Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae, Bembidiini)

TERRY L. ERWIN and DAVID H. KAVANAUGH

Ent. scand.

Erwin, T. L. & Kavanaugh, D. H.: Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae, Bembidiini).
Ent. scand. Suppl. 15: 33–72. Lund, Sweden 1 July 1981. ISSN 0105-3574.

The genus *Bembidion,* with its hundreds of described species whose cumulative ranges nearly cover terrestrial Earth, has fascinated biogeographers for decades because of its potential as an indicator of past geographic and climatic events. Unfortunately, no previous taxonomists attempted to work out systematics problems for the genus on a worldwide basis. Consequently, biogeographers have not adequately exploited the potential of the genus. The purpose of this paper, the first in a planned series which will meet the needs of biogeographers and other natural historians, provides a monographic treatment of two species groups of *Bembidion* of western North America. New study methods are adapted to this purpose and old methods are modified where necessary in order to fully treat the genus in a reasonable amount of time. Data are gathered and organized in such a way that a base is established so that a comprehensive phylogenetic and zoogeographic study of the genus can be made in the future. — Names are provided for four undescribed speieces [*B. carlhi,* type locality—Steamboat Creek (at Steamboat Falls, 410 m), Douglas County, Oregon; *B. lindrothellus,* type locality—Little Boulder Creek (Haines Highway Mile 31.5), Alaska; *B. lummi,* type locality—Friday Harbor, San Juan Island, San Juan County, Washington; and *B. chintimini,* type locality—Mary's Peak (8 miles W of Philomath, 1220 m), Benton County, Oregon]. Two Casey names, *B. brumale* and *B. vacivum,* are synonymized with *B. castum*. Ten species in two groups are fully discussed. Their cumulative range extends from southern Alaska to southern California and from the Pacific Coast east to Colorado; most species are fairly widespread within that range. A dot map is provided to illustrate the range of each taxon. A phylogenetic analysis based on 26 characters and their respective states demonstrates relationships among *erasum* group taxa, thereby providing grounds for recognition of four species subgroups. A cladogram is provided to illustrate relationships. Based on cladistic relationships and present ranges, a zoogeographic analysis suggests the following: The *erasum* species group arose in western North America no earlier than Miocene time, in association with general cooling trends and contemporary orogenic events, and is presently restricted to that region. Four included subgroups evolved sequentially, the first (the *osculans* subgroup) perhaps as early as Late Miocene, the last (the *erasum* subgroup) during Illinoian time. All extant species appear to have differentiated in Pleistocene or post-glacial time; and present distributions demonstrate a high incidence of sympatry which reflects widespread past dispersal of species and species groups.

T. L. Erwin, Department of Entomology #169, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.
D. H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

Introduction

The large, worldwide genus *Bembidion* Latreille (1802:82) received extensive taxonomic treatment from Hayward (1897), Lindroth (1939, 1945, 1962, 1963a), and Netolitzky (1935, 1942, 1943). Other authors such as Andrewes (1935), Erwin (MS), Erwin & Kavanaugh (1980), Jeannel (1941), and Nègre (unpublished manuscripts) dealt with smaller groups or with species in certain geographic regions. Despite this attention, *Bembidion* remains a genus of hundreds of species, tens of species groups, and many subgenera, among which relationships are poorly understood. Despite the group's potential as a zoogeographic treasure trove (see Darlington 1965; Erwin 1979; Lindroth 1957, 1963b, 1970, 1979), species distributions are poorly known. This is mainly because those who pioneered the taxonomy of *Bembidion* based their studies, by necessity, on small numbers of individuals per species. These pioneering efforts, however, provide the foundation from which we begin our treatment of the genus, group by group, for the fauna of the World. We intend to make our coverage as comprehensive as possible, utilizing all material available; and we will issue supplementary reports for groups already revised as new materials become available.

The study, as a whole, is dedicated to our friend, the late Carl H. Lindroth, whose favorite beetles were the *Bembidion*, and whose stimulus to carabidology and to us in particular is as strong in the works and memories he left behind as it was during his lifetime. Concerning *Bembidion*, Lindroth (1963a) wrote that "A satisfactory 'natural' division of genus *Bembidion* into groups or subgenera should be based ... upon the armature of the internal sac of penis ... Any lasting rearrangement of the genus implies ... a study of the World fauna." We adopt this as our *modus operandi*.

Methods.—Our methods are generally the same as we have outlined before (Erwin 1970, 1974; Kavanaugh 1978, 1979c). We intend to select groups for study based on need for taxonomic treatment, availability of material, or other criteria, but not on phylogenetic sequence. The latter cannot be determined until the species groups are better defined and understood.

We will alternate leading authorship group by group, the leader on a particular group being responsible for initiating the study, for gathering, preparing, and sorting the material, for initial dissections and drawings, and for preliminary and subsequent manuscript drafts. The junior author of each paper will provide review of sorted and dissected material, provide dissections and drawings where necessary, and review preliminary and subsequent manuscript drafts. Proper genitalic dissections and preparations require special techniques and expertise; and in order to make use of our respective previous experience in a most efficient manner, Erwin will dissect, prepare, and illustrate male genitalia and Kavanaugh will do likewise for female structures. Although division of tasks will be flexible, that outlined above will be the norm.

Systematic treatments will be numbered as they appear simply for convenience. Other contributions to our *Bembidion* project not revisionary in scope, such as Erwin & Kavanaugh (1980), will not be numbered, but will constitute part of the overall data base upon which we will make our final phylogenetic and zoogeographic statements. Revisional supplements will be assigned the number of the part supplemented plus a letter suffix. The purpose of such a numbering system is to allow the sum of reports to be organized and indexed as a single generic monograph. It is also for this reason that we assign each species a three-digit number code. Later, each species group will be assigned a code number that, when combined with the species number, will provide easy reference to the entire system and classification.

It will be some time yet before we are able to offer comprehensive keys to *Bembidion* species and species groups. We therefore will periodically provide modifications to existing keys where necessary so that collectors of these small but interesting beetles may keep up their determinations. For North America, Lindroth's key to species groups (Lindroth, 1963a:208–211) provides a beginning with which amateurs and professionals alike can sort their material to a workable level.

In order to provide reasonable usefulness, balance, and stability for an interim classification, we follow Lindroth's (1961, 1963a, 1974a) system of informal species groups and their names where possible. However, we deal with the World fauna whereas Lindroth dealt with regional groups and named these groups after a regional species. This often resulted in a Holarctic group having one name in the Palaearctic and another in the Nearctic Region (e.g. *biguttatum* group in Europe and *güttula* group in North America). Consequently, we use for the name of each species group that of the most commonly collected species, regardless of range, or in the case of groups with many common species, we adopt the name of the oldest described species. In most cases, this convention results in names currently in use; it also rids the nomenclature of synonyms.

Size ranges are presented (in millimeters) for several measures for each species. An electronic measuring device (Erwin 1978) was used as follows. Two measures of body length were recorded: ABL, apparent total body length (Kavanaugh 1979c), measured along midline from most anterior to most posterior point, that is, from apex of mandible to apex of elytron; and SBL, standardized body length (Kavanaugh 1979—modified from Ball 1972), the sum of fixed measurements along midline of head—from apical margin of clypeus to posterior margin of compound eye (left side)—pronotum—from apical to basal margin—and elytron—from apex of scutellum to apex of longer elytron. Size range was determined by visually selecting the largest and smallest specimens in the samples studied. ABL is a useful measure for field recognition and museum sorting; but SBL is essential for detailed comparative work. Other measures used include: total width, TW, viewed from dorsal aspect, measured at widest part of elytra when the latter are properly positioned and approximated medially; total depth, TD, viewed from left lateral aspect, measured from dorsum of elytra to venter of left hind coxa; and the ratio WPB/EL, length of longest elytron (see above) divided by width of pronotum across base.

In the study and identification of *Bembidion* adults, it is necessary to carefully and correctly observe dorsal microsculpture. This can be accomplished only with clean specimens. We use either a fine brush with a solvent, such as dilute ammonia, or an ultrasonic cleaner with dilute detergent solution. The specimen is then painted with glue (Corwin et al. 1979) which is allowed to dry for approximately five minutes. This glue layer is then easily peeled off in one piece, leaving the specimen absolutely free of debris. Whatever method is adopted, a specimen must be carefully cleaned before study with SEM or light microscopy.

Terms used in reference to form and structure of the pronotum and the elytra are illustrated in Fig. 2. Our use of terms referring to sclerites of the internal sac of the aedeagus (Fig. 9, elaborated in Tab. 1) generally follows that of Lindroth (1940) except where modifications are necessary. We attempt to homologize sclerites (e.g. the "CH" series) and maintain a consistent labelling scheme, whereas Lindroth apparently, at least in part, labelled for convenience. Terms used for structures in the female reproductive system are illustrated in Fig. 13.

Scenarios presented under the heading "Natural History" in species descriptions are the result of analyses of our unpublished field notes and specimen label data, as well as determination of the maturity of specimens (e.g. teneralness). We intend to integrate all available data on habitat range for *Bembidion* taxa, classifying these data with reference to both macrohabitat (i.e. gross altitudinal and/or life zone ranges) and microhabitat (i.e. the specific range of local conditions preferred by individuals within the macrohabitat range). This classification is especially useful in the present revision, in which we deal with species restricted mainly to montane areas. Our classification of macrohabitats follows that of Merriam (1892, 1894), as discussed by Kavanaugh (1978, 1979a, 1979b).

Data presented for specimens examined in this study include the following: locality (country, state or province, county, and particular locality—all arranged alphabetically—and elevation in meters), month(s) of collection, number of

Table 1. List of Structures of Male Aedeagus (after Lindroth 1940, in part)

Code	German	English
A	---	Apex of median lobe
BW	Borstenwulst	Elevated setiferous field
Bg	Basalteil CH_3	Basal piece of CH3
CH	Chitinstäbchen	Chitinous rod
Dk	mit Dörnern dicht bekleidetes Kissen	Elevated spinos callous
Dz	Chitinzähnchen	Chitinous dagger-like teeth
Fa	Längsfalte	Elongate chitinized fold
G	Geissel	Flagellum
Ge	Chitingerüst	Chitinous framework
H	Haarbesatz	Setiferous patch
Hf	Haarfeld	Setiferous field
Hg	Haargürtel	Setiferous belt
Hk	Kranz von Feinen Haaren	Setiferous crown
Hr	longitudinale Haarrinne	Setiferous rim
Lö	löffelformige Erweiterung	Spoon-like platelet
Mb	Membrane(-n)	Membrane(-s)
O	Ostium	Ostium
Of	---	Ostium flag
Pl	beilförmige Platte	Hatchet-like platelet
Rud	Chitinkörperchen	Small chitinous body
S	Schlauch	Hose-like sclerite
Sp	doppelte Spitze	Doubled tip
St	Stilett	Chinitous tooth

specimens seen from each locality, and depository(-ies). No attempt was made to add elevation data where same are not already noted on the specimen label(s), but all data provided were converted to their metric equivalents as necessary. Specimens which we have examined and which are from localities which we judge to be outside the geographical, altitudinal, or habitat ranges of their respective taxa are listed as "Doubtful record". Each such records is plotted on the distribution map for its taxon as a "?". Locality records from the literature which we have been unable to verify through examination of specimens are listed as "Additional Literature Records".

Acknowledgments.—We gratefully acknowledge the assistance of those curators and other individuals listed below who generously provided material on loan from collections in their care. Specimens from the following collections were examined: California Academy of Sciences, San Francisco (CAS), D. H. Kavanaugh; Canadian National Collection, Ottawa (CNC), A. Smetana; David H. Kavanaugh Collection, San Francisco (DHKa); Museum Of Comparative Zoology, Harvard University, Cambridge (MCZ), A. F. Newton, Jr. and M. Thayer; Oregon State University, Corvallis (OSUO), G. Peters; Strickland Museum, University of Alberta, Edmonton (UASM), G. E. Ball; Spencer Entomological Museum, University of British Columbia, Vancouver (UBC), S. G. Canning; University of California, Davis (UCD), R. O. Schuster; and United States National Museum of Natural History, Washington (USNM), T. L. Erwin.

Gloria Gordon Zimmer provided the habitus drawing of *B. carlhi*. All other illustrations, except those of female genitalic structures, are the work of George Venable. Scanning electron micrographs were obtained through the help of Susann Braden, Walter Brown, and Mary Jacques Mann. Linda Lea Sims recorded measurements, organized data for the reference list, and provided critical reading of manuscript drafts. Gay C. Hunter assisted with the transfer and handling of specimens; and Noreen Connell typed portions of manuscript drafts and tables. Joaquim Adis translated Carl Lindroth's (1940) table of terms for internal sac sclerites from German, and George Steyskal provided nomenclatural advice. We heartily thank each of these individuals for their competent and willing help.

Taxonomy

The *carlhi* group

Individuals of the single known member of the *carlhi* group are of medium size (ABL = 3.59—3.94 mm) for the genus. This species is intermediate in several characteristics between the *erasum* group and *guttula* group and shares features with the *vile* and *transparens* groups. Those character states shared with *erasum* group members include: 1) reduced number of visible elytral interneurs; 2) lateral margins of pronotum sinuate basally; 3) antennae short, antennomeres broad; and 4) configuration of armature of internal sac of aedeagus. Character states shared with *guttula* group members include: 1) elytral seta Ed6 associated with recurrent groove; 2) elytra iridescent; 3) elytra with pale spots; 4) interneurs 1–4 continuous beyond seta Ed5; 5) pronotum with basal margin sinuate; and 6) configuration and sclerotization of bursa copulatrix, spermatheca, and associated structures. The configuration of the male internal sac is nearly identical to that of *vile* group members; but these beetles, as well as members of the *transparens* group, have complex frontal furrows not found in *carlhi* group members. Thus *B. carlhi* cannot be assigned to either of these groups. Character states unique to *carlhi* group members include: 1) pronotal silhouette; and 2) each elytron with two pale spots. Based on these states, we conclude that *B. carlhi* cannot be placed in the *guttula* or *erasum* group, and that its unique combination of characters require that it be regarded as a group of its own. We predict that subsequent detailed study of members of the *vile, transparens, guttula,* and *championi* groups will permit a more complete analysis from which the intergroup relationships of *B. carlhi* can be ascertained.

Since only one species is included in this group, other character states, natural history, and geographical distribution and variation are described below in the species treatment.

Lindroth's key to species groups for North America (Lindroth 1963a: 208–211) can be modified as follows to include this new species group:

20(19). Upper surface of elytron microsculptured; elytra each with only preapical pale spot .... (p. 258) *guttula* group

— Upper surface of elytron quite smooth, microsculpture effaced; elytra each with two pale spots .... 20a.

20a(20). Pronotum highly convex, with lateral margins markedly arcuate; head with frontal furrows convergent anteriorly .... (key p. 17) *dilaticolle* group

— Pronotum subconvex, cordiform; head with frontal furrows parallel throughout their length .... *carlhi* group

Checklist of the *carlhi* group taxa

The **carlhi** group
001. *Bembidion carlhi* n.sp.

001. **Bembidion carlhi** n.sp.

Figs. 1, 4a, 5a, 6a, 7a–b, 8a, 10a, 11a, 12a, 13a, 15a, 16a, 18.

Type locality: U.S.A., Oregon: Douglas County, Steamboat Falls.

Type Material: Holotype ♀, U.S.A., Oregon, Douglas County, Steamboat Creek at Steamboat Falls, 410 m, 11 July 1971, Stop 71–260. Leg. D. H. Kavanaugh; Type No. 13657. in coll. CAS. — *Paratypes:* CALIFORNIA: Calaveras County, Calaveras Big Trees State Park [July] (6; CAS); Trinity County, Route 299 (small creek W of French Creek) [June] (2; CAS); Tuolumne County, Gardners [July] (21; CAS). OREGON: Douglas County, Steamboat Creek (at Steamboat Falls [410 m]) (1; DHKa).

Diagnostic features: Members of this species may be recognized immediately by the following combination of character states: elytra markedly iridescent, each with two distinct pale spots; pronotal silhouette as in Fig. 3.

Derivation of taxon name: We take great pleasure in naming this unique and colorful species after Carl H. Lindroth in recognition of his tremendous contributions towards a better understanding of *Bembidion*, carabidology, and experimental zoogeography. The name *carlhi* is a genitive patronym using Lindroth's first name and middle initial.

Description

Size.—ABL = 3.59–3.94 mm; SBL = 3.44–3.74 mm; TW = 1.58–1.81 mm; TD = 0.83–0.84 mm.

Color and luster.—Piceous, elytron with pale longitudinal humeral and transverse postmedial lunules; epipleura, legs, antennal scape, and basal palpomeres testaceous; antennal flagellum and apical palpomeres piceous. Dorsal and ventral surfaces shiny, venter and elytra markedly iridescent.

