rampart	25	—	—	—	—	—
2	199	AK: Wrangel	—	80	—	46	3	70
3	73	AK: Prince of Wales Island	—	49	1	14	3	4
4	25	BC: Lions Bay, Squamish	25	—	—	—	—	—
5	44	BC: Hope, Vancouver	44	—	—	—	—	—
	46	Other Alaska localities	17	2	3	7	1	16
	139	Other British Columbia localities	139	—	—	—	—	1

Elytral patterns refer to those illustrated in fig. 3. Sample numbers refer to those listed in fig. 6. 'Other localities' are those indicated by dots in fig. 6 but not represented by pie diagrams.

Table 6. Relative abundance of adult individuals of *Nicrophorus investigator* with different elytral colour patterns throughout the known Nearctic range.

Province or State	Total no. of individuals	Elytral pattern					
		A	B	C	D	E	F
Alberta	58	58	—	—	—	—	—
British Columbia	209	208	—	—	—	—	1
Manitoba	18	18	—	—	—	—	—
Newfoundland	8	8	—	—	—	—	—
Northwest Territories	7	7	—	—	—	—	—
Ontario	4	4	—	—	—	—	—
Quebec	14	14	—	—	—	—	—
Saskatchewan	22	22	—	—	—	—	—
Yukon Territory	46	46	—	—	—	—	—
Alaska	341	42	131	4	67	7	90
Montana	40	40	—	—	—	—	—
Total	768	468	131	4	67	7	91

Elytral patterns refer to those illustrated in fig. 3.

Geographic variation in the colour of the basal article of the antennal club in *N. guttula* is also evident (table 7). All specimens examined which possess a black basal article of the antennal club were from California except for a single specimen from Oregon. Although an antennal club with a black basal article was almost entirely restricted to California, individuals with an antennal club with a red basal article were also found within the state (table 7). A histogram showing association of the colour of the basal article of the antennal club with elytral pattern shows 94% of group F, 70% of group E, 10% of group D and 5% of group C individuals have this article black (fig. 7). No group A or B individuals possess an antennal club with a black basal article.

Discussion

Previous taxonomic problems in some *Nicrophorus* species were the result of overemphasis of colour patterns as primary diagnostic characters. Problems of species recognition in *Nicrophorus* have now been largely resolved as a result of examination of other structural features and of correlation of these features with elytral colour

Table 7. Distribution and relative abundance of adult individuals of *Nicrophorus guttula* with different colour of basal article of antennal club in California and Oregon. Individuals from all other states and provinces examined possessed a red basal article.

Colour of basal article of antennal club	Locality	
	California	Oregon
Red	106 (21·6%)	74 (99·0%)
Black	383 (78·4%)	1 (1·0%)

variation (Anderson and Peck, in press). For *N. defodiens*, *N. guttula* and *N. investigator*, elytral colour variants are largely sympatric, although differing in local relative abundances. Variation is extensive but, because it is continuous and represented by numerous intermediates, and cannot be associated with other structural features which differ among the colour variants, is interpreted as a result of local selection and not of reproductive isolation.

Results presented here also confirm conspecificity of *N. hecate* and *N. guttula* (Peck and Miller, 1982; Anderson and Peck, in press), previously distinguished solely on the basis of differences in colour of the basal article of the antennal club (Arnett, 1944; Miller and Peck, 1979). Differences in colour of the article are shown here to be associated with variation in elytral colour (fig. 7) and are very likely a secondary result of factors leading to the decreased maculation and darker elytral coloration of California specimens. We have not found other structural dissimilarities, and conclude that the two forms are conspecific.

Even though conspecificity of the variable forms is now largely accepted, the recognition of some forms as subspecies (Hatch, 1927; 1957) needs to be reevaluated. In the past, the subspecific taxon has been variously and inconsistently applied, but now usually refers to allopatric populations whose members are structurally different

