Trechus obtusus Erichson (Coleoptera: Carabidae), a European Ground Beetle, on the Pacific Coast of North America: Its Distribution, Introduction, and Spread

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Abstract.—The synanthropic European ground-beetle species Trechus obtusus Erichson was introduced to the West Coast of North America sometime in or prior to 1925 and presently occupies a partially disjunct range from southwestern British Columbia to the San Francisco Bay Area, California. A single primary introduction into the Seattle area is proposed through nursery stock originating in continental Europe. By 1950, the species had spread north to Vancouver and south to Portland, probably independent of human transport. Subsequent spread to disjunct regions in central and southern Oregon and the San Francisco Bay Area involved transport in nursery stock distributed from Portland. Recent range changes have involved minor spread from these secondary introduction centers. Records from undisturbed areas in California suggest marginal invasion of natural habitats; but presence of *T. obtusus* appears to have had no effect on the native carabid fauna to date.

Trechus obtusus Erichson is a morphologically varied and widespread ground beetle species in the Mediterranean region and in other parts of Europe, including the British Isles. Hatch (1933, 1949b) called attention to Trevor Kincaid's 1927 collection of members of this species in Seattle, Washington, the first published record for North America. Lindroth (1961) summarized the known distribution of the species, noting that it had been collected around port areas near Seattle and Vancouver and in southern Oregon (cf. Hatch, 1933). Erwin (1972) recorded its occurrence in the San Francisco Bay region.

In December 1978, we discovered and collected *Trechus obtusus* specimens in the cool, shaded canyon of Nicasio Creek, Marin County, California. A subsequent search through undetermined trechine material in the collection of the California Academy of Sciences (CAS) uncovered specimens from several other localities around the San Francisco Bay Area; and one of us (DHK) has recently collected additional specimens of T. obtusus in several other West Coast localities. An analysis of the distribution pattern apparent from these specimens indicated to us that this species is now more widespread than previously known.

In an effort to better establish its present distribution and the pattern of its introduction and spread and thereby address questions posed by Erwin (1972),

we obtained additional material on loan from the American Museum of Natural History (AMNH), J. K. Liebherr (JKLi) (University of California at Berkeley), J. R. Spence (JSpe) (University of Alberta), Oregon State University (OSUO), the University of Alberta, Strickland Museum (UASM), the University of British Columbia, Spencer Museum (UBC), and the United States National Museum of Natural History (USNM). The results of our study of available specimens of *Trechus obtusus* are presented here.

PRESENT DISTRIBUTION OF *TRECHUS OBTUSUS* IN NORTH AMERICA

Based on our study of 256 specimens and undoubted records from the literature, the present known distribution of T. obtusus in North America is as illustrated in Figure 1. Localities from which specimens have been collected and data for these specimens (including locality, date of collection, collection depository, and number of macropterous and brachypterous specimens) are provided in the Appendix.

PATTERN OF INTRODUCTION AND SPREAD

The earliest known record for *Trechus obtusus* in North America is based on one adult female collected on 12 May 1925 at North Creek (King County) Washington (OSUO; collector unknown), which is in the Bothell suburb of greater Seattle. Hatch (1933) credited Trevor Kincaid with collecting the first North American specimen on 26 May 1927 in Seattle itself. All subsequent records for *T. obtusus* through 1936 are restricted to the greater Seattle area (Fig. 2); and because there is no evidence to suggest its occurrence elsewhere in North America either before or during that period, the Seattle area appears to be the point of introduction to the continent.

In 1937, specimens were first collected at Cedar Mountain, some 20 miles southwest of Seattle. The first record of T. obtusus outside of King County is from a specimen collected in 1939 at Silver Lake (Snohomish County), Washington, 22 miles north of Seattle. The range of the species had extended to Everett (Snohomish County) by the mid-1940's and had spread south to Cowlitz County by the mid-1950's.

For at least 20 years after its original introduction (i.e., no later than 1925), *T. obtusus* was apparently confined to Washington, mainly to the area between Everett and Tacoma. But over only a seven-year subsequent period, this pattern changed profoundly. In September 1948 an adult was discovered in Vancouver, British Columbia; and the species became well-established in that area by the mid-1950's. Adults were found in Grants Pass (Josephine County), Oregon, in June 1951, and in Portland and vicinity (Multnomah County) in 1959. The first published record for California (Erwin, 1972) was based on a specimen collected in September 1971, at Niles Canyon (Alameda County). However, we recently examined a specimen (CAS) collected in San Francisco in April 1955; and by 1957, additional *T. obtusus* adults (CAS) had been collected in Mill Valley (Marin County), San Bruno Mountains (San Mateo County), and East Palo Alto (Santa Clara County), all San Francisco Bay Area localities.