Form.—Short, moderately broad, subconvex. Head moderately broad but narrower than pronotum; eyes large, rounded, not quite hemispheric; antennae short, not extended to seta Eo4 on elytra, antennomeres broad, median tooth of mentum acute. Pronotum (Fig. 5a) moderately wide, 1/3 wider than elytron, transverse, with markedly lobed base, lateral margin obliquely straight anterior to obtuse, denticulate posterior angle, anterior angle rounded and not produced. Elytra (Fig. 6a) with silhouette subrectangular basally, humeri squared, lateral

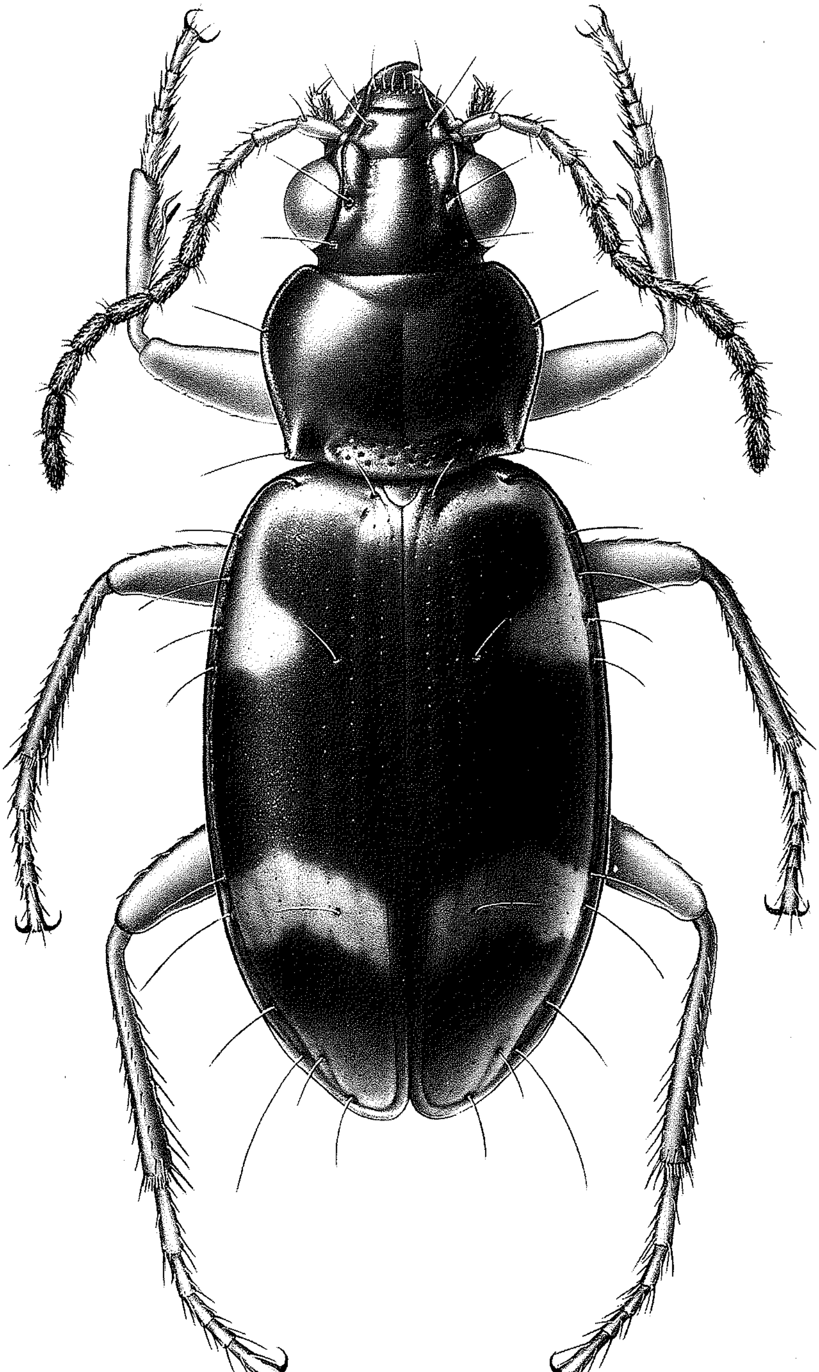
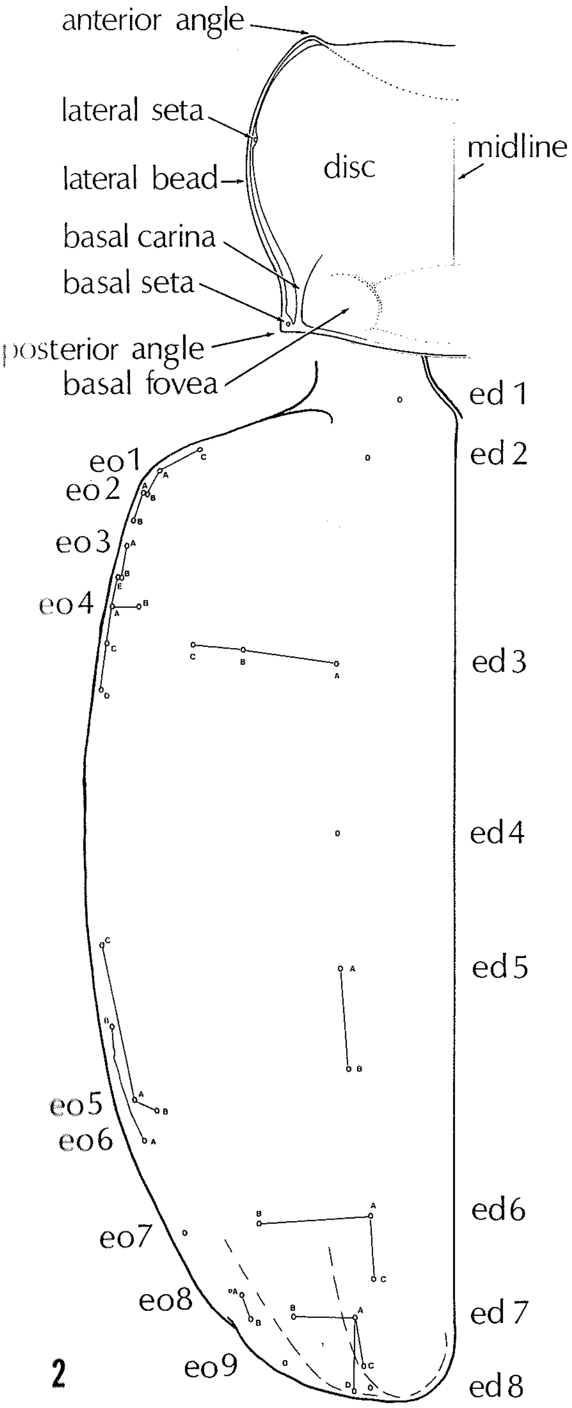


Fig. 1. *Bembidion carlhi* n.sp. male, habitus (Tuolumne County, California), ABL = 3.6 mm.



2

Fig. 2. Pronotum and elytron, diagramatic, dorsal aspect, with reference points used in text and chaetotaxy code.

margins slightly divergent at middle, intervals nearly flat. Foreleg of male with normally dilated basitarsus and tarsomere 2, the former slightly narrower than tibial apex.

Structure.—Microsculpture (Fig. 7a, b) effaced on frons and pronotum, comprised of large transverse meshes on vertex of head, and of finely engraved transverse lines on elytra. *Elytra* each with three (± 4) clearly traceable interneurs, 1 (± 2) extended to apex, interneurs punctulate, punctulae smaller laterally and apically. *Wings* fully developed. *Male genitalia* as in Fig. 10a; median lobe small, lightly pigmented and sclerotized, apex narrowly rounded, shaft uniformly tubular, basal constriction not well developed, ventral margin angulate near apex; internal sac with BW broad, nearly transverse, CH1 small, diagonally oriented, remote from BW, CH2 – CH5 well developed, OF very broad. Female genitalia as in Figs. 11a, 12a, 13a, 15a, and 16a; eighth tergum narrow, pigmentation pattern as in Fig. 11a; eighth sternum (Fig. 12a) narrow, with large, oval apical and small midmedial pale area on each hemisternite; coxostylus (Fig. 13a) with gonocoxite long and slender, gonostylus distinct, long and slender with ventromedial margin smooth; bursa copulatrix (Figs. 15a, 16a) with dorsal lobe distinct, large and ovoid, slightly deflected left, without dorsal sclerite, ventral lobe large, broad, V-shaped with ductal lobe present on anterodorsal surface in midline capped by a cylindrical sclerite at base of spermathecal duct; spermathecal duct with two full coils and two half coils (reversed), insertion on apex of ductal lobe; spermatheca short, vermiform, narrowed and bent apically; spermathecal gland long, slender, moderately convoluted, inserted on spermatheca through a long, tubular, slightly arcuate reservoir.

Natural history.—Members of this species are found along streams in stony areas at medium elevations in the Canadian Zone. They have been collected with members of the *erasum* group in the Sierra Nevada. Teneral adults from various localities collected in July and August suggest that overwintering takes place as an adult and that breeding occurs in Spring. The fully-developed flight wings indicate potential for dispersion through the air.

Geographical distribution.—The known range of *B. carlhi* (Fig. 18) extends from Douglas

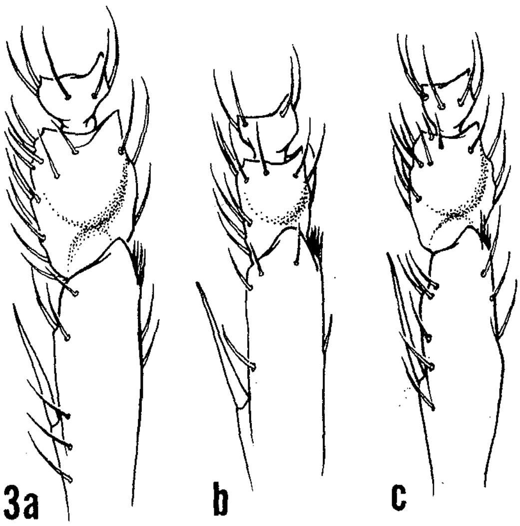


Fig. 3. Protarsus, male, basal tarsomeres and apex of tibia, dorsal aspect. — a. *Bembidion osculans* (Lassen Volcanic National Park, California). — b. *B. sequoiae* (Sequoia National Park, California). — c. *B. erasum* (Hood River, Oregon).

County, Oregon, south to Calaveras County, California, at low elevations in the Cascade Range, Sierra Nevada, and eastern slope of the Klamath Mountain system.

Geographical variation.—The small sample of specimens showed no variation between collecting sites except in size, which is also exhibited within sites.

The *erasum* group

Members of the *erasum* group are of medium size (ABL = 3.42–6.08 mm) for the genus. They are of somber, dark colors with pale or darkened appendages, and are short, stout, and subconvex in form. At present, there are nine species known. Their relationships with other groups are currently obscure, but evidence presented here indicates that they may be related to the *vile*, *transparens*, and *guttula* groups on one hand and to the *carlhi* group on the other. The *erasum* group is most likely monophyletic and the unique characteristics shared by its members substantiate its classification as a separate entity at the species group level.

These beetles are best recognized among *Bembidion* species by the following combination of features: 1) recurrent elytral groove short, preapical seta (Ed7B) free; 2) lateral elytral interneurs effaced, only sutural one entire, 2–5 increasingly shallower and shorter, 6–8 absent or nearly so; 3) elytral margination rounded and abruptly ended at humerus, not prolonged medially along base; 4) metasternal intercoxal process narrowly and completely margined laterally; 5) basal margin of pronotum very slightly lobed at middle, arcuate, straight or very slightly sinuate laterally; 6) foveae of dorsal elytral setae (Ed3 and Ed5) confluent with interneur 3; 7) base of pronotum carinate laterad of deep lateral fovea; 8) tooth of mentum narrowly rounded, surface with scaly microsculpture; and 9) head with frontal furrows parallel, not prolonged on clypeus.

In addition, the male genitalia (Fig. 10b–h) have CH1 of the internal sac well developed, plate-like, transversely oriented in apical curl of BW, OF doubled, narrow, well developed, basal constriction markedly developed.

Characteristics of genitalic structures of group females (Figs. 11b–j, 12b–j, 13b–j, 15b–j, 16b–j) include: eighth tergum broad, pigmentation pattern as in Fig. 11b–j; eighth sternum (Fig. 12b–j) broad or slightly narrow, with apical pale area more widespread on apical margin and irregular and medial pale area divided into apical and basal parts on each hemisternite; coxostylus (Fig. 13b–j) with gonocoxite moderate in length and width or short and dilated, gonostylus distinct, moderate in length or elongate with ventrolateral margin smooth or slightly crenulate; bursa copulatrix (Figs. 15b–j, 16b–j) with dorsal lobe distinct or not, dorsal sclerite present at least on dorsal surface, ventral lobe small or moderate in size, enlarged either on left or right with ductal lobe present or not, if present then on right ventrolateral surface and without sclerite at base of spermathecal duct; spermathecal duct with two half coils (reversed), insertion on apex of ductal lobe or directly on ventral lobe near midline; spermatheca short or more or less elongate, barrel-shaped; spermathecal gland long, slender, moderately convoluted, inserted on spermatheca through a long, tubular, slightly arcuate reservoir.

Natural history data indicate that *erasum* group members are best represented in stream-

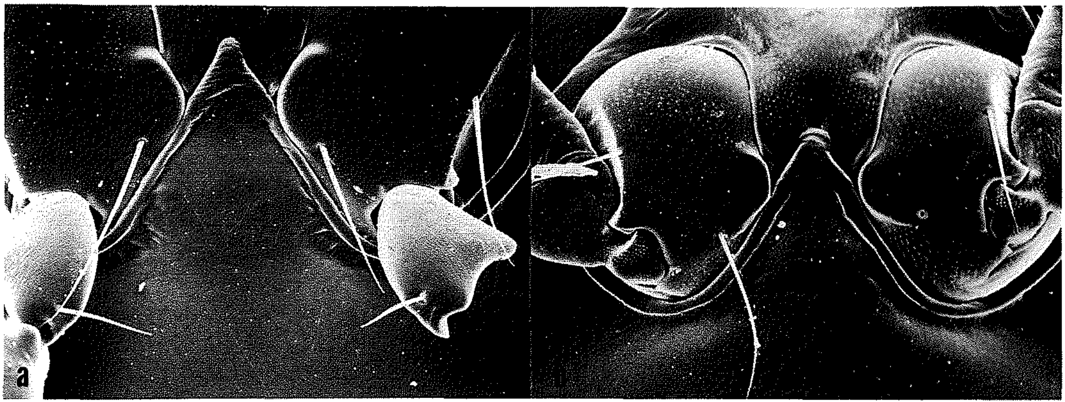


Fig. 4. Metasternal intercoxal process, male, ventral aspect, scanning electron micrographs. — a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. erasum* (Dodge Ridge, California).

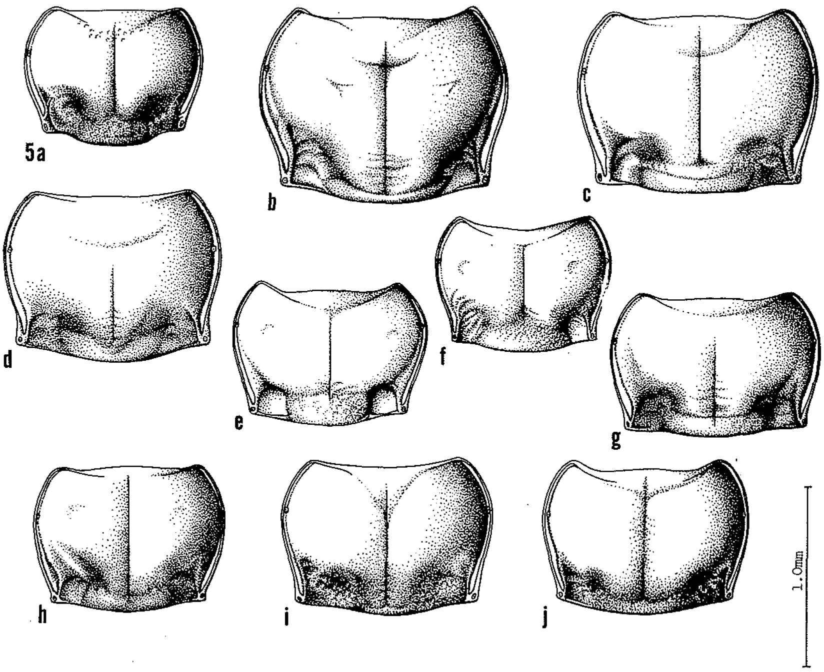


Fig. 5. Pronotum, dorsal aspect. — a. *Bembidion carlhi,* male (Tuolumne County, California. — b. *B. osculans,* male (Amador County, California). — c. *B. pseudoerasum,* male (El Dorado County, California). — d. *B. sequoiae,* male (Stevenson, Washington). — e. *B. castum,* male (Prince Rupert, British Columbia). — f. *B. disjunctum,* female (Eholt, British Columbia). — g. *B. erasum,* male (Hood River, Oregon). — h. *B. lindrothellus,* female (near Haines, Alaska). — i. *B. lummi,* male (Friday Harbor, Washington). — j. *B. chintimini,* female (Mary's Peak, Oregon).

side habitats in the Canadian Zone but extend into Hudsonian and Transition Zones in special microhabitats. For the most part, individuals overwinter as adults; but in some species larval overwintering also occurs. Only two species, *B. castum* and *B. lindrothellus* are wing dimorphic. According to our studies, one species, *B. chintimini,* has brachypterous members, and the others have only fully-winged adults which are probably capable of flight (but see *B. pseudoerasum*).

The geographical range of the *erasum* group (Fig. 19) is restricted to western North America, from southeastern Alaska in the north to southern California in the south, from the Pacific Coast east across the Columbia Plateau and

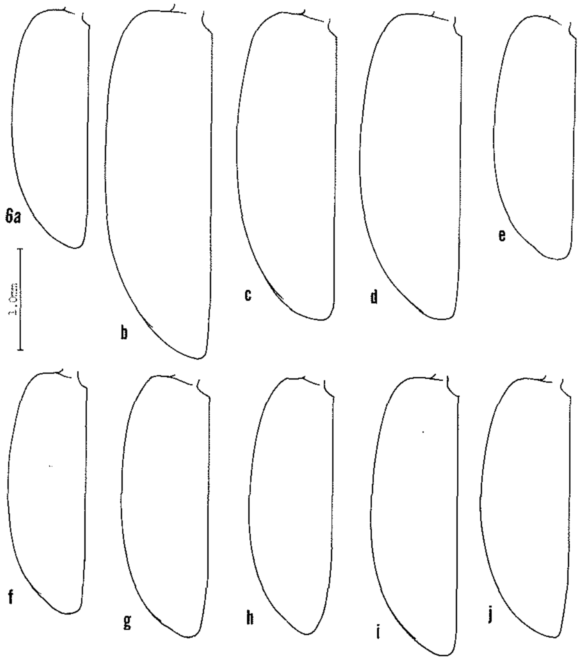


Fig. 6. Left elytron, silhouette, dorsal aspect. — a. *Bembidion carlhi,* male (Tuolumne County, California. — b. *B. osculans,* male (Amador County, California). — c. *B. pseudoerasum,* male (El Dorado County, California). — d. *B. sequoiae,* male (Stevenson, Washington). — e. *B. castum,* male (Prince Rupert, British Columbia). — f. *B. disjunctum,* female (Eholt, British Columbia). — g. *B. erasum,* male (Hood River, Oregon). — h. *B. lindrothellus,* female (near Haines, Alaska). — i. *B. lummi,* male (Friday Harbor, Washington). — j. *B. chintimini,* female (Mary's Peak, Oregon).

Great Basin to Alberta in the north and Colorado in the south.

The *erasum* group is sympatric with the *carlhi* group and allopatric with respect to the Palaearctic *guttula* group. There is considerable overlap of the ranges of *erasum* group species, especially in the central Sierra Nevada where five of the nine species are at least macrosympatric. Members of two species, *B. osculans* and *B. erasum,* were collected microsympatrically as well near Chester, California.

Taxonomic history of the *erasum* group

In his description of *B. erasum,* LeConte (1859) stated that his new species was "related to *B. tetraglyptus*", a Mannerheim species which Lindroth (1963a:273) later regarded as synonymous with *B. incertum* Motschulsky (see also Hayward 1897: 133). Hayward (1897) moved *B. erasum* into a group with *B. nitidum* Kirby because he thought that members of these taxa shared a "bifid mentum tooth and abbreviated outer striae of the elytra." Casey (1918) described several new species he regarded as related to *B. erasum* and erected the new subgenus *Lionepha* to contain them. He pointed out correctly that Hayward was in error in placing *B. erasum* with *B. nitidum* because the former lack "obtuse humeri". It should also be noted that Hayward was wrong in describing the simple, acute tooth of *B. erasum* adults as "bifid." Casey regarded *Lionepha* members as "closely allied to the *ustulatum* group", as well as to the *iridescens* group and to certain species of the *planatum* group. His "*Lionepha*" included three sections: *Lionepha* s. str., *Plataphus,* and *Trechnoepha.* Lindroth (1963a) brought order to chaos by limiting *Lionepha* to those species closely related to *B. erasum* based on sclerites of the internal sac of the aedeagus and external body features.