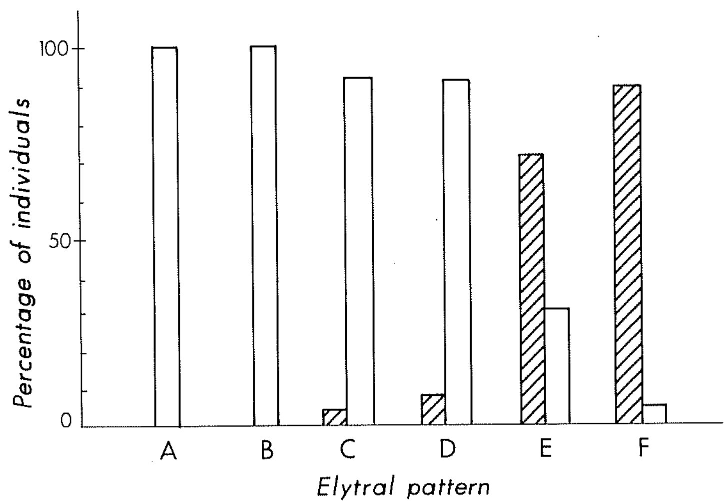

FIG. 7. Histogram showing association of colour of basal article of antennal club and elytral colour pattern in adult individuals of *Nicrophorus guttula*.
□, Red basal article; ▨, black basal article.

in some manner, yet if brought together are capable of interbreeding. We prefer, however, as do Whitehead (1972), Kavanaugh (1979) and others, to use subspecific names only to identify problematical patterns of structural variation in geographically isolated and disjunct populations where there is as yet no good evidence concerning reproductive isolation. Parapatric populations, although structurally distinct, in situations where there is good evidence of gene flow are not regarded as subspecies. Accordingly, our analysis of geographic variation in colour patterns in *N. defodiens, N. guttula* and *N. investigator* indicates that subspecific names should not be applied. We find that colour patterns, although generally geographically consistent are in part sympatric, continuous and represented by numerous intermediate forms. We also do not think it justified to recognize subspecies in *N. guttula* based on the antennal colour variation because, even though no intermediates are known, there is sympatry and a marked association of variation in this character with the variation in elytral colour.

In an attempt to justify his detailed enumeration and naming of intraspecific variants in various species of *Nicrophorus* Hatch (1940: 237) stated that 'The fundamental obligation of taxonomy is to describe accurately and precisely the variation presented. Many intraspecific variations are the materials out of which new species evolve in the course of geologic time.' Pursuit of an understanding of the diversity of life and its origins, however, must result in a classification and system of names which maximizes information content and stability, yet does so as simply as possible. Thus we concur with Arnett (1946) and Leech (1934, 1937) that while it is desirable to know the extent of variation, there is no need to name each colour variant individually as Hatch (1927, 1957) has done, especially since he (1940: 237) intended the variant names to be nomenclaturally equivalent to specific and subspecific names. Although we believe Hatch was justified in his ultimate intentions, it is not simply detailed naming of the variation which is necessary. More importantly, it is recognition of the patterns in the variation within species, and identification of their adaptive significance, which ultimately contributes to our knowledge of the origin of new species.

Unfortunately, for *Nicrophorus* species this is not at present possible. Although geographic patterns in the colour variation are given herein, any assessment of competing hypotheses concerning the adaptive significance of the elytral colour variation is at best preliminary. However, we do think that the general pattern of occurrence of the darker, less extensively maculated individuals at Pacific coastal localities, generally characterized by reduced levels of solar radiation (Hovanitz, 1940), and the limited and unpredictable nature of the carrion resource for which *Nicrophorus* species are competing, supports the notion of a thermoregulatory role. Under conditions of low solar radiation, darker individuals may predominate because they heat up and initiate foraging more rapidly than the lighter coloured, maculated individuals. Alternatively, the uniformity of the maculated colour pattern in the majority of species in the genus suggests a Müllerian mimicry complex, the contrasting black and orange pattern warning predators of distastefullness (Jones, 1932). Diurnal *Nicrophorus* are also known to mimic bumblebees (Milne and Milne, 1944; Lane and Rothschild, 1965) which might act to reinforce any mimicry complex based primarily on aposematism. Perhaps, as discussed for bumblebees by Stiles (1979) the observed colour patterns are an optimal result of the benefits accrued from both mimicry and thermoregulation. Clearly, detailed laboratory and especially field studies, such as those carried out on *Colias* butterflies (Watt, 1968, 1969; Roland, 1982) and *Adalia bipunctata* (Brakefield and Willmer, 1985, and references cited therein) are required to resolve the problem. We believe the undertaking of such studies to be a very promising area for future research on *Nicrophorus*.

Acknowledgements

We would like to thank G. R. Carmody, under whose guidance this study was first initiated, for his help and comments on an earlier draft of the manuscript; R. B. Madge and S. E. Miller for their continued assistance in our studies on the Silphidae; R. B. Aiken and J. Roland for their review of various drafts of the manuscript; and those curators who provided us with specimens upon which this study was largely based. J. Scott masterfully prepared the figures. Funding for all aspects of this study including field work was provided from a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to S. B. Peck.