The main features and full linear extent of the present distribution pattern of T. obtusus in North America were apparently established prior to 1960 (Fig. 3),

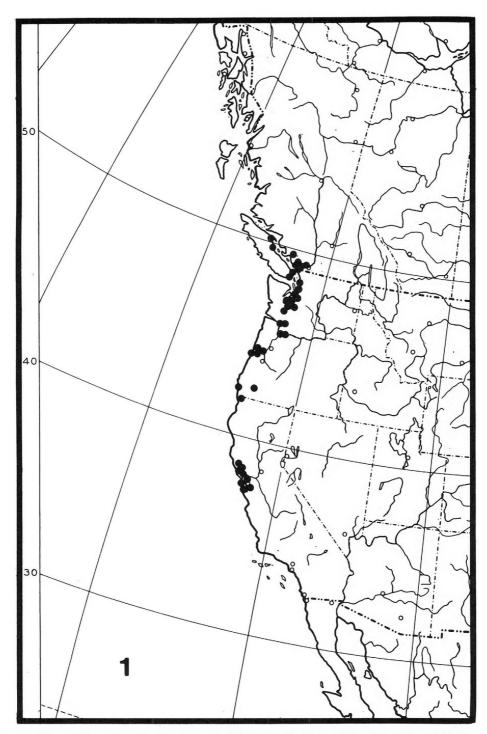
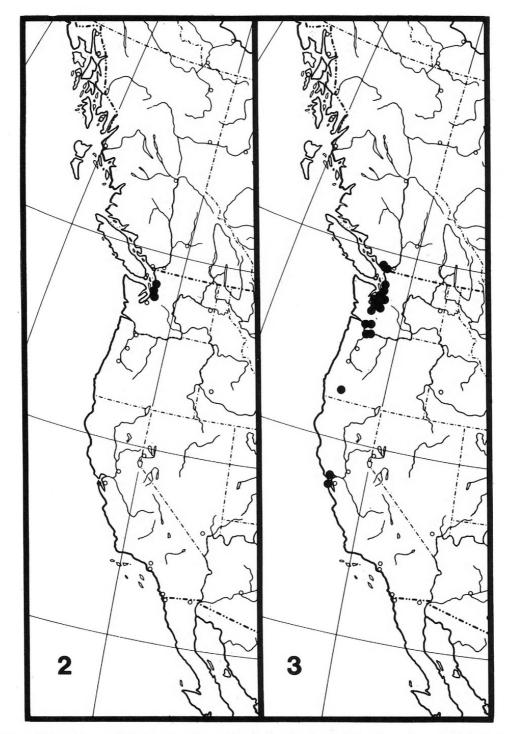


Figure 1. Map of the present known geographical distribution of *Trechus obtusus* Erichson in North America.

with disjunct occurrence in three main areas: (1) from Vancouver south through Seattle to Portland; (2) the Grants Pass area; and (3) the San Francisco Bay Area. The record provided by specimens in collections shows that subsequent spread of the species has been limited, with focal occurrence in several widely separate, intervening areas. Specimens were collected in the Corvallis area (Benton County) in 1967. Most recent significant additional records are from Alsea (1983), Lobster Valley (1972), Smith River (1978), and Winchester Bay (1978) (Benton County), Waldport (Lincoln County, 1971), and Gold Beach (Curry County, 1978), Oregon;



Figures 2–3. Maps of the known geographical distribution of *Trechus obtusus* Erichson in North America. 2. Records prior to 1945. 3. Records prior to 1960.

and from Jedediah Smith Redwoods State Park (Del Norte County, 1977), Nicasio Creek (Marin County, 1978), and Petaluma (1982) and Sebastopol (1983) (Sonoma County), California.