Lindroth (1963a) regarded *B. disjunctum* as representing a separate species group, but pointed out its close relationship with members of the *erasum* group. Here we include *B. disjunctum* as part of the *erasum* group based on shared features of the male and female genitalia and external characteristics. *Bembidion carlhi,* the new species described above, is apparently intermediate between and thus links the Nearctic *erasum* group and the Palaearctic *guttula* group. Lindroth (1963a:259) juxtaposed these two

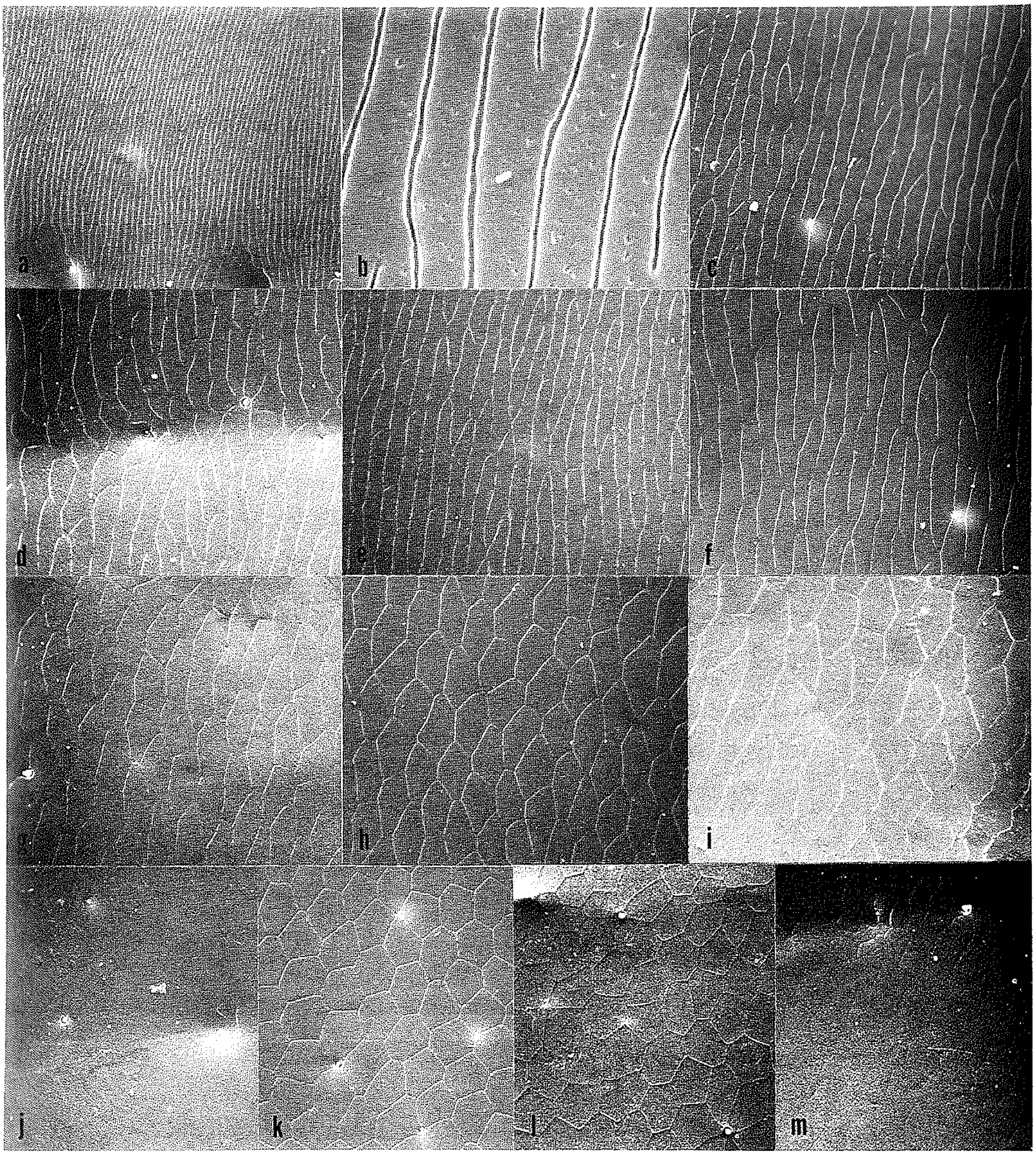


Fig. 7. Microsculpture, left elytron, disc posterior to seta Ed3, scanning electron micrographs. — a. *Bembidion carlhi*, male (Tuolumne County, California). — b. same. — c. *B. osculans*, female (Lassen Volcanic National Park). — d. *B. pseudoerasum*, male (Yosemite National Park, California). — e. *B. pseudoerasum*, female (Tuolumne County, California). — f. *B. sequoiae*, female (Yosemite National Park, California). — g. *B. castum*, male (Mendocino County, California). — h. *B. castum*, female (Mount Arrowsmith, British Columbia). — i. *B. disjunctum*, female (Pine Creek, Oregon). — j. *B. erasum*, male (Plumas County, California). — k. *B. erasum*, female (Modoc County, California). — l. *B. lindrothellus*, female (near Haines, Alaska). — m. *B. lummi*, male (Barkerville, British Columbia) [a and c through m = 1,000×; b = 10,000×].

groups but gave no reasons for doing so. We suspect that he saw a relationship but did not endeavour to explore it in his faunal coverage. Details of the hypothesized relationship are discussed below. Relationship between the *guttula* group (subgenus *Philochthus*) and the New World *championi* group (subgenus *Cyclolopha*) is presently undefined; and we therefore defer discussion of placement of the latter until later.

Lindroth's (1963a) sound faunal study of the *erasum* group provides an excellent starting point for our more detailed taxonomic coverage. This contribution supplements the former by correcting one improper nomenclatural assignment, expanding knowledge of the variation in and distributions of species, describing new species, clarifying key characters with detailed illustrations, and by demonstrating how the *carlhi* group ties the *erasum* and *guttula* groups together. We also add a phylogenetic and zoogeographic analysis of the *erasum* group and begin a character state data base for subsequent phylogenetic analysis at the generic level.

Lindroth's key to species groups (Lindroth, 1963a:208–211) does not discriminate the '*disjunctum*' group, nor does it treat the '*disjunctum*' group as part of the *erasum* group (both are here regarded as part of the *erasum* group). The following modification of Lindroth's key is suggested:

17(16). Elytron with only one to three evident interneurs OR preapical elytral seta Ed6 free, recurrent groove absent .... 18.
— Elytron with a least five evident interneurs (although abbreviated apically in some individuals); elytral seta Ed6 situated in or contiguous with recurrent groove .... 19.
18(17). Sutural interneur effaced toward apex; elytron with two spots .. (p.343) *mundum* group
— Sutural interneur entire; elytron not spotted, but may be paler apically .... (p. 259) *erasum* group

Checklist of the *erasum* group taxa

The **erasum** group
The *osculans* subgroup
001. *Bembidion osculans* Casey, 1918:20
002. *Bembidion pseudoerasum* Lindroth, 1963a:260
003. *Bembidion sequoiae* Lindroth, 1963a:160
The *castum* subgroup
004. *Bembidion castum* Casey, 1918:20

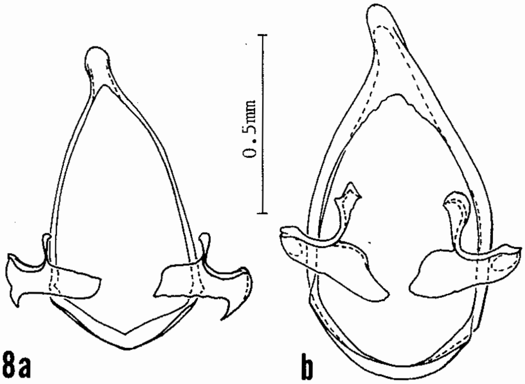


Fig. 8. Ring sclerite, male genitalia, dorsal aspect. — a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. erasum* (Humboldt County, California).

The *disjunctum* subgroup
005. *Bembidion disjunctum* Lindroth, 1963a: 264
The *erasum* subgroup
006. *Bembidion erasum* LeConte, 1859:83
007. *Bembidion lindrothellus* n.sp.
008. *Bembidion lummi* n.sp.
009. *Bembidion chintimini* n.sp.

Key to species of the *erasum* group

1. Elytron with five well-impressed striatopunctulate interneurs, lateral interneurs 6–8 finely punctulate, nearly effaced; body depressed; elytral microsculpture (Fig. 7f) comprised of irregularly isodiametric meshes, more deeply engraved in female than in male .... 005. *B. disjunctum* Lindroth
— Elytron with two or three well-impressed interneurs, lateral interneurs 4–8 much less impressed or effaced; body subconvex; elytral microsculpture varied .... 2.
2(1). Elytral microsculpture comprised of extremely fine transverse lines in both sexes (some lines formed into meshes); size larger (ABL = 4.71–6.08 mm) .... 3.
— Elytral microsculpture coarser, comprised of isodiametric or moderately transverse meshes (or in males of *erasum*, completely effaced); size smaller (ABL = 3.42–4.39 mm) .... 5.
3(2). Elytron with outer interneurs (3–8) effaced or nearly so, 3 barely traceable to posterior discal seta Ed5, 2 very shallow posterior to Ed5; elytral silhouette broadly ovoid, lateral margins arcuate posterior to humerus; male with apex of aedeagus (Fig. 10c) narrow, internal sac sclerite CH1 spoon-like (Fig. 10c) .... 002. *B. pseudoerasum* Lindroth

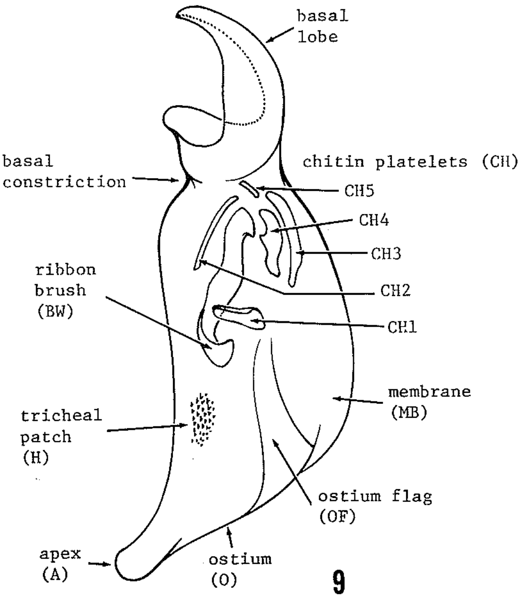


Fig. 9. Male aedeagus, diagramatic, left lateral aspect, with reference points used in text and Tab. 1 (in part).

— Elytron with outer interneurs (3–6) traceable (only 7 and 8 barely discernable) as rows of punctulae or striatopunctulae, 3 visible posterior to seta Ed5, 2 shallow but clearly extended to apex; elytral silhouette subrectangular, lateral margins straight at middle; male with apex of aedeagus (Fig. 10b,d) broad, internal sac sclerite CH1 narrower (Fig. 10b, d) .... 4.

4(3). Size large (ABL = 4.71–6.08 mm); male foreleg with broadly dilated basitarsus and tarsomere 2 (Fig. 3a), basitarsus wider than tibial apex; antennal scape infuscated dorsally (in most individuals); elytra faintly iridescent, elytral microsculpture (Fig. 7b) comprised of fine, shallowly engraved transverse lines .... 001. *B osculans* Casey

— Size smaller (ABL = 4.74–5.06 mm); male foreleg with normally broadened basitarsus and tarsomere 2 (Fig. 3b), basitarsus not wider than tibial apex; antennal scape rufous dorsally (in most individuals); elytra not iridescent, elytral microsculpture (Fig. 7d) comprised of thicker transverse lines formed irregularly into meshes .... 003. *B. sequoiae* Lindroth

5(2). Elytron with perfectly isodiametric meshes (Fig. 7k) AND fully winged, OR elytral microsculpture effaced (Fig. 7j); aedeagus of male as in Fig. 10f; bursa copulatrix of female as in Figs. 15g, 16g .... 006. *B. erasum* LeConte

— Elytron with microsculpture comprised of slightly or moderately transverse meshes in both sexes, more markedly developed in most females; if nearly isodiametric (Fig. 7g, l, m), flight wings short; aedeagus of male as in Fig. 10e, g, h, bursa copulatrix of female as in Figs. 15e, h, i, j; 16e, h, i, j .... 6.

6(5). Color dark flavous, legs slightly paler, antennae and mouthparts concolorous with head; elytral microsculpture comprised of nearly isodiametric meshes (Fig. 6h), granulate in females; male aedeagus as in Fig. 10g; female genitalia as in Figs. 15h, 16h .... 007. *B. lindrothellus* n.sp.

— Color piceous, appendages infuscated at least in part; elytral microsculpture comprised of transverse meshes; genitalia not as above .... 7.

7(6). Elytron with microsculpture comprised of moderately transverse meshes (Fig. 6e); male aedeagus as in Fig. 10e; female genitalia as in Figs. 15e, 16e; .... 004. *B. castum* Casey

— Elytron with microsculpture comprised of slightly transverse meshes as in Fig. 6i; genitalia not as above .... 8.

8(7). Flight wings full-sized; range: British Columbia and northern Washington ... 008. *B. lummi* n.sp.

— Flight wings short; range: Coastal Mountains of central Oregon (Mary's Peak) .... 009. *B. chintimini* n.sp.

The *osculans* subgroup

The three members of this subgroup, *B. sequoiae*, *B. pseudoerasum*, and *B. osculans*, differ from members of the *erasum* subgroup in having more transverse, less mesh-like microsculpture, larger size, and more broadly rounded apex of the male median lobe. They differ from members of the *disjunctum* subgroup in having fewer evident elytral interneurs and more convex form and from *castum* subgroup members in having much narrower and wider meshes of elytral microsculpture. Females of the *osculans* subgroup differ from those of all other subgroups in having the coxostylus (Fig. 13b–d) with gonocoxite short and dilated and the spermatheca slightly or moderately elongate.

The range of this species subgroup is more restricted than that of the *erasum* subgroup, but less restricted than the ranges of the *castum* and *disjunctum* subgroups. No species occurs north of southernmost British Columbia nor east of the Sierra Nevada and Cascade Range, except for the narrow incursion of *B. osculans* across the Columbia Plateau. Range overlap of species sub-

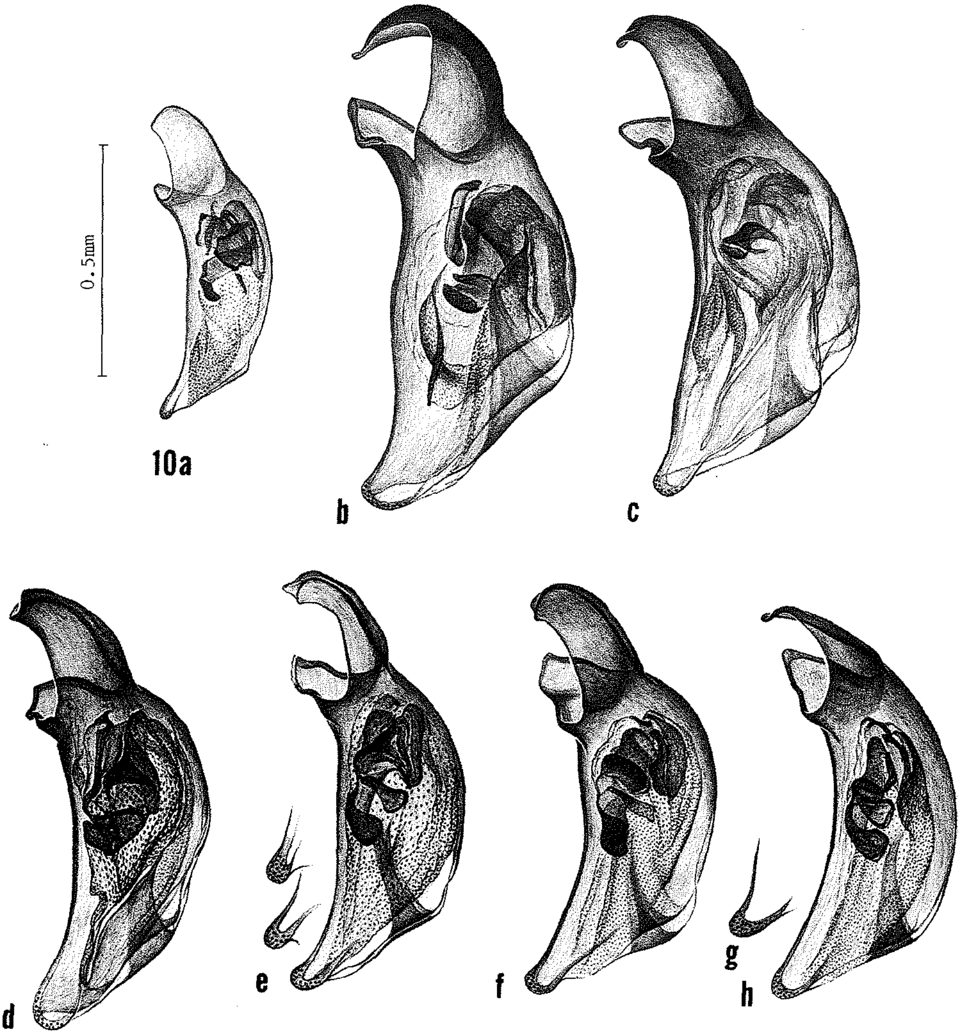


Fig. 10. Male aedeagus, left lateral aspect. — a. *Bembidion carlhi* (Calaveras County, California). — b. *B. osculans* (Marin County, California). — c. *B. pseudoerasum* (Tulare County, California). — d. *B. sequoiae* (Sequoia National Park, California). — e. *B. castum* (entire aedeagus, Vancouver, British Columbia; lower apex, Los Gatos, California; upper apex, Blodgett, Oregon). — f. *B. erasum* (Humboldt County, California). — g. *B. lindrothellus* apex (near Haines, Alaska). — h. *B. lummi* (Friday Harbor, Washington).

groups is discussed below in the introduction to the *erasum* subgroup. Ranges of all three species are at least macrosympatric in the Sierra Nevada; and *B. sequoiae* and *B. osculans* are also macrosympatric in the Cascade Range of Oregon. The nominal species, *B. osculans*, has the broadest longitudinal range and also appears to be the most varied.

001. **Bembidion osculans** Casey

Figs. 3a, 5b, 6b, 7c, 10b, 11b, 12b, 13b, 15b, 16b, 20, 29.

Bembidion osculans Casey, 1918:20. Lectotype (designated by Lindroth 1975:116), a female in USNM, Type No. 36816. Type locality: Marin County, California (as restricted by Lindroth 1963a:259).