References

ANDERSON, R. S., and PECK, S. B., in press, The Carrion Beetles of Canada and Alaska, Coleoptera: Silphidae, Agyrtidae. *The Insects and Arachnids of Canada.* Part 13. Agriculture Canada, Ottawa.

ANGEL, J. W., 1912, Two new North American species of *Necrophorus* (Coleop.), *Entomological News*, **23,** 307.

ARNETT, R. H., Jr, 1944, A revision of the Nearctic Silphini and Nicrophorini based upon the female genitalia (Coleoptera, Silphidae), *Journal of the New York Entomological Society*, **52,** 1–25.

—— 1946, Coleoptera notes 1: Silphidae, *Canadian Entomologist*, **78,** 131–134.

BRAKEFIELD, P. M., and WILLMER, P. G., 1985, The basis of thermal melanism in the ladybird *Adalia bipunctata*: Differences in reflectance and thermal properties between the morphs, *Heredity*, **54,** 9–14.

GOULET, H., and BAUM, B. R., 1981 Analysis of variation in the *Elaphrus americanus* complex of North America (Coleoptera: Carabidae), *Canadian Journal of Zoology*, **59,** 2253–2274.

HATCH, M. H., 1927, Studies on the Silphinae, *Journal of the New York Entomological Society*, **35,** 331–371.

—— 1940, Observations on Silphinae with a note on intraspecific variations and their designation, *Journal of the New York Entomological Society*, **48,** 233–244.

—— 1957, The beetles of the Pacific Northwest, Part II, Staphyliniformia, *University of Washington Publications in Biology*, **16,** 1–384.

HORN, G. H., 1880, Synopsis of the Silphidae of the United States with reference to the genera of other countries, *Transactions of the American Entomological Society*, **8,** 219–322, pls v–vii.

HOVANITZ, W., 1940, Parallel ecogenotypical colour variation in butterflies, *Ecology*, **22,** 259–284.

JONES, F. M., 1932, Insect coloration and the relative acceptability of insects to birds, *Transactions of the Entomological Society of London*, **80** (II), 345–386.

KAVANAUGH, D. H., 1979, Studies on the Nebriini (Coleoptera: Carabidae), III, New Nearctic *Nebria* species and subspecies, nomenclatorial notes, and lectotype designations, *Proceedings of the California Academy of Sciences*, **42,** 87–133.

LANE, C., and ROTHSCHILD, M., 1965, A case of Müllerian mimicry of sound, *Proceedings of the Royal Entomological Society of London, Series A*, **40**(10–12), 156–158 + 4 pls.

LEECH, H. B., 1934, The family history of *Nicrophorus conversator* Walker, *Proceedings of the British Columbia Entomological Society*, **31,** 36–40.

—— 1937, Notes on certain names in use in the *vespilloides*-group of *Nicrophorus* Fab. (Coleoptera: Silphidae), *Bulletin of the Brooklyn Entomological Society*, **32,** 156–159.

MILLER, S. E., and PECK, S. B., 1979, Fossil carrion beetles of Pleistocene California asphalt deposits, with a synopsis of Holocene California Silphidae, *Transactions of the San Diego Society of Natural History*, **19,** 85–106.

MILNE, L. J., and MILNE, M. J., 1944, Notes on the behaviour of burying beetles. (*Nicrophorus* spp.), *Journal of the New York Entomological Society*, **52,** 311–327.

PECK, S. B., and MILLER, S. E., 1982, Type designations and synonymies for North American Silphidae (Coleoptera), *Psyche*, **89,** 151–156.

ROLAND, J., 1982, Melanism and diel activity of alpine *Colias* (Lepidoptera: Pieridae), *Oecologia*, **53**, 214–221.

STILES, E. W., 1979, Evolution of colour patterns and pubescence characteristics in male bumblebees: automimicry vs thermoregulation, *Evolution*, **3**, 941–957.

WATT, W. B., 1968, Adaptive significance of pigment polymorphisms in *Colias* butterflies: I, Variation of melanin pigment in relation to thermoregulation, *Evolution*, **22**, 437–458.

—— 1969, Adaptive significance of pigment polymorphisms in *Colias* butterflies: II, Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*, *Proceedings of the National Academy of Sciences*, **63**, 767–774.

WHITEHEAD, D. R., 1972, Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini), *Quaestiones Entomologicae*, **8**, 131–348.