MODE OF INTRODUCTION

In his study of the faunal connections between Europe and North America, Lindroth (1957) discussed means by which Palaearctic species have been inadvertently introduced by man onto both the east and west coasts of North Americanamely, as stowaways in bulk rock and soil which was taken aboard commercial ships, mainly in the British Isles, as ballast for the trans-Atlantic crossing to North America. Several North American ports (particularly in Newfoundland) had rules which required that ballast be dumped on land so that the harbors themselves would not become filled over time. This practice was commonly employed from the 17th to 19th centuries on the East Coast of North America. After opening of the Panana Canal in 1914, ballast-laden ships could reach the West Coast relatively quickly as well. Lindroth (1957) cited one record (from the Portland area) which indicates that such ballast was at least occasionally deposited on shore during the second decade of the 20th century; but this practice was apparently abandoned after World War I and probably never employed around San Francisco Bay ports (Karl Kortum, National Maritime Museum, San Francisco (NMM), pers. comm.).

Although Lindroth (1957) believed that most introduced carabids in North America were ballast-transported, we do not think that *Trechus obtusus* arrived this way. Jeannel (1941) examined a small series of *T. obtusus* specimens, all of which were macropterous, that he had received from M. H. Hatch. He identified these, based on their full-sized hindwings, as subspecies *T. o. obtusoides* Jeannel (Hatch, 1949a; Jeannel, 1941) and suggested that the source area for the Seattle 'colony' was North Africa. However, at least some populations of *T. obtusus* in all parts of the present North American range of this species include both brachypterous and macropterous individuals (see Appendix). While the genetic basis for dimorphism in hindwing size has not yet been studied for *T. obtusus*, this suggests that the population (or populations) which served as the source for the North American colony(-ies) must also have included both brachypterous and macropterous individuals, or at least individuals heterozygous for genes determining this trait.

The problem of pin-pointing the source area for North American populations is much more difficult to solve than might be expected. Subspecific determinations for T. obtusus have been based mainly on hindwing size; and it has been routine for European workers to discuss the distributions of the different subspecies, hence different wing forms, separately (e.g., Jeannel, 1941). Lindroth (1974) noted that only the brachypterous form, subspecies T. o. obtusus Erichson, occurred in the British fauna. It therefore seems unlikely that the British Isles served as the source area for North American introduction; and because almost all of the trans-Atlantic ballast traffic described above originated in Britain (Lindroth, 1957), North American introduction was probably effected by some other means. Jeannel (1941) noted that only the macropterous form (subspecies *obtusoides*) occurs in North Africa. He also stated that this form also occurs in southwestern France, while the brachypterous form (subspecies *obtusus*) occurs in mountains and on Atlantic shores in France. We interpret this to mean that both forms co-exist at least in coastal parts of southwestern France. If so, then this region was a possible source area for the North American introduction. We suspect that other parts of mainland Europe also harbor dimorphic populations of T. obtusus and, therefore, could have served as source areas; but these are unknown to us at present. There is clearly no way to exclude the possibility of multiple introduction of this species into North America. However, a single primary introduction site, namely in the greater Seattle area (Washington), sometime prior to 1925 (but probably not much before that date), is sufficient to account for the present occurrence of this species

on the West Coast. In addition to dimorphism in wing size noted above, there is also considerable variation in size and body form among North American specimens. However, this variation is apparent in comparisons among individuals within populations to the same degree as between populations; and the full range in size and shape variation is represented throughout the North American range of the species. This suggests (1) a single European source area, one in which the *T. obtusus* population is highly varied; or (2) a single point of introduction into North America, at which point intrapopulational variation may have been increased through crossings among individuals from different European source areas; or (3) both a single source area and a single point of introduction. We prefer the last hypothesis as the least complex explanation for the observed pattern.

If *T. obtusus* members did not arrive in western North America in the ballast of ships, then how did they get here? A wide variety of human-assisted means can be envisioned, but one of these stands out as particularly likely: namely, transport in nursery stock. Hatch (1949a) and Lindroth (1957) suggested that this mode of introduction was particularly important in the Pacific Northwest; and Spence and Spence (in press) concluded that introduction and spread in nursery stock explained observed distribution patterns of some introduced species better than other plausible means. Trees and shrubs have been and continue to be shipped from Europe to North America with roots packed in large balls of loose soil wrapped in burlap. This would seem to be an ideal medium for long term survival of adult and larval carabids, perhaps also eggs deposited in the soil, in a medium which would permit long distance transport requiring weeks or even months. In fact, adult specimens of several different carabid species have been intercepted by quarantine officers in Vancouver (British Columbia) in nursery stock from Europe packed in just this manner (Spence and Spence, in press).