Bembidion speculum Casey, 1918:20. Lectotype (designated by Lindroth 1975:116), a female in USNM,

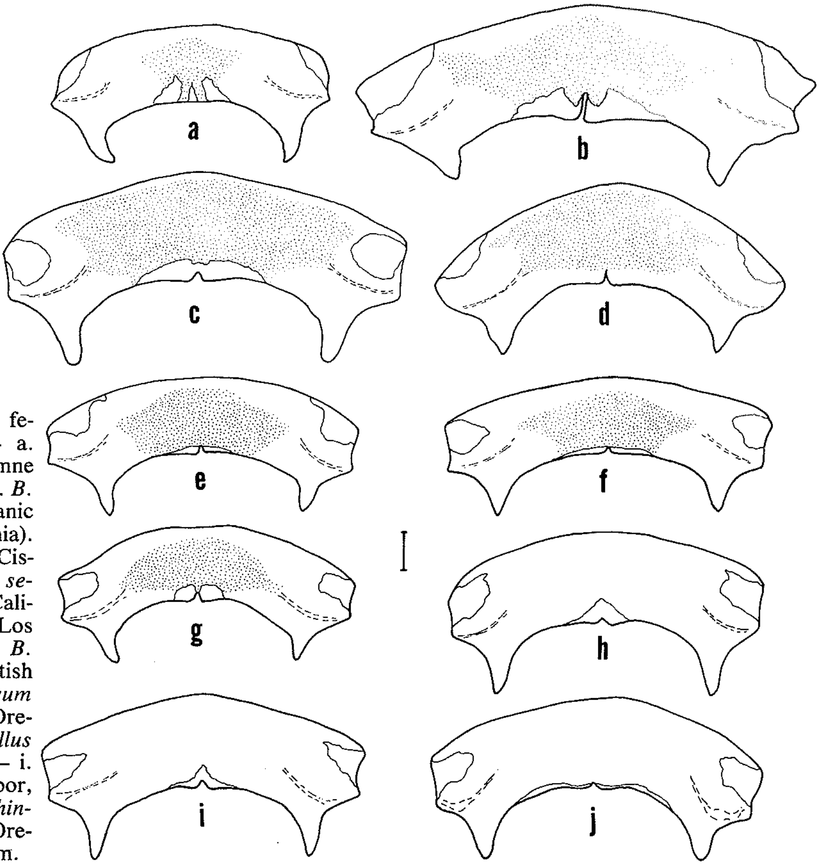


Fig. 11. Tergum eight, female, dorsal aspect. — a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. osculans* (Lassen Volcanic National Park, California). — c. *B. pseudoerasum* (Cisco, California). — d. *B. sequoiae* (Kings River, California). — e. *B. castum* (Los Gatos, California). — f. *B. disjunctum* (Creston, British Columbia). — g. *B. erasum* (Three Creeks Lake, Oregon). — h. *B. lindrothellus* (near Haines, Alaska). — i. *B. lummi* (Friday Harbor, Washington). — j. *B. chintimini* (Mary's Peak, Oregon). Scale line = 0.10 mm.

Type No. 36815. Type locality: Marin County, California. — Lindroth 1963a:259; 1975:116.

Diagnostic features: Members of this taxon are readily distinguished from all other members of the subgroup by the following combination of characteristics: markedly sinuate lateral margin of pronotum, piceous antennal scape, large size, and, in males, markedly expanded basitarsus. Most specimens have elytra faintly iridescent due to finely engraved transverse microsculpture.

Size.—ABL = 4.75–6.08 mm; SBL = 4.28–5.26 mm; TW = 1.93–2.50 mm; TD = 1.22–1.48 mm.

Color and Luster.—Piceous; antennae, elytra, and legs paler apically. Dorsal and ventral surfaces shiny, faintly iridescent.

Form.—Moderately long, broad, subconvex. Head broad but narrower than pronotal base; eyes medium-sized, well rounded; antennae short, not extended to seta Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5b) wide, one-fourth wider than elytron, transverse, with slightly lobed base, lateral margin markedly sinuate at basal 1/3, straight before rectangular, minutely pointed posterior angle, anterior angle rounded, slightly produced. Elytra (Fig. 6b) with silhouette subrectangulate, humeri squared, lateral margins slightly divergent at middle, intervals slightly convex. Foreleg of male with broadly dilated basitarsus and tarsomere 2 (Fig. 3a), the former slightly broader than tibial apex.

Structure.—*Microsculpture* (Fig. 7c) of male and female dorsum comprised of broadly transverse meshes, finely engraved on elytra, nearly effaced from pronotum, of large, slightly transverse meshes on occiput. *Elytra* each with four (±5, 6) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate,

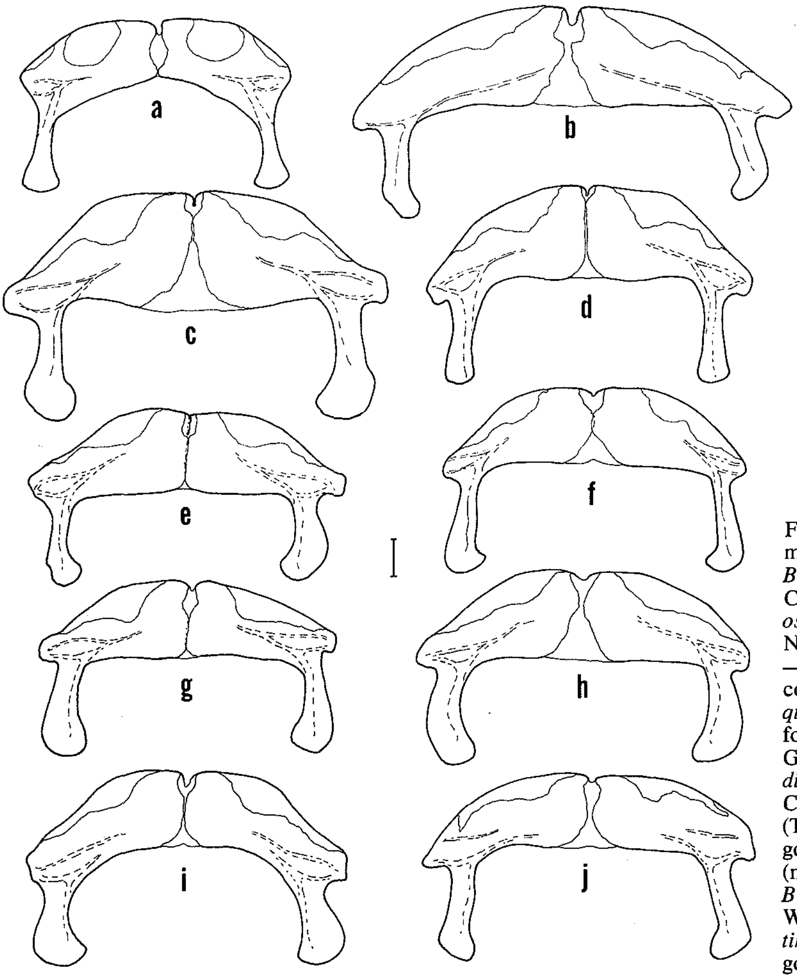


Fig. 12. Sternum eight, female, ventral aspect. —. a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. osculans* (Lassen Volcanic National Park, California). — c. *B. pseudoerasum* (Cisco, California). — d. *B. sequoiae* (Kings River, California). — e. *B. castum* (Los Gatos, California). — f. *B. disjunctum* (Creston, British Columbia). — g. *B. erasum* (Three Creeks Lake, Oregon). — h. *B. lindrothellus* (near Haines, Alaska). — i. *B. lummi* (Friday Harbor, Washington). — j. *B. chintimini* (Mary's Peak, Oregon). Scale line = 0.10 mm.

striae more effaced laterally, punctuale smaller laterally. *Wings* fully developed. *Male genitalia* as in Fig. 10b; median lobe with broadly dilated apex which is squared ventrally, shaft robust, tubular, ventral margin bisinuate; internal sac complex, BW large, CH1 small and transverse, CH2 long and broad, CH3 small, CH4 large, CH5 long and narrow, H collar-like when everted, OF doubled, narrow, well defined. *Female genitalia* as in Figs. 11b, 12b, 13b, 15b, 16b; coxostylus (Fig. 13b) with gonocoxite moderately short, gonostylus moderate in length with ventrolateral margin smooth; bursa copulatrix (Figs. 15b, 16b) with dorsal sclerite very deeply folded and extended onto lateral surface and dorsum of ventral lobe, ventral lobe greatly enlarged on left; spermatheca slightly elongate.

Natural history.—Members of *B. osculans* are found at low to medium elevations under stones at margins of small, cool or cold streams, usually in densely shaded areas. Most individuals overwinter as larvae, as suggested by the frequent occurrence of teneral adults from March to July (1463m). However, fully pigmented and hardened adults were also collected in December and March, and a teneral female was found in August (Idaho); therefore, some adults may also overwinter. The fully developed wings present in all adults examined and the wide geographical range of this species indicate that dispersion by flight is probable. *Bembidion osculans* members are apparently restricted to the Transition and Canadian Zones along cold rills and streams.

Geographical distribution.—(Fig. 20). The range of this species extends from central California northward to northern Oregon, then eastward along the lower Columbia River drainage to northeastern Oregon, southeastern Washington, and northwestern Idaho. Although widespread in both the Sierra Nevada and Coast Ranges (as far south as Monterey) of California and the Cascade and Coast Ranges of Oregon, the species is apparently absent from the Cascade Range (and all other parts of western Washington) north of the Columbia River. This distribution pattern, characterized by an abrupt northern limit and a narrow eastward extension across the Columbia Plateau, is remarkably similar to that of *Nebria eschscholtzii* Ménétriés (Kavanaugh 1979b), although the latter is slightly more wide-ranging in all directions.

We have examined a total of 206 males and 170 females from the following localities:

CALIFORNIA: Alpine County, Bloods [July] (6; CAS); Butte County, Brush Creek (0.5 miles N) [July] (1; CAS); Amador County, Corral Flats (Highway 88) [May] (3; USNM); Calaveras County, Big Meadows [June] (1; CAS), Calaveras Big Trees State Park [May, July] (6; CAS), Camp Connell (2 miles N) [May] (7; CDAS), Mokelumne Hill (1; CAS); Colusa County, Paradise Creek ([730 m]) (1; CAS); El Dorado County (2; USNM), Kyburz [May] (3; CNC), Pollock Pines [July] (3; UCD), Riverton (3 miles W on South Fork American River [910 m]) [July] (1; DHKa), Strawberry (1; CAS); Fresno County, Kings River ([1460 m]) [July] (1; USNM), Huckleberry Meadow ([1980 m]) [Aug.] (4; CAS); Glenn County, Board Tree Camp [Aug.] (3; CAS); Lake County (2; CAS), Adams Springs [June] (1; CAS), Bartlett Springs [June] (1; CAS), Lower Lake (Hereondon Creek) [May] (1; CAS); Kings Canyon National Park, General Grant Grove [June, Aug.] (8; CAS); Lassen Volcanic National Park ([2440 m]) [July] (1; UCD), Lost Creek (at Highway 87 [1840 m]) [Aug.] (7; DHKa), Sulphur Works Area (West Sulphur Creek [2130 m]) [Aug.] (11; DHKa), Mirror Lake [Aug.] (4; CAS); Madera County, Boggy Meadow ([1830 m]) [July] (1; CAS); Marin County (17; CAS, MCZ, USNM), Alpine Dam [Apr.] (1; CAS), Coldrill [July] (8; CAS), Cypress Ridge [Apr.] (5; CAS), Fairfax (1; CAS), Lagunitas [Apr.] (2; CAS), Mill Valley [May–June, Aug.] (15; CAS, MCZ), Mount Tamalpais (1; CAS), Muir Woods [May] (1; USNM); Mariposa County, Fish Camp (7 miles NW [2130 m]) [July] (1; CAS), Stove Pipe Campground ([1860 m]) [Aug.] (3; CAS); Mendocino County, Mill Creek (W of Mailliard Redwoods State Park) [Sept.] (1; CAS), Willits [July] (1; CAS); Monterey County, Salmon Creek [Aug.] (1; CAS); Napa County (7; CAS, MCZ, OSUO, USNM), Calistoga [June–July] (3; CAS); Placer County, Benner Creek (NW of Chester) [Aug.] (1; USNM); San Mateo County, Crystal Springs Wildlife Refuge (w. of San Andreas Lake) [June] (1; DHKa); Santa Clara County, Congress Springs [Apr.] (1; CAS), Corte Madera Creek [Apr.–May] (61; CAS), Los Gatos [Aug.] (4; CAS, USNM), Pacheco Creek [July] (1; CAS), Stanford University Campus (Corte Madera Creek, Los Tancos Creek) [Mar., June, Dec.] (10; CAS, USNM), Sunset Park [May] (1; CAS), Sveadal [Apr.] (1; USNM); Santa Cruz County (1; CAS), Boulder Creek (4; CAS); Shasta County, Eiler Lake [Sept.] (1; CAS), Hat Creek [July] (1; UCD), Highway 44 (E of Redding) [June] (1; CAS), Old Station (Hat Creek at Highway 89 [1400 m]) [Aug.] (1; DHKa), Viola ([1370 m]) [June] (1; CAS); Sierra County, Frogpond Public Camp (Highway 49 at North Fork Yuba River) [July] (10; CAS), Indian Creek (at Highway 49) [Aug.] (1; CAS); Siskiyou County, Big Springs ([1120 m]) [June] (2; CAS); Sonoma County, Camp Meeker (1; CAS), Fort Ross [July] (1; CAS), Healdsburg [July] (1; CAS), Santa Rosa [May] (2; MCZ); Tehama County, Battle Creek (1.4 miles W Mineral on Highway 36 [1460 m]) [May] (3; DHKa), Deer Creek Meadow [June] (1; CAS), Mineral (4 miles ENE at Summit Creek [1710 m]) [Aug.] (5; DHKa); Trinity County, Hyampom (2 miles SE at Butter Creek Road [550 m]) [July] (1; CAS); Tuolumne County, Dodge Ridge [Aug.–Sept.] (2; CAS), Gardners [July] (23; CAS), Long Barn (Rush Creek) [Aug.–Sept.] (5; CAS), Niagara Creek Campground (tributary to Niagara Creek) [Aug.] (1; CAS); Yosemite National Park, White Wolf Campground (2 miles W [2470 m]) [July] (6; USNM); County unknown, Big Meadow [June] (1; CAS), Lassen National Forest [June] (5; CAS). IDAHO: Benewah County, St. Joe [July] (1; OSUO); Latah County, Potlach [Aug.] (1; CAS). OREGON: Benton County, Berry Creek (9 miles N of Corvallis) [June] (4; OSUO), Corvallis [July] (1; OSUO); Douglas County, Steamboat Creek (at North Umqua River [310 m]) [July] (1; DHKa); Grant County, Beech Creek ([1520 m]) [July] (1; CAS); Hood River County, Hood River [May] (1; USNM); Jackson County, Butte Falls (0.3 miles E on South Fork Butte Creek [730 m], 6.1 miles SE at Willow Creek [820 m]) [July] (4; DHKa), Shady Cove (4.9 miles S on Highway 62 at Reese Creek [400 m] (1; DHKa), West Branch Willow Creek (0.7 miles N of Highway 140 [1070 m]) [July] (1; DHKa); Klamatch County, Lake of the Woods [July] (1; CAS); Lane County, Cottage Grove [June] (4; OSUO); Umatilla County, S of Kooskooskie (Washington) [June] (1; OSUO); Wheeler County, Spray (10 miles NNE at Northeast Fork Deadhorse Creek [980 m]) [July (1; CAS); Yamhill County, McMinnville [Mar., July] (4; OSUO). WASHINGTON: Asotin County, Asotin (Snake River) [June] (1; CAS); Klickitat County, Bickelton (10 miles SW at Spring reek [1010 m]) [May] (11 DHKa); Walla Walla County, Walla Walla (Mill Creek) [June–July, Sept.] (29; CAS, MCZ, OSUO); Whitman County, Wawawai [May] (1; CAS).

Doubtful Records: WASHINGTON: Olympic National Park, Sol Duc Hot Springs ([610 m]) [June] (1; OSUO).

Specimens without locality: (1; CAS).

Geographical variation.—We could not detect any clinal variation in this species. Intrapopulational variation occurs most notably in size, coloration of elytra (i.e. extent of apical rufinistic area), and pronotal width in proportion to elytral width.

002. **Bembidion pseudoerasum** Lindroth

Figs. 5c, 6c, 7d–e, 10c, 11c, 12c, 13c, 15c, 16c, 21, 29.

Bembidion pseudoerasum Lindroth, 1963a:260. Holotype, a male in USNM, Type No. 76638. Type locality: Truckee, Placer County, California.

Diagnostic features: Members of *B. pseudoerasum* are easily distinguished from all other group members by presence of markedly transverse microsculpture, large quadrate pronotum, arcuate lateral margin of elytron, and reduced number of visible interneurs (only interneurs 1 and 2, ± 3).

Size.—ABL = 4.73–4.94 mm; SBL = 4.28–4.57 mm; TW =1.81–2.12 mm; TD = 1.14–1.22 mm.

Color and luster.—Piceous; antennal scape, mandibles, elytra, and legs paler in some specimens, especially scape and apical one-half of elytra which are rufinistic. Dorsal and ventral surfaces shiny.

Form.—Moderately robust and subconvex. Head broad but considerably narrower than pronotal base; eyes medium-sized, slightly to moderately rounded, antennae short, extended to seta Eo3 on elytron, antennomeres less broad than members of other species in group. Pronotum (Fig. 5c) wide, at least one-third wider than elytron, quadrate, with barely arcuate base, lateral margins markedly sinuate in basal 1/3 with sinuation continued to the sharp posterior angle, anterior angle rounded, moderately produced. Elytra (Fig. 6c) with silhouette subovoid to subrectangulate, humeri squared, lateral margins divergent at middle, interneurs flat (except sutural which is convex apically). Foreleg of male with broadly dilated basitarsus and tarsomere 2 (as in Fig. 3a), the former slightly wider than tibial apex.

Structure.—*Microsculpture* (Fig. 7d–e) of male and female dorsum comprised of broadly transverse meshes, finely engraved on elytra, nearly effaced from frons and pronotum, meshes coarser on occiput. *Elytra* each with two (± 3, 4) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate, striae more effaced laterally, punctulae smaller laterally. *Wings* fully developed. *Male genitalia* as in Fig. 10c; median lobe with narrowly rounded apex, shaft robust, tubular, basal constriction well developed, ventral margin slightly arcuate near apex; internal sac with BW small, CH1 Y-shaped, CH2–CH5 lightly pigmented, H extensive and convoluted, OF doubled, narrow, and well defined. *Female genitalia* as in Figs. 11c, 12c, 13c, 15c, 16c; coxostylus (Fig. 13c) with gonocoxite very short, gonostylus elongate with ventrolateral margin slightly crenulate; bursa copulatrix (Figs. 15c, 16c) with dorsal sclerite deeply folded and extended onto lateral surface, ventral lobe slightly enlarged on left; spermatheca moderately elongate.

Natural history.—Members of *B. pseudoerasum* are found at medium elevations in the central and southern Sierra Nevada of California. Their precise microhabitat is unknown. One fully pigmented male was collected in May at 1220 m; thus it is likely that at least some individuals overwinter as adults. The fully developed wings present in all individuals examined indicates that dispersion by flight is probable. *Bembidion pseudoerasum* members are apparently restricted to microhabitats of the Canadian and Hudsonian Zones.

Geographical distribution.—(Fig. 21). The range of this species is restricted to the Sierra Nevada of California, in which it extends from Nevada County in the north to Sequoia National Park in the south.

We have examined a total of 6 males and 11 females from the following localities:

CALIFORNIA: El Dorado County, Fallen Leaf Lake [June] (1; CAS), Kyburz (5 miles SW [1220 m]) [May] (1; CNC), Strawberry (1; CAS); Kings Canyon National Park, Kings River (at Paradise Valley) [July] (1; CAS); Nevada County, Truckee (5; USNM); Placer County, Cisco [Aug.] (1; CAS); Sequoia National Park, Mount Silliman ([2440 m]) [Aug.] (4; CAS); Tuolumne County, Gardners [July] (1; CAS), Pinecrest ([July] (1; CAS); Yosemite National Park, Nevada Falls ([1800 m]) [July] (1; CAS), Tioga Pass ([2740 m]) [Aug.] (1; OSUO).