Appendix I

List of localities for Nicrophorus defodiens

CANADA. British Columbia. Aldergrove, Agassiz, Bowser, Cranbrook, Creston, Delta, Duncan, Genoa Bay, Golden, Hope, Jones Creek, Kamloops, Kikomun Creek Provincial Park, Kootenay Lake, Lilloet, Lions Bay, Masset, Merritt, Mission City, Nanaimo, New Westminster, Oliver, Powell River, Robson, Saanich, Salmon Arm, Skagit Valley, Squamish, Steelhead, Summerland, Terrace, Trail, Vancouver, Vernon, White Rock, Youbou.

USA. Alaska. Haines, Ketchikan, Kodiak Island, Wrangell. **California.** Lake Tahoe, Marin County, Quincy, Sagehen, San Mateo County. **Oregon.** Corvallis, Turner. **Washington.** Bremerton, Monroe, Ocean Park, Pullman, Seattle, Spokane.

Appendix 2

List of localities for Nicrophorus guttula

CANADA. British Columbia. Agassiz, Chilcotin, Comox, Creston, Foulder, Hatzic, Kamloops, Kikomun Creek Provincial Park, Langford, Marritt, Mission, Nanaimo, New Westminster, Oliver, Osoyoos, Peachland, Penticton, Princeton, Riondel, Saanich, Salmon Arm, Sardis, Sidney, Summerland, Trail, Vancouver, Vernon, Victoria, Wellington.

USA. California. Aguanga, Alameda County, Alpine, Alturas, Anaheim, Anza, Atwater, Bakersfield, Banning, Bass Lake, Benton, Berkeley, Borrego Springs, Calveras County, Carmel, Caspar, China Lake, Chino Canyon, Claremont, Colma, Davis, Eldorado County, El Toro, Escondido, Eureka Valley, Fairfax, Fairmont, Fontana, Fort Bidwell, Fort Bragg, Fresno, Glendora, Guatay, Half Moon Bay, Humboldt County, Huron, Idyllwild, Indio, Independendence, Kaweah, Kern County, Laguna Beach, La Mesa, Lebec, Lemon Cove, Lone Pine, Los Angeles, Lytle Creek, Madeline, Mariposa County, McFarland, Mendocino County, Milpitas, Mono County, Monterrey, Moss Beach, Nevada County, Onyx, Pacific Grove, Palmdale, Palm Springs, Palo Alto, Pasadena, Pescadero, Poway, Pinnacles National Monument, Riverside, San Bruno Mountains, San Clemente Island, San Diego, San Francisco, San Gregorio State Park, San Jacinto, San Joachin, San Lorenzo, San Mateo, San Simeon, Santa Barbara, Santa Cruz, Santa Monica, Santa Rosa, Sebastopol, Sequoia National Park, Shafter, Shasta County, Siskiyou County, Susanville, Trinity County, Tulare County, Victorville, Watsonville, Weldon, Wendel, White Pine County, Whitewater Canyon, Woodford, Yorba Linda, Yosemite National Park.

Oregon. Boardman, Camp Umatilla, Corvallis, Eugene, Forest Grove, Fort Klamath, Glenada, Goose Lake, Hermiston, Hood River, Manns Lake, Marrion, McDermitt, McMinnville, Portland, Sisters, Roseburg, Umatilla, Weston, Yam hill.

Washington. Almota, Blue Mountains, Cheney, Colton, Coulee City, Coupeville, Dayton, Everett, Friday Harbour, Grand Coulee, Granger, Kahlotus Lake, Kookskooskie, Nespelem, Olympia, Oroville, O'Sullivan Dam, Pasco, Palouse, Port Townsend, Pulman, Renton, Ritzville, Seattle. Spokane, Steptoe Butte, Vantage, Walla Walla, Wallula, Washtucna.

Appendix 3

List of localities for Nicrophorus investigator

CANADA. British Columbia. Agassiz, Aldergrove, Bella Coola, Castlegar, Chilcotin, Chilliwack, Courtenay, Cranbrook, Creston, Delta, Duncan, Genoa Bay, Golden, Hazelton, Hope, Kamloops, Kaslo, Kikomun Creek Provincial Park, Lilloet, Lions Bay, Masset, Merritt, New Westminster, Nicola, Peachland, Queen Charlotte City, Radium Hot Springs, Robson, Salmon Arm, Shushwap Lake, Smithers, Squamish, Terrace, Tlell, Trinity Valley, Vancouver, Victoria.

USA. Alaska. Anchorage, College, Homer, Juneau, Ketchikan, Kodiak Island, Palmer, Prince of Wales Island, Rampart, Sitka, Unalaska Island, Wrangell.