Hatch (1949a) studied the faunas of greenhouses in the Seattle area and found T. obtusus to be well-represented in this 'habitat'; and all the early records for this species in North America were markedly synanthropic. The habitat distribution of this species in Europe (Lindroth, 1957, 1961, 1974), on both open and shaded ground and frequently in association with man and his cultivation, would qualify members of this species as likely candidates for transport in soil associated with nursery stock. We therefore suggest that the initial introduction of T. obtusus into North America was through this means.

MEANS OF SPREAD IN NORTH AMERICA

The range of T. obtusus in time and space is illustrated in Figures 2, 3, and 1. Thus, the history of the spread of this species in North America can be divided into three periods. The first of these began no later than 1925, with the hypothesized initial introduction event in Seattle, and extended into the mid-1940's. During this period of 25 years or more, the range of T. obtusus expanded slowly north and south of the Seattle area (Fig. 2) in Washington in the lowland west of the Cascade Range. The second phase extends from the late 1940's or early 1950's to the middle of the latter decade. By 1948, T. obtusus was in Vancouver (British Columbia). It had reached Grants Pass (Oregon) by 1951 and the San Francisco Bay Area by 1955. This latter period, although relatively brief, was one of profound change in geographical distribution (Fig. 3). The third and final period began in the late 1950's and continues to the present. During this period, one significant extension to the range of T. obtusus has occurred. By 1967, it was in the Corvallis (Oregon) area and, shortly thereafter, at localities west of Corvallis. But other distributional extensions are minor expansions from centers established during the second period.

That the first period was one of slow, progressive spread north and south of the original introduction site suggests to us that range expansion was effected by natural dispersal of T. obtusus, unaided by human transport, into areas of suitable habitat. Such habitats were chiefly those provided by humans through their modification of the natural environment. While we cannot rule out the possibility that this spread was assisted by human transport, at least in part, such means do not appear to have been an essential factor in our view.

Following the period of slow spread, T. obtusus adults suddenly appeared in Grants Pass (1951), Portland (1959), and the San Francisco Bay Area (1955). What happened in the late 1940's or early 1950's to alter the range of T. obtusus in western North America so rapidly and profoundly? In an attempt to answer this question, we contacted the California Department of Food and Agriculture, Sacramento (CDFA) and nurserymen in the San Francisco Bay Area to learn more about the sources of nursery stock in California and the means and geography of transport and redistribution of this stock within the state.

Bill Callison (Pest Exclusion Unit, CDFA, pers. comm.) noted that there has been a steady, high-volume influx of nursery stock into California from the Pacific Northwest for many years. Apparently little of this stock originates in the Seattle area or in other parts of coastal Washington (Tim Talamantes, Dandylion Nursery, Petaluma, CA, pers. comm.); but numerous large nurseries in the Portland area have been the main suppliers of nursery stock for California and the entire West Coast for decades (Ben Heller, Heller Nursery Company, Morgan Hill, CA, pers. comm.). Of particular interest to us are commercial ventures such as California Garden Supply, which was active in the late 1940's (1947–1949), importing large quantities of stock directly from Portland to secondary distribution centers in the San Francisco Bay Area. Nurseries receiving and/or redistributing Portland stock through such suppliers during that period were located in Alameda, Marin, San Francisco, and San Mateo counties (Ben Heller, pers. comm.); and *Trechus obtusus* specimens have been collected in each of these areas (records from 1955 through the present; see Appendix).

It seems clear from the above discussion that the distribution network of the commercial nursery business during the late 1940's could have served as the means by which the range of T. obtusus was abruptly changed. Of course, other means could also be proposed; but none, we think, would account so well for the distributional and temporal data available. The fact that the Portland area, rather than Seattle or other areas in coastal Washington, was the major exporter of nursery stock on the West Coast may explain why a change in the tempo of T. obtusus range expansion occurred in the late 1940's. We proposed above that primary introduction from Europe was in nursery stock. It apparently took several decades for the range of this species to spread from Seattle to Portland, probably by dispersal of individuals under their own power. It was not until T. obtusus became established in the Portland area that an efficient human distribution system, the commercial nursery trade, was again available to assist with rapid, long-distance spread. Unfortunately, the earliest known records for the Portland

area are from 1959; but for reasons outlined above, we think that T. obtusus was represented there by 1950. This is supported by the Vancouver record of 1948 and the probability that spread from Seattle, north and south, was not human assisted.