Geographical variation.—We had too few specimens with which to determine any clinal variation, and most locality samples were limited to a single specimen. Therefore, both inter- and intrapopulational variation could not be adequately assessed. However, of interest to us is the elytra silhouette, which is either subovoid or subrectangulate. Subovoid elytra are normally associated with brachypterous individuals, but all *B. pseudoerasum* adults examined are fully winged. The restricted range of this species together with the subovioid body form may indicate that some members at least are functionally flightless. This change in elytral shape, which in most carabid groups studied to date (see Darlington 1936, 1943; Lindroth 1945, 1963b) either follows or appears simultaneously with flight wing reduction, appears to have preceded actual wing reduction in some *B. pseudoerasum* members and also in some *B. castum* and *B. lindrothellus* members (see below). This unusual sequence of structural change leading to brachyptery is presently known otherwise only in some species of *Nebria* (Kavanaugh 1978).

003. **Bembidion sequoiae** Lindroth

Figs. 3b, 5d, 6d, 7f, 10d, 11d, 12d, 13d, 15d, 16d, 22, 29.

Bembidion sequoiae Lindroth, 1963a:260. Holotype, a male in MCZ, Type No. 32532. Type locality: Sequoia National Park, Californa.

Diagnostic features: Members of *B. sequoiae* are very similar to members of *B. osculans,* and reliable determination of specimens requires dissection of genitalia. However, most specimens may be distinguished on the basis of elytral microsculpture, which is finer and more transverse in *B. osculans* members. The anterior basitarsus of *B. sequoiae* males is subequal in width to foretibial apex, whereas it is wider than the tibial apex in *B. osculans* males. *B. sequoiae* members have a greater number of traceable interneurs than *B. pseudoerasum* members (six as opposed to three) and a rectangulate elytral silhouette (*B. pseudoerasum* members have a subovoid or subrectangulate elytral silhouette).

Size.—ABL = 4.74–5.06 mm; SBL = 4.47–4.57 mm; TW = 1.99–2.09 mm; TD = 1.09–1.21 mm.

Color and luster.—Piceous; antennal scape, elytral apex, and legs rufopiceous; head with occiput and mouthparts rufous in some individuals. Dorsal and ventral surfaces shiny.

Form.—Medium-sized, broad, subconvex. Head broad, but narrower than pronotal base; eyes medium-sized, rounded; antennae short, not extended to seta Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5d) wide, one-third wider than elytron, transverse, with slightly arcuate base, lateral margin sinuate in basal 1/3 with sinuation continued to the slightly obtuse posterior angle, anterior angle rounded, barely produced. Elytra (Fig. 6d) with silhouette subrectangulate, humeri squared, lateral margin straight, not widened apically, intervals flat. Male foreleg with basitarsus subequal in width to apex of tibia (Fig. 3b).

Structure.—Microsculpture (Fig. 7f) of male and female dorsum comprised of transverse meshes, finely engraved on elytra, nearly effaced from pronotum, with meshes slightly transverse on occiput. Elytra each with three (± 4, 5, 6) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate, striae more effaced laterally, punctulae smaller laterally. Wings fully developed. *Male genitalia* as in Fig. 10d; median lobe with broadly rounded apex, shaft tubular, narrow, basal constriction moderately well developed, ventral margin shallowly arcuate; internal sac with BW broad and well developed, CH1 broad and plate-like, CH2–CH5 well developed, OF doubled, narrow, well defined. *Female genitalia* as in Figs. 11d, 12d, 13d, 15d, 16d; coxostylus (Fig. 13d) with gonocoxite very short, gonostylus elongate with ventrolateral margin slightly crenulate; bursa copulatrix (Figs. 15d and 16d) with dorsal sclerite deeply folded and slightly extended onto lateral surface, ventral lobe moderately enlarged on left; spermatheca moderately elongate.

Natural history.—Members of *B. sequoiae* are found at medium elevations in the central Sierra Nevada and northern Cascade Range. Their precise microhabitat is unknown, but labels on some specimens suggest association with streams and meadows. One subteneral specimen was collected in July at high elevation, suggesting adult hibernation. The fully developed wings present in all individuals examined suggests that dispersion by flight is probable. *Bembidion sequoiae* members are apparently restricted to microhabitats of the Canadian Zone.

Geographical distribution.—(Fig. 22). The range of this species extends along the Cascade Range and Sierra Nevada from extreme southern British Columbia to central California. Its apparent distribution pattern is notably disjunct; but because individuals are rarely collected even in areas where the species is known to occur, gaps between known localities may be due to poor sampling, at least in part. We predict that populations of this species will eventually be discovered in the northern Sierra Nevada and in the Cascade Range of southern Oregon and Central Washington. The range of *B. sequoiae* is broadly sympatric with that of *B. osculans* from southern Washington to central California and macrosympatric with that of *B. pseudoerasum* in the Sierra Nevada, California.

We have examined a total of 13 males and 4 females from the following localities:

BRITISH COLUMBIA: Hope (15.2 miles W on Route 1) [Aug.] (1; UASM). CALIFORNIA (1;MCZ): Fresno County, Camp Greeley ([1850 m]) [Mar.] (1; CAS), Huckleberry Meadow ([1980 m]) (1; CAS); Kings Canyon National Park, Kings River ([1460 m] [July] (1; USNM); Mariposa County, Mariposa Grove (2 miles ESE [2130 m]) [July] (1; CAS); Sequoia National Park [June–July] (4; CAS, MCZ), Marble Fork Kaweah River ([2130 m]) (1; CAS); Tulare County, Kaweah ([300 m]) (1; CAS); Yosemite National Park [Aug.] (1; CAS), Yosemite Valley [June] (1; CAS). OREGON: Marion County, Silver Creek Falls [Aug.] (1; OSUO); Multnomah County, Troutdale (2 miles E) [July] (1; OSUO). WASHINGTON: Skamania County, Stevenson [June] (1; OSUO).
Additional Literature Records: BRITISH COLUMBIA: Vancouver (1; ZMUL) [Lindroth 1963a].

Geographical variation.—We could not detect any significant variation, except in color, among the specimens of this species examined; and color variation is no doubt related to degree of teneralness (i.e. time since the molt to adult stage and resultant amount of pigment deposition).

The *castum* subgroup

Adults of *B. castum,* the single member of this subgroup, differ from members of the other *erasum* group species primarily in genitalic structures (see Figs. 10–16). Elytral microsculpture is moderately transverse. Form and structure of head, prothorax, and elytra are very similar to *erasum* subgroup members; however; based on features of the genitalia of females, we place this species in a separate subgroup.

The range of this subgroup is restricted to the Coast Mountain System and adjacent lowlands from central California to central British Columbia, with an eastern extension only to the western slope of the Cascade Range in Oregon and Washington. This subgroup is sympatric with some members of the *osculans* and *erasum* subgroups in parts of its range and allopatric with respect to the range of the *disjunctum* subgroup.

004. **Bembidion castum** Casey

Figs. 5e, 6e, 7g–h, 10e, 11e, 12e, 13e, 15e, 16e, 17, 23, 29.

Bembidion castum Casey, 1918:20. Lectotype (designated by Lindroth 1975:116), a male in USNM, Type No. 36818. Type locality: Santa Cruz Mountains, California.
Bembidion serenum Casey, 1918:21. Lectotype (designated by Lindroth 1975:116), a female in USNM, Type No. 36819. Type locality: Arcata, Humboldt County, California.—Lindroth 1963a:261; 1975:116.
Bembidion brumale Casey, 1918:22. Lectotype (designated by Lindroth 1975:116), a female in USNM, Type No. 36823. Type locality: Metlakatla, British Columbia, Canada. NEW SYNONYMY.
Bembidion vacivum Casey, 1918:22. Lectotype (designated by Lindroth 1975:116), a female, in USNM, Type No. 36822. Type locality: Skeena River, Terrace, British Columbia, Canada.—Lindroth 1963a:262; 1975:116. NEW SYNONYMY.
Bembidion nesicum Casey, 1918:30. Lectotype (designated by Lindroth 1975:116), a male in USNM, Type No. 36845. Type locality: Metlakatla, British Columbia, Canada.—Lindroth 1963a:261; 1975:116.

Diagnostic features: Members of *B. castum* are somewhat varied and possess characteristics which grade into those possessed by *B. lummi, B. chintimini, B. lindrothellus,* and *B. erasum* members. However, they may be distinguished by presence of moderately transverse meshes of elytral microsculpture, length of elytron in proportion to width of pronotal base, geographical range, and configuration of genitalic structures.

Size.—ABL= 3.65–4.18 mm; SBL = 3.34–3.37 mm; TW = 1.56–1.82 mm; TD = 0.87–1.0 mm; WPB/EL: $\bar{X}$ = 0.392, s = 0.012, c.v. = 3.032 (N = 30).

Color and luster.—Piceous; elytra and mandibles paler apically, legs flavous. Dorsal and ventral surfaces shiny.

Form.—Moderately short and broad, subconvex. Head broad but narrower than pronotal base; eyes medium-sized, barely to slightly rounded; antennae short, not extended to seta Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5e) moderately broad, 1/3 wider than elytron, quadrate, with slightly arcuate base, lateral margin straight or very slightly sinuate in basal 1/3, posterior angle sharp, obtuse anterior angle rounded, barely produced. Elytra (Fig. 6e) with silhouette subrectangulate, subspatulate, or spatulate, humeri squared or sloped, lateral margins divergent at middle, intervals nearly flat. Foreleg of male with moderately dilated basitarsus and tarsomere 2, the former subequal in width to tibial apex.

Structure.—Microsculpture (Fig. 7g–h) of male and female dorsum comprised of transverse meshes, finely engraved on elytra, nearly effaced from pronotum and frons, meshes less transverse and larger on occiput. *Elytra* each with three (± 4, 5, 6) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate, striae more effaced laterally, punctulae smaller laterally. *Wings* fully developed or reduced to a minute, veinless pad. *Male genitalia* as in Fig. 10e; median lobe with narrow apex of varied shape, shaft narrowly tubular, markedly constricted before base, ventral margin markedly arcuate at basal 1/4; internal sac with BW long and broad with apex narrowly curled transversely, CH1 plate-like, medially constricted, CH2–CH5 more lightly pigmented than in two preceding species, OF as in preceding species. *Female genitalia* as in Figs. 11e, 12e, 13e, 15e, 16e; bursa copulatrix (Figs. 15e, 16e) with dorsal lobe indistinct, dorsal sclerite longitudinal and shallowly folded, restricted to dorsal surface, ventral lobe large, enlarged on left, with ductal lobe present; spermatheca short.

Natural history.—Members of *B. castum* are found at low to medium elevations, not directly associated with water, but in leaf litter (T.L.E., Humboldt County, California) or gravel bars (D.H.K., Clackamas County, Oregon) on upper floodplains. Most individuals overwinter as adults, with the next generation emerging in July and August. However, three teneral females were collected in Oregon in May, suggesting that immature stage individuals may also overwinter. Wing dimorphism among members of this species indicates that some individuals fly and other do not. Wingless specimens are known only from Portland (Oregon) and localities farther north. *Bembidion castum* is normally an inhabitant of Canadian Zone microhabitats.

Geographical distribution.—(Fig 23). This species is restricted to the extreme West Coast of North America, from central British Columbia to central California. In Oregon and Washington, its range extends east only to the western slope of the Cascade Range. It is even more restricted in California, where it occurs only in the coast mountain systems and is absent from even the western slope of the Sierra Nevada. The range of *B. castum* is sympatric with that of *B. lindrothellus* in the southern half of coastal British Columbia (including Vancouver Island), with *B. chintimini* in westcentral Oregon, and with *B. erasum* in the Puget lowland and Cowlitz Valley of southwestern Washington and on the eastern slope of the Klamath Mountain system in northwestern California. *Bembidion castum* and *B. erasum* are otherwise apparently parapatric.

We have examined a total of 128 males and 138 females from the following localities:

BRITISH COLUMBIA: Inverness [July] (1; CNC), Ladner (and 10 miles E) [June] (3; CNC, MCZ, UASM), Metlakatla [Apr.] (10; USNM), Prince Rupert [July] (4; CNC), Terrace (Skeena River) (1; USNM), Vancouver (University of British Columbia campus) [Jan., Mar.–May, Sept.] (7; CNC, MCZ, OSUO, UBC); Queen Charlotte Islands, Massett (1; USNM); Vancouver Island, Abernathy Bridge (E of Youbou) [Aug.] (1; UASM), Bowser [June] (3; CNC), Cowichan Lake [July] (3; CNC, UBC), Errington [Oct.] (1; UBC), John Deane Provincial Park ([290 m]) [Aug.] (4; UASM), Macmillan Provincial Park (10 miles E of Alberni) [May] (2; CNC), Mount Arrowsmith (Mount Arrowsmith Trail [300 m — 980 m]) [July–Aug] (4; UASM), Mount Benson [May] (1; UBC), Victoria (Royal Oak) [May] (3; MCZ, UBC, USNM), Wellington (Lost Lake) [May, Sept.-Oct.] (3; OSUO).
CALIFORNIA: Humboldt County (4; CAS, MCZ), Arcata (1; USNM), Carlotta (6 miles E on Highway 36) [June] (4; USNM), Fieldbrook [May] (2; USNM), Green Point [June] (3; CAS), Hoopa Valley (Trinity River at Fort Gaston) (3; USNM), Willow Creek [June] (2; CAS); Marin County, Lagunitas [Apr.] (1; CAS); Mendocino County (17; CAS, MCZ), Fort Bragg (4 miles E) [June] (1; CAS); Monterey County, Carmel River [Aug.] (1; CAS); Santa Clara County, Hecker Pass (SW of San Martin) [June] (1; CAS), Los Gatos (6; USNM); Santa Cruz County (1; USNM), Boulder Creek (2; CAS, MCZ); Siskiyou County (1; USNM); Sonoma County, Duncan Mills [June–July] (2; CAS), Healdsburg (and W at Mill Creek) [Apr., July] (3; CAS); Sylvania [Aug.] (2; MCZ); Trinity County, Coffee Creek [July] (1; CAS), French Creek (small tributary at Highway 299) [June] (2; CAS); County unknown, Santa Cruz Mountains (1; USNM). OREGON (14; CAS, MCZ, USNM): Benton County, Blodgett [June] (2; MCZ), Corvallis [Mar, May–June] (6; OSUO), Mary's Peak (1760 m]) [May, Aug.] (5; OSUO), Monroe [June] (4; OSUO), Philomath (9 miles W) [Sept.] (1; OSUO); Clackamas County, Zig Zag River (1 mile SE of Rhododendron [600 m]) [Aug.] (1; DHKa); Hood River County, Hood River [May, July] (3; CAS, USNM), Mount Hood (Sand Creek) [July] (1; CAS); Jackson County, Dead Indian Soda Spring (E of Copper) [May] (2; OSUO); Josephine County, O'Brien [May] (24; OSUO); Klamath County, Lake of the Woods (Ashland Road) [June] (1; OSUO); Lincoln County, Depot Bay [May] (1; OSUO); Linn County, Sweet Home (32 miles E [1130 m]) [Aug.] (1; OSUO); Multnomah County, Portland [May] (9; MCZ, USNM), Starvation Creek State Park [June] (2; OSUO); Tillamook County, Sand Lake [May, Nov.]

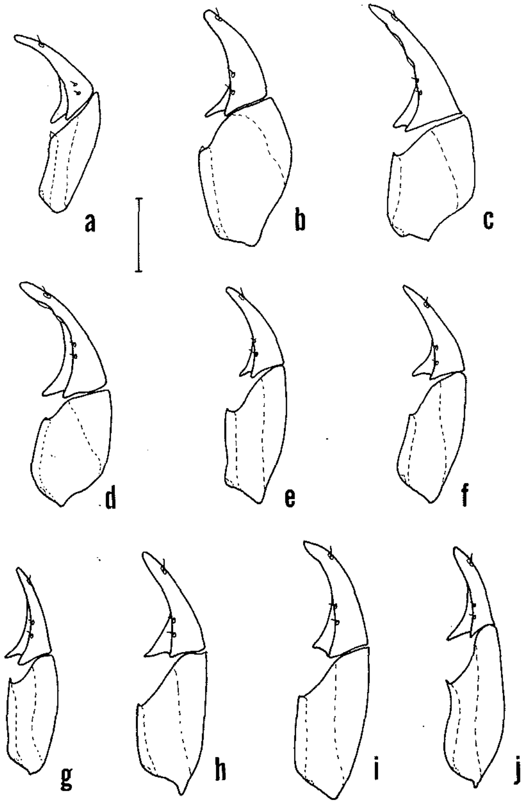


Fig. 13. Left coxostylus, female, ventral aspect. — a. *Bembidion carlhi* Tuolumne County, California). — b. *B. osculans* (Lassen Volcanic National Park, California). — c. *B. pseudoerasum* (Cisco, California). — d. *B. sequoiae* (Kings River, California). — e. *B. castum* (Los Gatos, California). — f. *B. disjunctum* (Creston, British Columbia). — g. *B. erasum* (Three Creeks Lake, Oregon). — h. *B. lindrothellus* (near Haines, Alaska). — i. *B. lummi* (Friday Harbor, Washington). — j. *B. chintimini* (Mary's Peak, Oregon). Scale line = 0.10 mm.

(2; OSUO); Washington County, Dilley (11; USNM), Forest Grove [Mar.] (2; OSUO); Yamhill County, McMinnville (and Peavine Ridge) [June–Aug., Oct.] (15; OSUO). WASHINGTON: Clallam County, Mora [May] (1; OSUO), Port Angeles [May] (1; CAS); Cowlitz County, Castle Rock [July] (1; OSUO); Grays Harbor County, Hoquiam [May] (1; CAS); King County, Cedar Mountain [May] (1; OSUO), Green River Gorge [May] (1; OSUO), Seattle [Apr.–May] (3; OSUO); Mount Rainier National Park, Louise Lake ([1430 m]) [May] (1; CNC), Nisqually River ([1220 m]) [May] (1; CNC), White River (at Silver Springs Campground [790 m]) [Aug.] (1; DHKa); Olympic National Park, Lake Quinault [June] (1; CAS); Pacific County, Willapa Harbor (Long Island) [Aug.] (1; OSUO), Pierce County, Elbe [June] (2; CAS), Fort Lewis [June] (1; OSUO); Skamania County, Little Huckleberry Mountain [July] (1; OSUO); Snohomish County, Chase Lake [Apr.] (1; OSUO); Thurston County, Olympia [Apr., Aug.] (7; MCZ, OSUO); County unknown, "Olympia" ([1520 m]) [Aug.] (CNC). STATE UNKNOWN: Washington Territory (1; USNM).
Anomalous records: OREGON: County unknown, Blue Mountains (Lewis Peak) [June] (1; OSUO).
Doubtful records: CALIFORNIA: Nevada County [June] (1; USNM). WASHINGTON: Yakima County, Naches [May] (1; OSUO).
Additional literature records: BRITISH COLUMBIA: Barkerville [doubtful record], Boundary Bay (Vancouver), Essondale [all Lindroth 1963].
ALASKA: Ketchikan [June–July, Sept.] [Lindroth 1963].

Geographical variation.—We could not detect any geographical variation in this species except in flight wing development. Brachypterous individuals apparently do not occur south of Portland, Oregon, whereas fully winged individuals are found throughout the range of the species. Intrapopulational variation occurs in coloration (but this seems tied to gradual development of pigmentation following molt to the adult stage), width of pronotum, and overall size. Some individuals in the Mary's Peak region of western Oregon and parts of western Washington and extreme southwestern British Columbia (i.e. in and adjacent to the Puget lowland) have their humeri narrowed, a feature usually associated with wing reduction, but have full-sized flight wings.

A single female specimen labelled as from the Blue Mountains of eastern Oregon, listed above as an "Anomalous Record", is unique in its possession of nearly isodiametric microsculpture and genitalic structures typical of *B. castum* females. Its presence so far outside the known range of *B. castum* is suspect; but, because of its microsculpture, we cannot suggest where the specimen may have been collected within the known range of this species.

TAXONOMIC NOTES.—Our study of Casey's type specimens showed that *B. brumale* and *B. vacivum* are conspecific with *B. castum*. These two names are based on brachypterous specimens which have the different body form described above. Unfortunately, Lindroth applied the name *B. brumale* to specimens of another brachyterous form he collected near Haines, Alaska. We here recognize the synonymy and describe below Lindroth's new species, *B. lindrothellus*, in his honor.

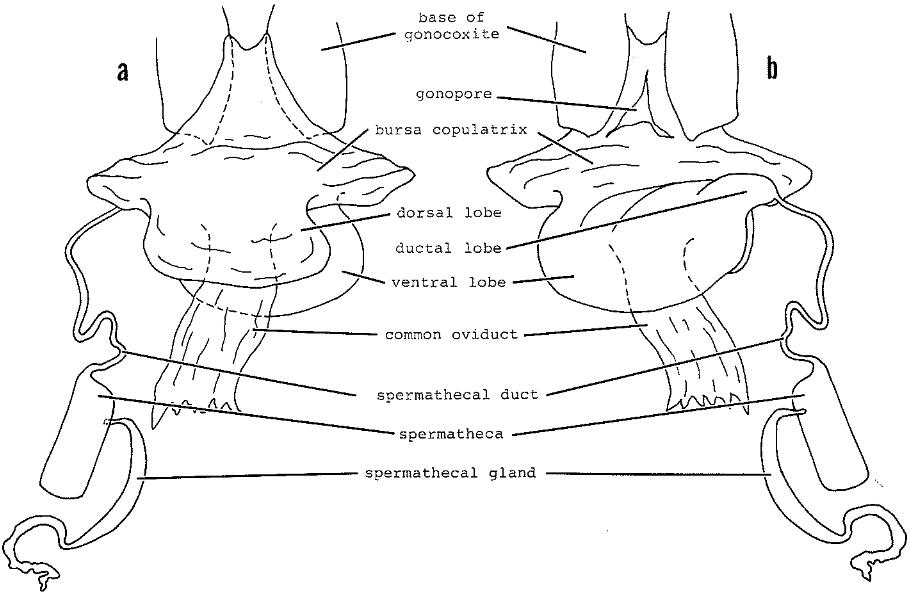


Fig. 14. Female genitalia, diagramatic, illustration of structures and points of reference used in text. — a. Dorsal aspect. — b. Ventral aspect.

The *disjunctum* subgroup

Adults of *B. disjunctum,* the single member of this subgroup, differ from members of the other *erasum* group species in having better-developed elytral interneurs and a flatter body form. Elytral microsculpture is nearly isodiametric, but not as perfectly so as in *B. erasum,* a condition regarded by Lindroth (1974b) as plesiotypic. *Bembidion disjunctum* adults share with *osculans, castum,* and *erasum* subgroup members pronotal form and structure, the apparent absence of interneurs 7 and 8, absence of recurrent groove, elytral seta Ed6 free (i.e. not associated with a recurrent groove), complete lateral margination of the metasternal intercoxal process, relatively short antennae with broad antennomeres, configuration of the sclerites of the male internal sac, and configuration and scleritization of the female bursa copulatrix and associated structures. Based on these shared derived character states, we include *B. disjunctum* in the *erasum* group. However, we place it in its own subgroup because of derived character states exhibited by its members, such as their more completely expressed elytral interneurs and depressed form. We place this subgroup between the *castum* and *erasum* subgroups based on the unique combination of primitive and derived features of the bursa copulatrix of females.

The *disjunctum* subgroup is sympatric with both the *erasum* and *osculans* subgroups and allopatric with respect to the range of the *castum* subgroup (except for the possible presence of *B. castum* in the Blue Mountains, see above). As the name implies, the range of *B. disjunctum* is apparently "disjunct"—southern British Columbia, Blue Mountains of northeastern Oregon, and mid-Sierra Nevada of California.

005. **Bembidion disjunctum** Lindroth

Figs. 5f, 6f, 7i, 11f, 12f, 13f, 15f, 16f, 24, 29.

Bembidion disjunctum Lindroth, 1963a:264. Holotype, a male, in MCZ, Type No. 32533. Type locality: Sonora Pass (west side, 2440 m), Tuolumne County, California.

Diagnostic features: Members of this species can be distinguished from other *erasum* group members by the following combination of character states: form depressed; five well-impressed striatopunctulate interneurs, lateral interneurs (6–8) finely punctulate, not quite effaced; narrow head and prothorax; and irregular, nearly isodiametric elytral microsculpture.

Size.—ABL = 3.86–4.21 mm; SBL = 3.28–3.81 mm; TW = 1.58–1.76 mm; TD = 0.59–0.79 mm.

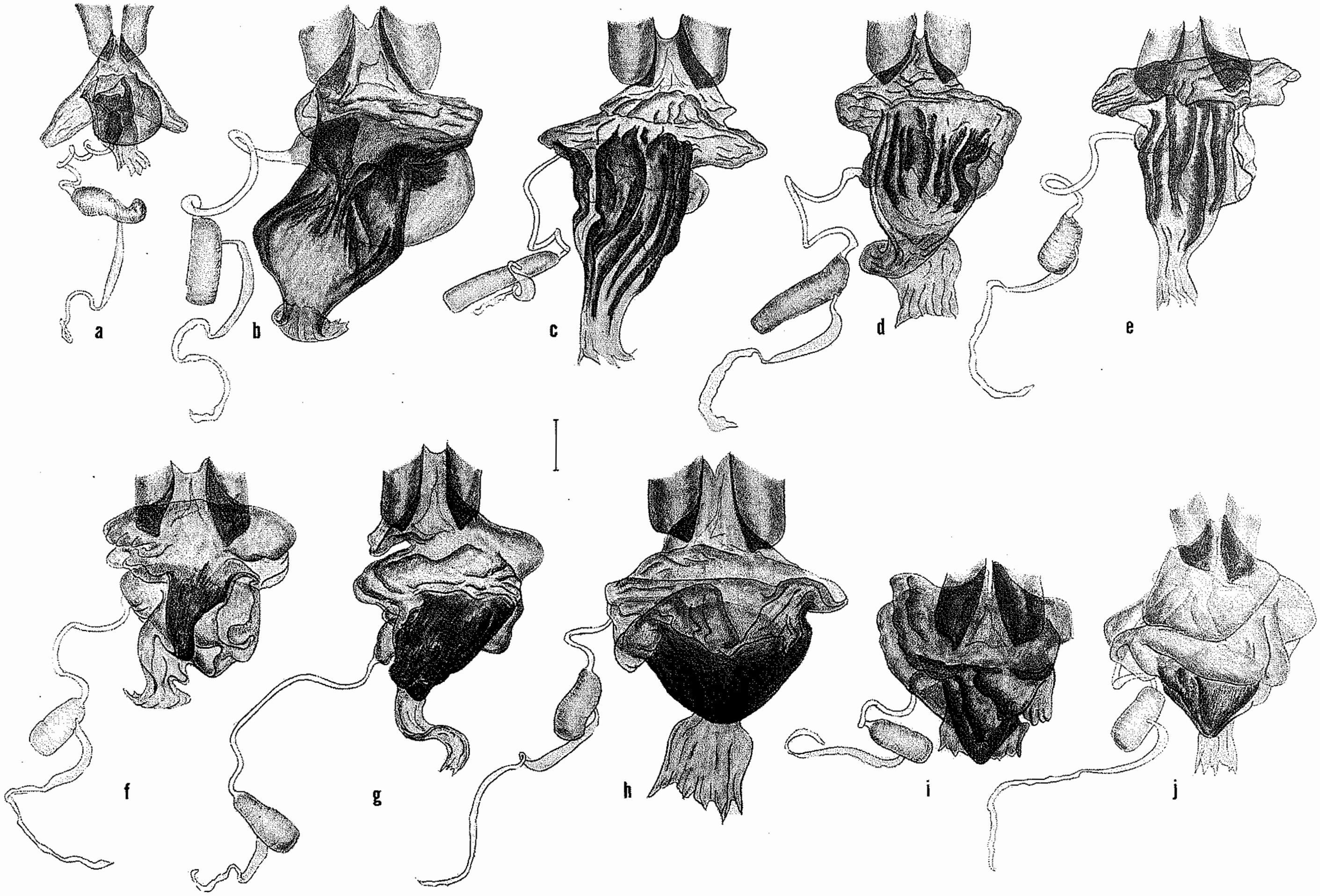


Fig. 15. Bursa copulatrix and associated structures, female, dorsal aspect. — a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. osculans* (Lassen Volcanic National Park, California). — c. *B. pseudoerasum* (Cisco, California). — d. *B. sequoiae* (Kings River, California). — e. *B. castum* (Los Gatos, California). — f. *B. disjunctum* (Creston, British Columbia). — g. *B. erasum* (Three Creeks Lake, Oregon). — h. *B. lindrothellus* (near Haines, Alaska). — i. *B. lummi* (Friday Harbor, Washington). — j. *B. chintimini* (Mary's Peak, Oregon). Scale line = 0.10 mm.

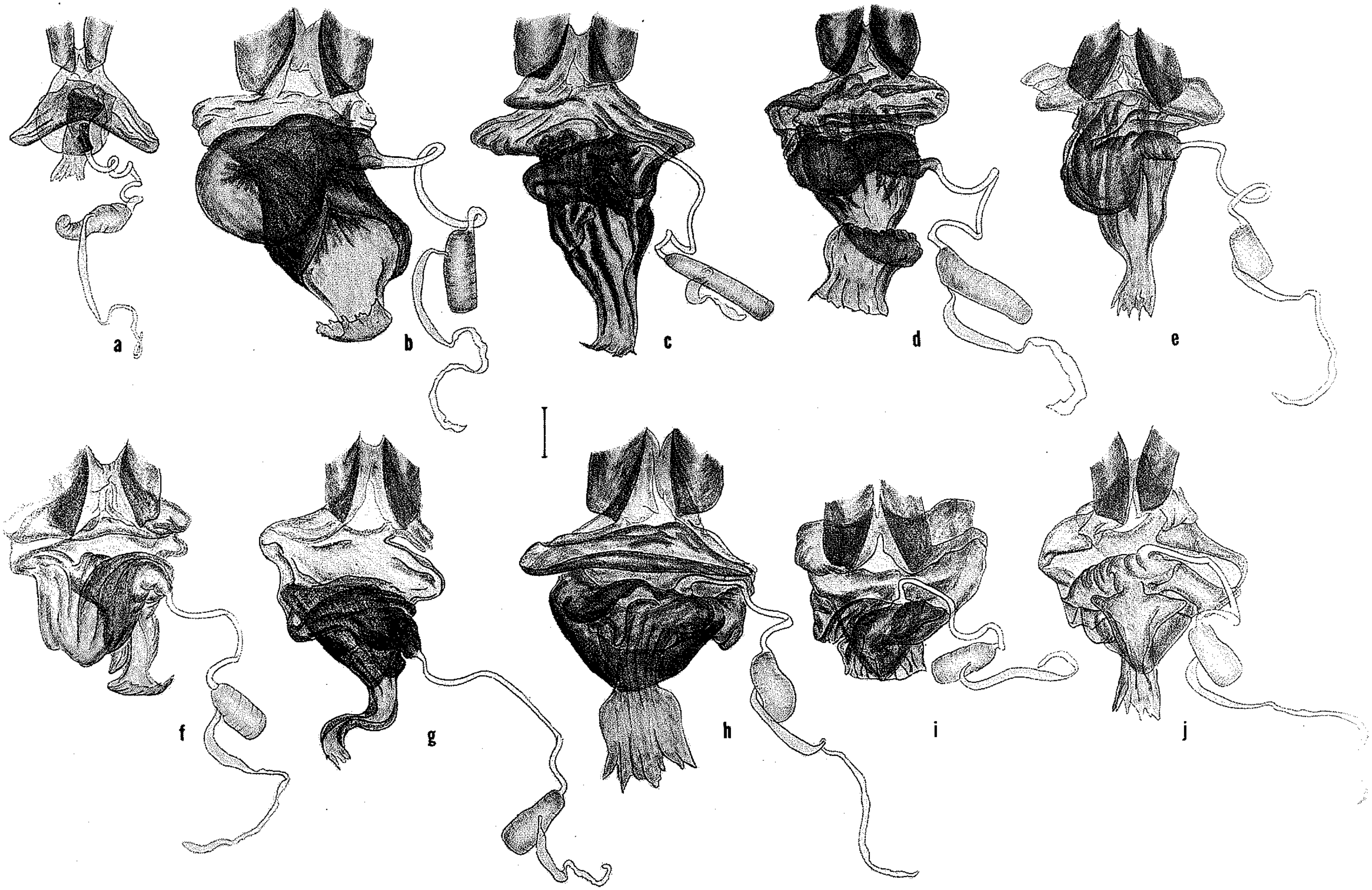


Fig. 16. Bursa copulatrix and associated structures, female, ventral aspect. — a. *Bembidion carlhi* (Tuolumne County, California). — b. *B. osculans* (Lassen Volcanic National Park, California). — c. *B. pseudoerasum* (Cisco, California). — d. *B. sequoiae* (Kings River, California). — e. *B. castum* (Los Gatos, California). — f. *B. disjunctum* (Creston, British Columbia). — g. *B. erasum* (Three Creeks Lake, Oregon). — h. *B. lindrothellus* (near Haines, Alaska). — i. *B. lummi* (Friday Harbor, Washington). — j. *B. chintimini* (Mary's Peak, Oregon). Scale line = 0.10 m.

Color and luster.—Rufopiceous, legs flavous, mouthparts and antennae rufopiceous. Dorsal surface shiny, especially head and pronotum, which have faint metallic reflections, elytra duller, especially in females, due to microsculpture.

Form.—Short, moderately broad and depressed. Head moderately narrow, narrower than pronotal base; eyes small, rounded; antennae short, not extended to seta Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5f) moderately narrow, but more than 1/3 wider than elytron, transverse, with moderately arcuate base, lateral margin sinuate anterior to the nearly rectangular posterior angle, anterior angle rounded, moderately produced. Elytra (Fig. 6f) with silhouette subrectangular, humeri squared, lateral margins slightly divergent beyond middle, intervals moderately convex. Foreleg of male with broadly dilated basitarsus about equal in width to tibial apex.

Structure.—Microsculpture (Fig. 7i) comprised of well-engraved, irregular, nearly isodiametric meshes on elytra, of finely engraved, slightly transverse meshes on head and pronotum. Elytra each with five (± 6, 7) clearly traceable interneurs, only 1 (± 2) extended to apex; interneurs striatopunctulate, striae more effaced laterally, punctulae smaller laterally and apically. Wings fully developed. *Male genitalia* as in Lindroth (1963a:264, fig. 128); median lobe with narrowly rounded and prolonged apex, shaft robust, tubular, basal constriction well-developed, ventral margin arcuate; internal sac with BW well developed, markedly curled at apex, CH1 plate-like, CH2–CH5 well developed. *Female genitalia* as in Figs. 11f, 12f, 13f, 15f, 16f; bursa copulatrix (Figs. 15f, 16f) with dorsal lobe distinct, small, dorsal sclerite transverse, lobate or triangulate, ventral lobe large, enlarged on left, with ductal lobe present; spermatheca short.

Notes on material examined.—The only male specimen available to us was the holotype. Lindroth dissected and figured the aedeagus of this specimen then glued it to a card and pinned it with the specimen. We did not think it wise to attempt extraction of the internal sac from this glue-dried aedeagus, thus we defer offering a comparative illustration at this time. Figure 128 in Lindroth (1963a) must suffice until additional males are discovered. Also for this reason, we were unable to prepare an electron scanning micrograph of elytral microsculpture of a male, but this appears to be the same as in females.

Natural history.—Lindroth (1963a) found the beetles "among gravel along a quite small cold-water brook" at 2440 m in the Sierra Nevada and along a "flooded creek" in British Columbia, both localities in the Canadian Zone. Two subteneral adult females (CAS) were collected in September and Lindroth's specimen from British Columbia (CNC), probably mature, was collected in May. Thus it is probable that adults overwinter. All specimens studied had fully developed flight wings, indicating potential for dispersion through the air.

Geographical distribution.—(Fig. 24). Members of this species are known from only three disjunct localities, the northernmost in southern British Columbia and the southernmost in the mid-Sierra Nevada at Sonora Pass. Because individuals are so rarely collected, even in areas where the species is known to occur, it is likely that this disjunct distribution pattern is at least partially due to incomplete sampling. However, this pattern is still a curious one, linking faunistically, as it does, the central Sierra Nevada directly with the Blue Mountains and western slope of the Rocky Mountains of southern British Columbia diagonally across the northern Great Basin. A more probable route of continuity of populations of *B. disjunctum* would be from the Sierra Nevada northward through the Cascade Range and then eastward through mountain ranges rimming the Columbia Plateau. To date, no specimens of *B. disjunctum* have been collected from any point along this route.

We have examined a total of 1 male and 5 females from the following localities:

BRITISH COLUMBIA: Creston (8 miles W) [June] (1; CNC), Eholt (NW of Grand Forsk) [May] (1; CNC). CALIFORNIA: Tuolumne County, Sonora Pass ([2440 m]) [Sept.] (3; CAS, MCZ). OREGON: Baker County, Baker (Pine Creek) [July] (1; USNM).

Geographical variation.—Too few specimens are presently available to assess either inter- or intrasite variation.

The *erasum* subgroup

The four members of this subgroup, *B. erasum, B. lindrothellus, B. lummi,* and *B. chin-*

timini, differ from members of the *osculans* subgroup in having less transverse, more mesh-like microsculpture of the elytra, and smaller size (ABL). They differ from members of the *disjunctum* subgroup in having fewer visible interneurs and more convex form and from *castum* subgroup females in having the bursa copulatrix (Figs. 15g–j and 16g–j) with a distinct dorsal lobe, dorsal sclerite transverse, and ventral lobe small, slightly enlarged on right.

The range of this species subgroup is the same as the total range for the *erasum* group (see above). The *erasum* subgroup members are sympatric, at least in part, with members of all the other subgroups. There is also some range overlap among species of the *erasum* subgroup. The range of *B. lindrothellus* narrowly overlaps the range of *B. lummi*. Geographical ranges of *B. erasum* and *B. castum* of the *castum* subgroup are allopatric except in a few areas where the range of the former reaches the coastal mountains or lowlands of northern California and central Washington (see below). The range of *B. erasum* does not overlap the ranges of any other species in the subgroup. The nominal species, *B. erasum*, has the broadest range of the entire species group and also appears to be the most varied in form.

006. **Bembidion erasum** LeConte

Figs. 3c, 4b, 5g, 6g, 7j–k, 8b, 10f, 11g, 12g, 13g, 15g, 16g, 17, 25, 29.

Bembidium erasum LeConte, 1859:83. Lectotype (here designated), a female, in MCZ, Type No. 5490. Type area: Oregon, as given by LeConte (1859:83) and Lindroth (1963a:261), herewith restricted to Fort Klamath, Klamath County, Oregon.

Bembidion lacivum Casey, 1918:21. Lectotype (designated by Lindroth 1975:116), a male, in USNM, Type No. 36821. Type locality: Lake Tahoe, California.—Lindroth 1963a:261; 1975:116.