Since the 1950's, spread of *T. obtusus* has been modest, confined chiefly to areas adjacent to centers occupied by the mid-1950's. Recent records (see Appendix) from Gold Beach (Oregon) and Jedediah Smith Redwoods State Park (California) probably represent dispersal from the Grants Pass area; and those from Vancouver Island represent expansion from mainland British Columbia or Washington. To what (if any) extent these range changes have been assisted by human transport is unclear; but local redistribution of nursery stock may well have been involved. Because *T. obtusus* has never been recorded from the area between Portland and Corvallis, in spite of significant collecting activity in that area in recent years, we suggest that records from the latter area represent a separate introduction, again probably from the Portland area, sometime prior to 1967 (date of first record from that area; see Appendix). Records from Alsea, Lobster Valley, Smith River, Waldport, and Winchester Bay may all represent dispersal from the Corvallis area or one or more additional independent secondary introductions.

PLACE IN THE NORTH AMERICAN ENVIRONMENT

At least four different European species of genus *Trechus* Clairville are now recorded as introduced into North America. Three of these, *T. discus* Fabricius (Lindroth, 1961), *T. rubens* Fabricius (Lindroth, 1961), and *T. quadristriatus* (Schrank) (Bousquet and Smetana, 1984) are established in the northeastern United States and/or southeastern Canada. *Trechus obtusus* is the fourth. There is little evidence to suggest that the three eastern species have been able to invade relatively undisturbed native habitats. For example, *T. rubens* members are "probably confined to cultivated ground" (Lindroth, 1961); and those of *T. quadristriatus* in North America have been collected "at the edges of onion fields and cornfields, in gardens, vacant fields, ... etc." (Bousquet and Smetana, 1984).

While most collections of *T. obtusus* members have also been from synanthropic situations, recent discoveries suggest that this species is expanding its range, at least in California, to include adjacent native habitats. For example, specimens collected at Nicasio Creek (Marin County) in 1978 were found under *Salix* leaf litter on sandy substrate on a secondary floodplain of the creek. This area, situated in a thickly wooded, deeply shaded canyon, has remained relatively undisturbed by human activity and contains an otherwise typical California woodland carabid fauna. No other open-land or commonly synanthropic species were represented there; and *T. obtusus* adults were found together with numerous specimens of the native species, *Trechus ovipennis* Motschulsky. Other records from northern California and westcentral and southwestern Oregon are also from rural areas; but these may be associated with roadsides, state parks, etc., which may have been slightly changed by human activity and cannot be classified as strictly native habitat.

There is no evidence to suggest that the presence of T. obtusus in North America has had any effect on the native fauna. As noted above, T. obtusus and T. ovipennis members were found co-existing at Nicasio Creek, with the latter represented in numbers typically encountered in that habitat during December. At this point,

we can only concur with findings of Spence and Spence (in press) for western Canada that the inadvertent introduction of T. obtusus and other European carabids to the West Coast of North America appears to represent an enrichment of the native fauna with no evident deleterious effects on the latter. It will no doubt be interesting to continue to monitor the geographical expansion of this species and the interactions of its members with the native fauna in future years.

ACKNOWLEDGMENTS

Lee H. Herman, Jr. (AMNH), J. K. Liebherr, J. R. Spence, G. L. Peters (OSUO), G. E. Ball (UASM), and S. G. Cannings (UBC) gave us access, through loans, to important specimens in their care. Karl Kortum (NMM) furnished useful information on the history of shipping practices on the West Coast, specifically in San Francisco Bay; and information and personal insights provided by Bill Callison (CDFA), Ben Heller, and Tim Talamantes gave us an understanding of past and present commerce in nursery stock in western North America. John Spence generously provided specimens, his own data and notes, and useful comments based on his field and laboratory experience with synanthropic carabid beetles in western Canada. We thank each of these individuals most heartily for their assistance during the preparation of this paper.

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APPENDIX. SELECTED DATA FROM TRECHUS OBTUSUS SPECIMENS EXAMINED¹

CANADA

BRITISH COLUMBIA: Boundary Bay (10 mi E of Ladner, 1 Jun. 58, UBC, 1L), Delta (11 Jun. 79, JSpe, 1L/3S), Galiano Island (Spanish Hills, 6 Jun. 81, UBC, 1L), Mission (24 May 79, JSpe, 4L/1S) (31 May 79, JSpe, 1L/1S), Squamish (10 Jun. 79, JSpe, 1L/1S), New Westminster (2 Jun. 58–

¹ For each entry, format for data is as follows: locality (qualifier, date of collection, collection depository, number of long-winged (macropterous) specimens (L)/ number of short-winged (brachypterous) specimens (S)).

Lindroth (1961), specimens not seen), Vancouver (Second Beach, Sep. 48 – Lindroth (1961), specimens not seen) (20 May 51 – Lindroth (1961), specimens not seen) (18 Sep. 51 – Lindroth (1961); specimens not seen) (Spanish Banks, 19 Jul. 52, UBC, 1S) (University of B.C. Campus, 15 Aug. 59, UBC, 1L/ 5S) (8 Aug. 62, UBC, 1S) (9 Aug. 62, UBC, 1L) (University of B.C. Campus, 15 Aug. 62, UBC, 1L) (University of B.C. Campus, 15 Aug. 62, UBC, 1L) (University of B.C. Campus, 15 Aug. 62, UBC, 1L) (University of B.C. Campus, Sep. 65, UBC, 1L) (28 Sep. 65, UBC, 1L) (17 Oct. 65, CAS, 1S) (Wreck Beach, 19 Jul. 80, CAS, 1S), Whistler (10 Jun. 79, JSpe, 1L), Vancouver Island (Campbell River, 21 May 79, JSpe, 3L/1S) (Courtenay, 21 May 79, JSpe, 5L) (Victoria, 15 May 79, JSpe, 9L/7S).