Bembidion lubricum Casey, 1918:21. Lectotype (designated by Lindroth 1975:116), a male, in USNM, Type No. 36820. Type locality: Truckee, Nevada County, California.—Lindroth 1963a:261; 1975:116.

Bembidion probatum Casey, 1918:22. Lectotype (designated by Lindroth 1975:116), a female, in USNM, Type No. 36817. Type locality: Boulder, Boulder County, Colorado.—Lindroth 1963a:261; 1975:116.

Diagnostic features: Female members of this species can be identified most easily among group members by their regular isodiametric elytral microsculpture. Although the microsculpture is variously impressed among individuals, the meshes are visible in all but a very few specimens. In males, the meshes are nearly effaced from the elytra, thus making males easily identified among group members, the rest of which have evident transverse elytral microsculpture. In both sexes of *B. erasum*, most post-teneral (i.e. fully pigmented) individuals have black mouthparts and legs. In addition, the lateral pronotal margin is obliquely straight anterior to the obtuse, denticulate posterior angle (Fig. 5g).

Size.—ABL = 3.42–4.25 mm; SBL = 3.03–3.85 mm; TW = 1.51–1.65 mm; TD = 0.75–0.98 mm; WPB/EL: $\bar{X} = 0.406$, s = 0.014, c.v. = 3.53 (N = 30).

Color and luster.—Fully mature specimens black, appendages and elytral apices piceous or rufinistic in most individuals, tibiae paler than femora, palpi and antennal scape infuscated dorsally but rufous ventrally in some individuals. Dorsal surface shiny in males, females with elytra duller due to isodiametric microsculpture. Some individuals with slight blue or green metallic reflection.

Form.—Short, broad, subconvex. Head broad but narrower than pronotum; eyes small, rounded; antennae short, not extended to seta Eo4 on elytron, antennomeres broad. Pronotum (Fig. 5g) wide, 1/3 wider than elytron, transverse, with slightly arcuate base, lateral margin obliquely straight anterior to the obtuse, denticulate posterior angle, anterior angle rounded, slightly produced. Elytra (Fig. 6g) with silhouette subrectangular basally, humeri squared, lateral margins slightly divergent at middle, intervals nearly flat. Foreleg of male with normally dilated basitarsus and tarsomere 2 (Fig. 3c), the former slightly narrower than tibial apex.

Structure.—*Microsculpture* (Fig. 7j–k) of dorsum of most females comprised of perfectly isodiametric meshes, well-engraved on elytra, less so on head and pronotum (few females with elytral microsculpture nearly effaced); males without or with nearly effaced microsculpture on elytra and pronotum. *Elytra* each with four (± 5, 6) clearly traceable interneurs, only 1 (± 2) extended to apex; interneurs striatopunctulate, striae more effaced laterally, punctulae smaller laterally. Wings fully developed. *Male genitalia* as in Fig. 10f; median lobe with apex slightly flared and squared, shaft robust, tubular, basal constriction markedly well developed, ventral margin angulate at middle; internal sac with BW broad and long with its apex broadly curled transversely, CH1 narrowly spatulate, CH2–CH5 well developed, OF doubled, narrow, well defined. *Female genitalia* as in Figs. 11g, 12g, 13g, 15g, 16g; eight tergum (Fig. 12g) with discal macula evident; bursa copulatrix (Figs. 15g, 16g) with dorsal lobe moderate in size, dorsal sclerite lobate or triangulate, not dorsoventrally deepened, ventral lobe with evident ductal lobe; spermathecal duct inserted on apex of ductal lobe.

Natural history.—These beetles are found at medium to high elevations at the margins of cold water rills, streams, and snowfields, and (in northern localities) also along small rivers in drift debris on banks. During daylight hours, they hide under stones at water's edge, among leaves, or in moss. *B. erasum* members are normally inhabitants of the Canadian Zone; but they may also be found in the Transition Zone at the margins of very cold streams in heavily shaded areas. They apparently also disperse upward into the Hudsonian Zone, where they are found at receding snowfield and lake margins. Most individuals overwinter as adults, which emerge in May, mate, and oviposite. Teneral adults of the subsequent generation emerge by July or August. It appears that larval and pupal individuals are present from late May through August, depending on latitude and elevation. The fully developed wings of all individuals and the wide geographical range of the species suggest that these beetles may disperse by flight.

Geographical distribution.—(Fig. 25). *Bembidion erasum* is the most widespread species of the *erasum* group, with a range extended from southeastern British Columbia and southwestern Alberta southward along the Cascade Range, Sierra Nevada, and beyond to the San Jacinto Mountains in southern California, east through Idaho, Nevada, and Utah, and south along the Rocky Mountains to northern Colorado. This distribution pattern is almost completely confined to the mountainous areas of the Great Basin and its perimeter. For example, *B. erasum* is restricted in Oregon to the area east of and including the eastern slope of the Cascade Range. However, its range extends out of the Great Basin region (including the latter's western mountainous perimeter—i.e. the Cascade Range and Sierra Nevada) and into the Cowlitz Valley, Puget lowland (Olympia), and northeast flank of the Olympic Mountains in western Washington, and onto the eastern slope of the Klamath Mountain system in northwestern California. In both of these general areas, it is at least macrosympatric with *B. castum*.

We have examined a total of 130 males and 181 females from the following localities:

ALBERTA: Crowsnest Pass (4; CNC, USNM, Kananaskis Forest Experiment Station (10 miles SW [1520 m]) [July–Aug.] (3; CNC). BRITISH COLUMBIA: Kootenay National Park, Kootenay River (at Route 1B) [Aug.] (1; UASM); Mount Revelstoke National Park ([1370 m]) [Aug.] (1; CNC); Other localities: Cabin Creek (tributary of Flathead River [1520 m]) [Aug.] (1; UBC), Cherryville (Twelvemile Creek at Monashee Road) [July] (1; CAS), Christina Lake (15 miles E [1620 m]) [May] (2; UASM), Copper Mountain (Similkameen River) [Sept.–Oct.] (5; UBC), Creston (8 miles W) [June] (4; CNC), Fernie [July] (1; CAS), Kingsgate [Apr., July] (7; CNC, UASM, UBC), Oliver (McIntyre Road [910 m]) [June] (1; CNC), Osoyoos (12 miles E) [May] (1; UASM), Rock Creek [May] (11; UASM), Rossland trail [May] (7; CNC, MCZ), Spious Creek [July] (1; CAS), St. Mary's Lake (near Kimberley [910 m]) [Aug.] (1; UASM), Trinity Valley [May] (1; CAS) CALIFORNIA (1; CAS): Alpine County, Blue Lakes [Aug.] (4; CAS); Calaveras County, Big Meadows [June] (1; CAS), Calaveras Big Trees State Park [July] (1; CAS); El Dorado County (1; CAS), Glen Alpine [July] (1; CAS), Meeks Creek [Aug.] (1; CAS), Strawberry (1; CAS), Tallac (Taylor Creek [1890 m]) [June] (1; CAS); Fresno County, Kings River ([1460 m]) [July] (1; USNM), Huckleberry Meadow ([1980 m]) [Aug.] (2; CAS); Glenn County, Board Tree Camp [Aug.] (1; CAS); Humboldt County (1; CAS); Inyo County, Big Pine Creek (at First Lake) [May] (1; CAS), Bishop [June] (1; CAS), Death Valley National Monument (Eagle Spring on Telescope Peak [2900 m]) [July] (1; CAS), Horton Lake (W of Bishop [3050 m]) [Aug.] (1; CAS), Onion Valley (Independence Creek [2550 m]) [July] (1; DHKa), Wyman Creek ([2470 m]) [Sept.] (1; CAS); Kings Canyon National Park, General Grant Grove [Aug.] (1; CAS); Lassen County, Silver Lake [Aug.] (1; CDAS); Lassen Volcanic National Park, Emerald Lake ([2450 m]) [Aug.] (2; DHKa); Madera County, Boggy Meadow (4.8 miles ESE of Fish Camp [1950 m]) [Aug.] (1; CAS), Chiquito Creek (at Clover Meadow Road [2070 m]) [Aug.] (3; CAS); Mendocino County (1; MCZ); Modoc County, Cedar Creek (E of Cedear Pass [1620 m] [Aug.] (8; CAS), Cedar Pass ([1830 m]) [Aug.] (1; CNC), Davis Creek [July] (1; CAS); Mono County, Crooked Creek ([3090 m]) [June] (1; CAS), Lundy ([2130 m–2440 m]) [July] (1; USNM), Sonora Pass [Sept.] (1; USNM), Robinson Creek (trail above Twin Lakes [2286 m]) [Aug.] (3; CAS); Nevada County, Prosser Creek (1 mile SW of Hobart Mills [1770 m], 1 mile W of Hobart Mills) [June–July] (2; DHKa, USNM), Truckee ([1770 m], Truckee River [1750 m]) [July–Aug.] (20; CAS, DHKa, USNM), Upper Truckee River [Aug.] (1; CAS); Placer County [Aug.] (1; USNM); Plumas County, Benner Creek (6 miles NW of Chester) [July–Aug.] (4; USNM); Riverside County, San Jacinto Mountains [July] (1; CAS); Sequoia National Park (1; CAS), Gray Meadow [July]

(1; CAS), Mount Silliman (Twin Lakes [2990 m]) [Aug.] (1; CAS); Shasta County, Hat Creek [Aug.] (1; CAS); Sierra County, Independence Creek [July] (1; CDAS); Siskiyou County [July] (2; CAS), Big Flat Campground [Sept.] (1; CAS), East Fork of South Fork Salmon River (at lake above headwaters [2030 m]) [Aug.] (2; CAS), Josephine Creek (at Carter's Trinity Alps Lodge [1570 m]) [Aug.] (1; CAS), Mount Shasta ([2440 m]) (Aug.] (1; CAS), Shasta Retreat [July] (2; CAS), Sisson (=town of Mount Shasta) [July] (1; USNM), Taylor Lake Road (small tributary of Taylor Creek [1750 m]) [Aug.] (1; CAS), Wolf Creek (S of Callahan [1580 m]) [Aug.] (1; CAS); Tehama County, Summit Creek (4 miles ENE of Mineral on Highway 36 [1710 m]) [Aug.] (1; DHKa); Tulare County, Franklin Lakes [Sept.] (1; CAS), Mineral King (Tar Gap Trail) [Sept.] (1; CAS); Tuolumne County (1; CAS), Dodge Ridge [Aug.] (19; CAS), Gardners [July] (4; CAS), Long Barn (Rush Creek) [Sept.] (1; CAS), Sonora Pass [Aug.–Sept.] (3; CAS), Strawberry [Aug.–Sept.] (3; CAS, UCD), Sugarpine [Aug.] (2; CAS); County unknown, Lake Tahoe [July] (21; USNM), San Bernardino Mountains (2; CAS, MCZ). COLORADO: Boulder County, Boulder (8, USNM); Clear Creek County, Silver Plume [June] (1; USNM); Mesa County (1; USNM); Routt County, Steamboat Springs ([2070m]) [July] (1; CAS); IDAHO: Blaine County, Big Wood River (3 miles N of Ketchum) [July] (1; CAS), North Fork Warm Springs Creek (1 mile E of Dollarhide Summit [2440 m–2500 m]) [Aug.] (1; DHKa); Camas County, South Fork Boise River (34 miles E of Featherville at Bear Creek [1830 m]) [Aug.] (2; DHKa); Custer County, Wet Creek (2 miles WSW of Pass Creek Pass [2410 m]) [Aug.] (1; DHKa); Latah County, Cedar Mountain [May] (1; OSUO); Twin Falls County (1; CAS). MONTANA: Sweetgrass County, Big Timber Creek (at Half Moon Campground [2230 m — 2290 m]) [July] (1; DHKa). NEVADA (2; MCZ, USNM): Elko County, Thomas Creek (8 miles SE of Lamoille at Thomas Creek Campground [2320 m — 2380 m]) [Aug.] (1; DHKa); Pershing County, Oreana (7 miles E) [Aug.] (1; CDAS); White Pine County, Duckwater Peak (east slope 13 miles W of Highway 6 [2440 m]) [July] (1; DHKa). OREGON (4; MCZ): Baker County, Baker (Pine Creek) [July] (5; OSUO, USNM); Deschutes County, Elk Lake ([1170 m]) [July] (14; OSUO), Indian Fork Creek (4 miles NW of Sisters) [May–June] (9; OSUO), Three Creek Lake (17 miles S of Sisters [1950 m]) [July] (2; OSUO); Grant County, Austin [June] (1; OSUO), Strawberry Lake [June] (1; OSUO); Hood River County, Hood River [July] (1; CAS); Jefferson County, McKenzie Pass [June] (1; OSUO), Metolius River [May] (1; OSUO); Klamath County, Fort Klamath (7.5 miles SW) [May] (4; CNC), Wood River (headwaters) [Sept.] (2; CAS); Lake County, Lakeview [June] (2; OSUO); Umatilla County, Meacham [May] (1; OSUO), Mottet Meadow [Sept.] (1; OSUO), Wildwoman Spring (3 miles ENE of Tollgate [1550 m]) [July] (1; OSUO); Wallowa County, Lostine River (17 miles S of Lostine [1650 m]) [July–Aug.] (3; OSUO), Wallowa Lake (inlet at S end [1340 m]) [July] (1; OSUO); Wasco County, Tygh Valley [June] (1; OSUO); Wheeler County, North Fork Deadhorse Creek (10 miles NNE of Spary [970 m]) [July] (1; CAS); County unknown, Bear Springs [June] (1; OSUO), Mount Hood ([1680 m]) [June] (1; OSDUO). UTAH: Summit County, Park City [June] (1; USNM); Utah County, Aspen Grove ([2130 m]) [May] (1; CAS). WASHINGTON: Olympic National Park, Hurricane Hill [July] (2; OSUO); Skamania County, Mount St. Helens (northeast slope [1520 m–1620 m]) [Aug.] (1; DHKa); Thurston County, Olympia (1; MCZ); Whatcom County, Mount Baker (Razor Hone Creek [1680 m]) [Aug.] (1; DHKa); Yakima County, American River (Lodgepole Campground) [June–July] (2; OSUO); County unknown, Blue Mountains [July] (2; OSUO). WYOMING: Yellowstone National Park [Aug.] (1; USNM). STATE UNKNOWN: Washington Territory (3; USNM). *Specimens without locality data:* (1; CNC).

Geographical variation.—We could not detect clinal variation among population of this species for any characters studied. Intrapopulational variation occurs in form and structure of the following characters: width of pronotum relative to elytral width; relative width of lateral explanation of pronotum; degree of development, depth of impression, and punctation of elytral interneurs; and degree of impression of elytral microsculpture (especially in males).

Taxonomic notes.—Lindroth (1963a) designated this species as the type of subgenus *Lionepha* Casey, 1918. Although Casey designated "erasum LeC" as type species, his concept of *B. erasum* LeConte, as is evident from a study of his collection, was wrong. Lindroth (1963a) described Casey's "*erasum*" specimens as a distinct species, *B. pseudoerasum*. Casey's three synonyms were based on individual variation in form and color and, in the case of *B. lacivum,* on his judgment that specimens from the Lake Tahoe, California, area had especially long and narrow antennae. We could not recognize such a distinguishing feature among members of Lake Tahoe samples.

007. **Bembidion lindrothellus** n.sp.

Figs. 5h, 6h, 7l, 10g, 11h, 12h, 13h, 15h, 16h, 17, 26, 29.

Type locality: U.S.A., Alaska: Little Boulder Creek, Haines Highway Mile 31.5.
Type material: Holotype ♂, U.S.A., Alaska, Little Boulder Creek, Haines Highway Mile 31.5, 24–25 June 1958, Stop 314. Leg. C. H. Lindroth, in coll. MCZ, Type No. 32549. — Paratypes: BRITISH COLUMBIA: Terrace [Aug.] (1; CNC); Vancouver Island, Saanich [June] (1; CNC). ALASKA: Haines Highway (Mile 4.5) [June] (1; UASM), Little Boulder Creek (Haines Highway Mile 31) [June] (2; MCZ). WASHINGTON: Pierce County, Fort Lewis [June] (1; OSUO).

Diagnostic features: Members of *B. lindrothellus* may be distinguished from other group members by their brown color, elongate form in proportion to the width pronotal base (see *size* below), presence of nearly isodiametric microsculpture, geographical range, and configuration of genitalic structures.

Derivation of taxon name: We take great pleasure in naming this species for Carl H. Lindroth, who collected the type specimen and actually described the species but used an old name for it, not recognizing it to be undescribed. The epithet *lindrothellus* is a noun in apposition meaning "little Lindroth", in reference to the small size of these and other *Bembidion* beetles for which Carl held such fascination.

Size.—ABL = 3.81–4.48 mm; SBL = 3.49–4.18 mm; TW = 1.53–1.90 mm; TD = 0.90–1.05 mm; WPB/EL: $\bar{X} = 0.370$, s = 0.017, c. v. = 4.595 (N = 6).

Color and luster.—Flavous, legs flavotestaceous, antennae and mouthparts flavopiceous. Dorsal surface shiny, more so in males than females due to more deeply engraved microsculpture in the latter.

Form.—Moderately elongate and narrow, subconvex. Head moderately narrow, narrower than pronotal base; eyes medium-sized, rounded; antennae short, not extended to seta Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5h) moderately broad, less than 1/3 wider than elytron, transverse, with slightly arcuate base, lateral margin broadly explanate in females, slightly sinuate anterior to slightly obtuse posterior angle, anterior angle rounded, moderately produced. Elytra (Fig. 6h) with silhouette spatulate, humeri markedly narrowed, lateral margins markedly arcuate, intervals flat. Foreleg of male with broadly dilated basitarsus, about equal in width to tibial apex.

Structure.—*Microsculpture* (Fig. 71) comprised of moderately well-engraved, nearly isodiametric meshes on elytra, fine and transverse meshes on pronotum and head. *Elytra* each with two (± 3, 4, 5) clearly traceable interneurs, only 1 (± 2) extended to apex; interneurs striatopunctulate, striae effaced laterally, punctulae smaller laterally and apically. *Wings* either fully developed or reduced to minute, veinless pad. *Male genitalia* as in Fig. 127f in Lindroth (1963a); median lobe with broadly squared apex (Fig. 10g), shaft tubular, broad apically, narrowed to shallow basal constriction, ventral margin evenly arcuate; internal sac similar to that of *B. erasum* male, except BW narrowly curled transversely and CH1 broad and spoon-like. *Female genitalia* as in Figs. 11h, 12h, 13h, 15h, 16h; eight tergum (Fig. 12h) with discal macula obscure; bursa copulatrix (Figs. 15h, 16h) with dorsal lobe moderate in size, dorsal sclerite lobate, not dorsoventrally deepened, ventral lobe without ductal lobe; spermathecal duct inserted directly on ventral lobe near midline.

Natural history.—Specimens collected by Ball and Lindroth near Haines, Alaska were found beneath "rosettes of *Taraxacum* on dry, hard, sun-exposed gravel near a creek." One of four specimens from Haines collected in June was teneral; thus at this high latitude it is likely that overwintering takes place in the larval stage, at least in part. All localities from which *B. lindrothellus* were recorded are in the Canadian Zone. Specimens from the Haines, Alaska area and from Terrace, British Columbia have highly reduced wings, but specimens from the other known localities are fully winged.

Geographical distribution.—(Fig. 26). This species is presently known from only a few widely separated, coastal localities in southeastern Alaska, British Columbia (including Vancouver Island), and Washington. Areas between these known locality records are among the most poorly sampled areas in North America, and it is likely that the distribution of this species is much more nearly continuous than is presently apparent.