UNITED STATES OF AMERICA

CALIFORNIA: Alameda County, Berkeley (Woolsey Canyon, 21 Dec. 83, CAS, 1L), Niles Canyon (12 Sep. 71, USNM, 1L), El Cerrito (6 May 79, CAS, 2S), Wildcat Canyon Regional Park (3 Jun. 79, JKLi, 4L) (10 Nov. 79, JKLi, 1L); Del Norte County, Jedediah Smith Redwoods State Park (22 Sep. 77, CAS, 1L); Marin County, Lagunitas Creek (at Tocaloma, 8 Jul. 79, JKLi, 5L), Laurel Canyon (1 mile W of Nicasio Reservoir, 8 Jul. 79, JKLi, 3L), Mill Valley (25 May 57, CAS, 2S), Nicasio Creek (0.5 miles W of Nicasio Reservoir, 12 Dec. 78, CAS/USNM, 11L) (0.5 miles W of Nicasio Reservoir, 28 Dec. 78, CAS, 1L); San Francisco County, San Francisco (8 Apr. 55, CAS, 1L); San Mateo County, Crystal Springs Reservoir (2 Jul. 81, CAS, 1L), Junipero Serra Park (28 Jun. 64, CAS, 1L), San Bruno Mountains (30 May 57, CAS, 1L), South San Francisco (25 Sep. 77, CAS, 1S); Santa Clara County, East Palo Alto (17 May 57, CAS, 1L); Sonoma County, Petaluma (3.5 miles NW, Jun. 82, CAS, 1L), Sebastopol (4 May 83, CAS, 1S) (10 Aug. 83, CAS, 2L/2S). OREGON: Benton County, Alsea (3 miles SE, 15 May 83, CAS, 1L), Corvallis (7 Oct. 67, OSUO, 1L), Lobster Valley (15 miles SW of Alsea, 28 Jun. 72, OSUO, 1L); Curry County, Gold Beach (9 miles S, 1978, AMNH, 1L/1S); Douglas County, Smith River (5.5 miles NE of Reedsport, 29 Jun. 78, AMNH, 1L/1S) (27.5 miles NE of Reedsport, 29 Jun. 78, AMNH, 2L), Winchester Bay (28 Jun. 78, AMNH, 2L); Josephine County, Grants Pass (2 Jun. 51, OSUO, 3L) (31 Aug. 68, USNM, 1L); Lincoln County, Waldport (2.5 miles N, 1 Jun. 71, CAS, 1S); Multnomah County, Portland (27th & W Front, 16 Jul. 59, OSUO, 2L), Rooster Rock State Park (20 May 59, OSUO, 4L). WASHINGTON: Cowlitz County, Lake Merwin (3 miles S of Yale, 15 Sep. 57, OSUO, 1L), Lewis and Clark State Park (11 Sep. 56, USNM, 1L), Lewis River (4 miles E of Woodland, 15 Sep. 57, OSUO, 1L); King County, Bothell (1 Jul. 41, OSUO, 1S) (4 Aug. 44, OSUO, 2L) (15 Jun. 49, CAS, 1L/5S), Cedar Mountain (18 May 37, OSUO, 1L) (12 May 39, OSUO, 1S) (7 Jul. 39, OSUO, 1L) (22 May 41, OSUO, 1L) (29 May 45, OSUO, 3L) (16 May 46, OSUO, 1L/2S), North Creek (12 May 25, OSUO, 1L), Renton (Lake McDonald, May 39, OSUO, 1S) (Cedar River, 22 May 41, OSUO, 1L) (Cedar River, 16 May 46, OSUO, 1S), Seattle (26 May 27, OSUO, 1L) (8 Oct. 27, OSUO, 1L) (1 Mar. 28, CAS, 1S) (17 May 28, OSUO, 2L) (21 Jun. 29, OSUO, 2L) (25 Apr. 31, OSUO, 1L) (30 Apr. 31, OSUO, 1S) (10 May 31, OSUO, 1L) (23 May 31, OSUO, 18L) (24 May 31, OSUO, 3L/2S) (2 Apr. 32, OSUO, 1S) (2 Aug. 32, OSUO, 1L) (10 Jun. 33, OSUO, 1L) (11 Sep. 33, OSUO, 1L) (28 Apr. 34, OSUO, 1L/1S) (17 May 34, OSUO, 3L/2S) (9 Jun. 34, OSUO, 1L) (14 Sep. 34, OSUO, 1L) (10 Apr. 35, OSUO, 1S) (14 Apr. 35, OSUO, 1L) (11 May 35, OSUO, 1S) (19 May 35, OSUO, 1L) (11 Apr. 36, OSUO, 1L) (Univ. of Washington Campus, 22 Apr. 37, OSUO, 1S) (Univ. of Washington Campus, 27 May 37, OSUO, 1L) (Univ. of Washington Campus, 22 Jun. 37, OSUO, 1L) (Univ. of Washington Campus, 7 Apr. 38, OSUO, 1L) (20 May 38, OSUO, 1L) (8 Jun. 38, OSUO, 2L/3S) (2 Aug. 38, OSUO, 2L) (7 Sep. 38, OSUO, 1S) (22 Jun. 39, OSUO, 1S) (Univ. of Washington Campus, 26 Jun. 39, OSUO, 1L) (Univ. of Washington Campus, 15 Apr. 41, OSUO, 1S) (30 Apr. 41, OSUO, 1L) (Univ. of Washington Campus, 27 May 41, OSUO, 2S) (3 Aug. 41, OSUO, 3S) (2 May 42, OSUO, 1L) (Harbor Island, Apr. 44, OSUO, 1S) (Saxe Greenhouse, 5 Jan. 46, OSUO, 1L) (2 Apr. 46, OSUO, 1L) (Carkeek Park, 18 Feb. 48, OSUO, 1S) (Univ. of Washington Campus, 8 Apr. 48, OSUO, 1L) (Univ. of Washington Campus, 13 Apr. 49, OSUO, 2S) (22 May 49, OSUO, 1L/3S) (Saxe Greenhouse, 28 May 49, OSUO, 1L) (Univ. of Washington Campus, 14 Sep. 56, OSUO, 1L) (Innis Arden, 29 Mar. 59, AMNH, 1L); Mason County, Hartstine Island (30 Aug. 57, OSUO, 1L); Pierce County, La Grande (Pack Forest, 7 Jun. 60, OSUO, 1L), North Fort Lewis (26 Jun. 44, CAS, 4L) (15 Jul. 44, CAS, 4L/1S), Puyallup (30 Jun. 53, OSUO, 1L), Tacoma (29 Jun. 41, OSUO, 4L/1S) (29 May 47, OSUO, 1L); Snohomish County, Everett (Staiff Greenhouse, 26 Aug. 46, OSUO, 1S), Silver Lake (20 Jul. 39, OSUO, 1S); Thurston County, Nisqually (10 Jun. 57, OSUO, 1S).



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