Geographical variation.—In the small sample available, we could not detect geographical variation in any features studied. However, we note here that sexual dimorphism is apparent in degree of development of dorsal microsculpture. Females have more deeply engraved meshes than males.

Taxonomic notes.—Lindroth (1963a) described this species and illustrated its pronotum and male aedeagus. However, he thought it to be *B. brumale* Casey and applied that name. Our study shows that the type of *B. brumale* is a brachypterous *B. castum* female and not conspecific with individuals from the Haines, Alaska area upon which Lindroth's concept of *B. brumale* was formed.

008. **Bembidion lummi** n.sp.

Figs. 5i, 6i, 7m, 10h, 11i, 12i, 13i, 15i, 16i, 27, 29.

Type locality: U.S.A., Washington: San Juan Island, Friday Harbour.

Type material: Holotype ♀, U.S.A., Washington, Friday Harbor, San Juan Island, San Juan County, 10 August 1926. Leg. Unknown, in coll. CAS (on permanent deposit from OSUO), Type No. 13652. — *Paratypes:* BRITISH COLUMBIA: Barkerville (Grouse Creek [1280 m — 1310 m]) [Sept.] (2; UBC). WASHINGTON: San Juan County, San Juan Island (American Camp, Friday Harbor) [Apr.–May, Aug.] (4; CAS, OSUO, USNM).
Diagnostic features: Members of *B. lummi* are superficially very similar to *B. castum* members (winged form) and can reliably distinguished only by features of either male or female genitalia.
Derivation of taxon name: This species is named for the Lummi Tribe—the people native to the area including San Juan Island, on which the type locality is located.

Size.—ABL = 3.99–4.58 mm; SBL = 3.73–4.00 mm; TW = 1.68–1.89 mm; TD = 0.92–1.14 mm; WPB/EL: $\bar{X} = 0.381$, s = 0.012, c.v. = 3.196 (N = 6).

Color and luster.—Piceous, legs flavotestaceous, infuscated in part, antennae and mouthparts piceous. Dorsal surface shiny.

Form.—Moderately elongate and broad, subconvex. Head moderately narrow, slightly narrower than pronotal base; eyes medium-sized, rounded; antennae short, not extended to Eo3 on elytron, antennomeres broad. Pronotum (Fig. 5i) moderately broad, less than 1/3 wider than elytron, transverse, with slightly arcuate base, lateral margin behind middle straight to slightly obtuse posterior angle, anterior angle rounded, moderately produced. Elytra (Fig. 6i) with silhouette subrectangulate, humeri squared, lateral margin slightly arcuate, intervals flat. Foreleg of male with broadly dilated basitarsus, about equal in width to tibial apex.

Structure.—*Microsculpture* (Fig. 7m) comprised of moderately well-engraved, irregular and slightly transverse meshes on elytron, pronotum, and head. *Elytra* each with two (+ 3, 4, 5) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate, striae and punctulae effaced laterally and apically. *Wings* fully developed. *Male genitalia* as in Fig. 10h; median lobe with broadly rounded apex, shaft tubular, broad apically, narrowed slightly to shallow basal constriction, ventral margin evenly, shallowly arcuate; internal sac similar to that of *B. castum* males except BW apical curl narrower, more well developed. *Female genitalia* as in Figs. 11i, 12i, 13i, 15i, 16i; eighth tergum (Fig. 12i) with discal macula obscure; bursa copulatrix (Figs. 15i, 16i) with dorsal lobe small, dorsal sclerite triangulate, not dorsoventrally deepened, ventral lobe without ductal lobe; spermathecal duct inserted directly on ventral lobe near midline.

Natural history.—Members of *B. lummi* are found at low elevation in western Washington and at mid-elevation in eastern British Columbia (ca. 1300 m). Their precise microhabitat is unknown, although two specimens from Barkerville (British Columbia) are labelled as from "Grouse Creek". From this information and known microhabitat requirements of related species, we predict that these beetles will be found in the same kinds of microhabitats as *B. castum* adults (see above). None of the specimens studied was teneral; all had fully developed wings which suggest that dispersion by flight is probable.

Geographical distribution.—(Fig. 27). This species is presently known from only two widely separated and environmentally different areas—one on an island on Puget Sound, Washington, the other on the eastern edge of the Central Plateau in eastern British Columbia. This unusual disjunction is perhaps more apparent than real. Intervening areas, especially in western British Columbia, have been very poorly sampled to date. However, if the disjunction is real, the pattern is most likely a relict one, and one not shared with any other carabid species known at present.

Geographical variation.—Too few specimens were available to adequately study geographical variation; however, we noted that specimens from San Juan Island are more robust in body form than specimens from Barkerville.

009. **Bembidion chintimini** n.sp.

Figs. 5j, 6j, 11j, 12j, 13, 15j, 16j, 17, 27, 29.

Type locality: U.S.A., Oregon, Benton County, Mary's Peak.
Type material: Holotype ♀, U.S.A., Oregon, Mary's Peak (8 miles W of Philomath, 1220 m), Benton County, 9 May 1968. Leg. J. M. Campell & A. Smetana, in coll. CNC, Type No. 16452 No other specimens known.
Diagnostic features: Members of *B. chintimini* are superficially similar to members of *B. lindrothellus* and can only be distinguished from the latter reliably by characters of female (male unknown) genitalic structure. However, the specimen of *B. chintimini* has infiscated legs, antennomeres, and mouthparts, while all

specimens of *B. lindrothellus* studied have these appendages flavous. In addition, the latter have the elytral microsculpture nearly isodiametric whereas the *B. chintimini* specimen has slightly transverse meshes. *Derivation of taxon name:* For this species, we have selected the name given to Mary's Peak by local native peoples—*Chintimini,* the meaning of which is unknown.

Size.—ABL = 3.99 mm; SBL = 3.90; TW = 1.77; TD = 0.98.

Color and luster.—Piceous, appendages rufotestaceous, infuscated in part. Dorsal surface of head and prothorax shiny; elytra dull due to more deeply-engraved microsculpture.

Form.—Moderately elongate and broad, subconvex. Head moderately broad, slightly narrower than pronotal base; eyes medium-sized, rounded; antennae unknown (missing from unique type), except basal two antennomeres, these broad as in *B. erasum* members. Pronotum (Fig. 5j) broad, 1/4 wider than elytron, transverse, with slightly arcuate base, lateral margin behind middle straight to obtuse, denticulate posterior angle, anterior angle rounded, moderately produced. Elytra (Fig. 6j) with silhouette subspatulate, humeri moderately sloped, lateral margin moderately arcuate, intervals flat. Foreleg of male unknown.

Structure.—*Microsculpture* (not figured) comprised of slightly transverse, well-engraved, irregular meshes on elytron, more transverse and less deeply engraved on pronotum and head. *Elytra* each with two (+ 3, 4) clearly traceable interneurs, only 1 extended to apex; interneurs striatopunctulate, striae and punctulae effaced laterally and apically. *Wings* short. *Male genitalia* unknown. *Female genitalia* as in Figs. 11j, 12j, 13j, 15j 16j; eight tergum (Fig. 12j) with discal macula obscure; bursa copulatrix (Figs. 15j, 16j) with dorsal lobe small, dorsal sclerite triangulate and dorsoventrally deepened, ventral lobe without ductal lobe; spermathecal duct inserted directly on ventral lobe near midline.

Natural history.—The single known specimen of this species was collected in May at 1220 m elevation on Mary's Peak, Oregon, in some unknown microhabitat in the upper Canadian Zone. However, from its relationships among *erasum* group members, we predict that it will be found on tertiary floodplain or adjacent forest margins in leaf litter or other debris on sandy soil. We predict further that all members of *B. chintimini* will be found to be brachypterous, based on the nature of the presumed microhabitat and the degree of isolation of the locality.

Geographical distribution.—Fig. 27. This species is known only from the type locality in the Coast Range of central Oregon. Mary's Peak, a mountain which is low by all but regional standards, nonetheless provides sufficiently isolated mid-altitude habitats that it harbors numerous other endemic and/or at least differentiated forms of carabid beetles and other organisms. We therefore suspect that *B. chintimini,* with its members presumably all brachypterous, fits this pattern and is unlikely to occur elsewhere.

Geographical variation.—Unknown and unlikely (see above).

Phylogeny and zoogeography

Phylogeny

These are the first species groups we have studied thoroughly; and therefore data for outgroup comparisons (necessarily) were gleaned from varied literature sources, particularly from papers by Lindroth and Netolitzky. Despite this difficulty, we here present a hypothesis and its supporting evidence regarding phylogenetic relationships among members of the *erasum* group, and between the *carlhi* and *erasum* groups. At this time, we cannot say where these groups belong within genus *Bembidion.*

Configurations of the armature of the internal sac of the male aedeagus and of the female reproductive system constitute two major suites of characters important for phylogenetic analysis. In addition, several other characters of external form seem useful for they exhibit states which lend themselves to analysis (Tab. 2).

Out-group comparisons within genus *Bembidion* indicate that at least five groups—*guttula, carlhi, erasum, vile,* and *transparens*—may constitute a monophyletic lineage, all male members of which share the apotypic feature CH1 present and located near apex of BW. We have not yet studied the *guttula, vile,* and *transparens* groups at the species level, and therefore intergroup relationships are yet unclear. Consequently, these relationships are not depicted in the cladogram, Fig. 29, nor are they discussed

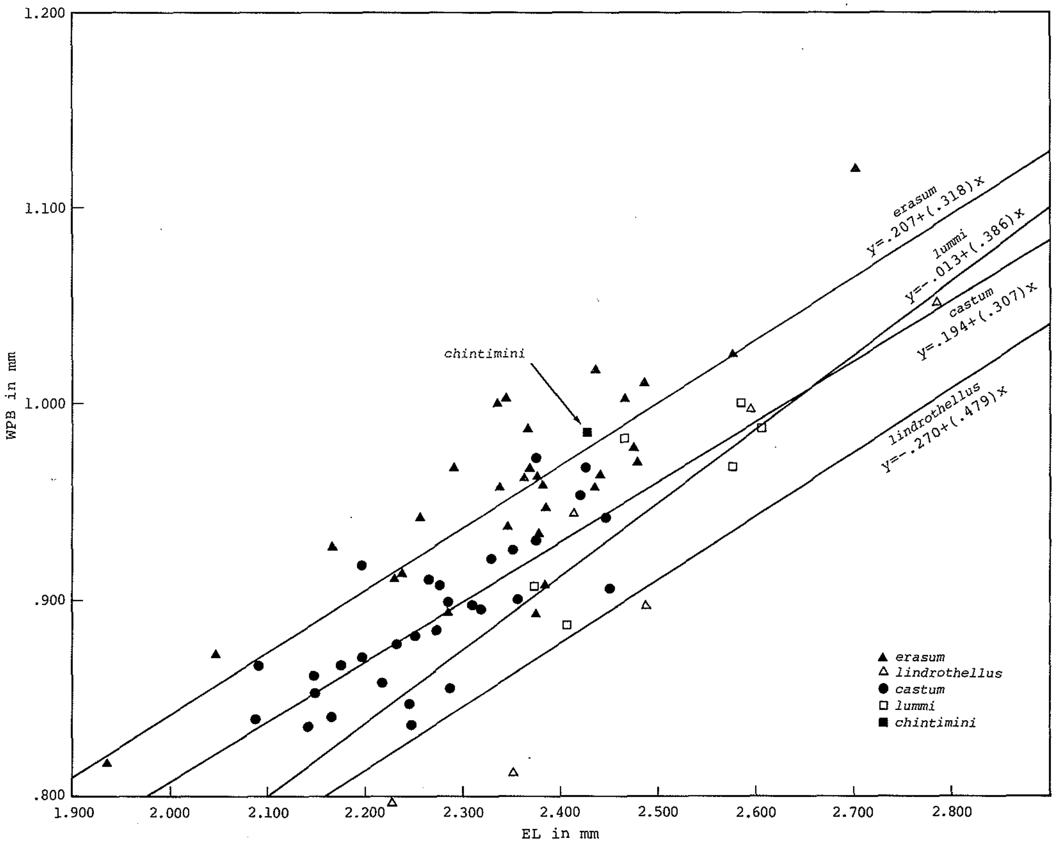


Fig. 17. Linear regression fitted to data plotted on scattergram illustrating relationship between WPB and EL (WPB/EL) for *castum* and *erasum* subgroup taxa.

further here. At this point in our study, we must consider the *carlhi* and *erasum* groups to be sisters, all other groups being ignored until the we have dealt with them in detail. Because the *carlhi* group is monotypic, its inclusion in the cladogram contributes nothing; and we therefore represent and discuss only intragroup relationships among *erasum* group members.

The distribution of character states among members of the *erasum* group for characters used in our cladistic analysis in presented in Tab. 3. Generally, within this group, *osculans* subgroup members represent the plesion level of evolution; but species of this subgroup share numerous apotypic features (see cladogram, Fig. 29). In contrast, *castum, disjunctum,* and *erasum* subgroup members share apotypic feature N (Tab. 2). In their descent from a common ancestor, *castum* subgroup members acquired Gb, Jb, Ob, and Pb as apotypic features, and *disjunctum*/*erasum* subgroup members acquired apotypic features Xc and W. *Disjunctum* subgroup members subsequently acquired apotypic features A, B, Fb, I, and Xc, d while *erasum* subgroup members acquired apotypic feature U. Hypothetical relationships among these four species subgroups are illustrated in the cladogram, Fig. 29.

We discuss below, in a context of historical zoogeography, the hypothetical sequence in acquisition of additional apotypic features, and therefore the subsequent branching sequence, at the species level.

Table 2. Cladistic classification of character states for members of the *erasum* species group of *Bembidion*

Character		Plesiotypic state	Apotypic state	Criterion (-a)
Head				
A	Antenna	short	long	I
B	Antennomeres	broad	narrow	I
Prothorax				
C	Basitarsus, male	broadly dilated	moderately dilated	V
Pronotum				
D	Shape	quadrate	broadly transverse	V
E	Lateral margination	narrowly explanate	broadly explanate	V
Elytron				
F	Interneurs, number	eight complete	three or four complete (a)^{1} seven complete (b)^{2} two complete (c)$^{2'}$	I, II
G	Microsculpture	slightly transverse	isodiametric, effaced (a)$^{1'}$ moderately transverse (b)^{1} markedly transverse (c)^{2}	II, III
H	Recurrent groove	present	absent	I
I	Form	subconvex	depressed	I
Flight wings				
J	Length	full	short (a)^{1} *dimorphic* (b)$^{1'}$	IV
Color				
K	Body	piceous	flavous	V
Male aedeagus				
L	CH1, form	rod-shaped	plate-shaped (a)^{1} Y-shaped (b)^{2}	I
M	CH1, position	distinct from BW	in curl of BW	I
N	BW, shape	straight	curled apically	I
O	BW, apex	curled transversely	curled longitudinally (a)^{1} curled diagonally (b)$^{1'}$	I, II
P	Apex	squared, dorsally hooked	squared, not hooked dorsally (a)^{1} narrowly rounded (b)^{2} broadly rounded (c)$^{2'}$	I, II
Q	H	absent	present	I
Female genitalia				
Coxostylus				
R	gonocoxite shape	long, slender	short, dilated	I
S	gonostylus length	moderate	elongate	I
T	gonostylus margin	smooth ventrolaterally	slightly crenulate	I
Bursa copulatrix				
U	ventral lobe shape	enlarged left	enlarged right	I, V
V	ductal lobe	present	absent	I
W	dorsal lobe	indistinct	distinct	II, V
X	dorsal sclerite	longitudinal, shallowly folded, on dorsal surface only	longitudinal, more deeply folded, on dorsal and lateral surfaces (a)$^{1'}$ longitudinal, very deeply folded, extended onto ventral lobe (b)$^{2'}$ transverse, lobate (c)^{1} transverse, triangulate (d)^{2} transverse, triangulate, deepened (e)^{3}	II, V
Spermatheca and duct				
Y	duct insertion	far right ventral	near midline	II, V
Z	length spermatheca	short	slightly elongate (a)^{1} moderately elongate (b)^{2}	II, V

For characters with more than one apotypic state, a code system for defining suggested direction and/or branching pattern of transformation series is as follows. Different apotypic character states are denoted by different lower case letters. If different apotypic states represent a linear transformation sequence, the sequence is noted by a superscript numeric sequence. If different states represent a branched transformation from the same relatively plesiotypic state, then these states have the same numeric superscipt, but one will be designated by a prime (') mark. If apotypic states represent a combination of linear and branched transformations, the linear sequences are first noted by numeric sequences and can then be identified by prime (') marks (e.g. states with superscripts 1, 2, etc. form one linear branch, states 1', 2', etc. form a second linear branch).

The code for criteria by which polarities of character transformations were determined is as follows (see also Kavanaugh 1978): I = out-group comparisons; II = character correlations; III = group trends; IV = correlation with adaptive significance; and V = in-group comparisons.

Zoogeography

In order to adequately assess the biogeographic history of a group of organisms, three criteria must be met by the data base. First, one must be able to formulate some hypothesis of the phylogenetic relationships of all the members of the group in question and of the group as a whole with respect to other groups at the same or higher levels. Second, one must know the geographical ranges of included extant species with a fair degree of completeness. Third, one must have a large enough pool of taxa with which to work so that concordant or discordant patterns may manifest themselves in relation to some biotic or abiotic patterns (e.g distribution of vegetation types, distribution of pertinent predators, etc. or climate, topography, etc.).

In our analysis of the *erasum* group, we have met the first two criteria but not the third. We have shown that the *erasum* group is likely related to the *carlhi, guttula, transparens,* and *vile* groups (perhaps also the *championi* group); but we have yet to study in-group relationships and distributions of members of the these other groups. We therefore must deal with patterns evident from distributions of only nine species—all quite closely related. While this data base may permit analysis of regional patterns and perhaps provide insight into the relative timing of evolutionary events for the group, we cannot determine how these patterns developed nor the precise timing of their antecedents. Until we have dealt with other *Bembidion* species groups, it will be impossible to ascertain with clarity zoogeographic antecedents and trends in this genus.

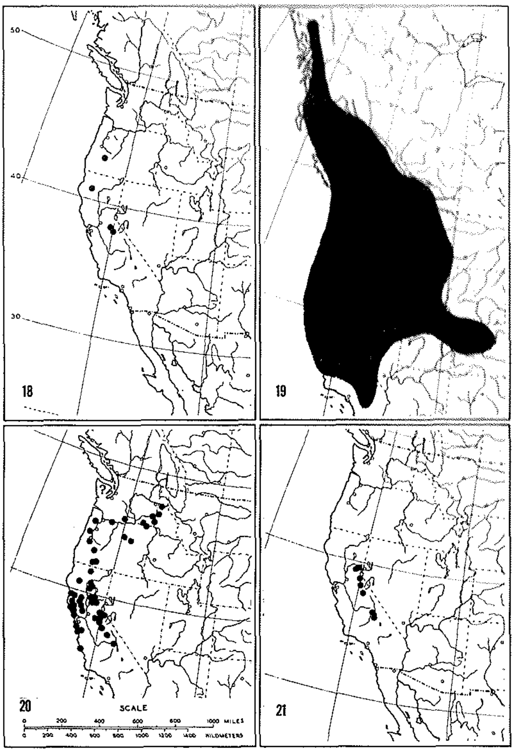


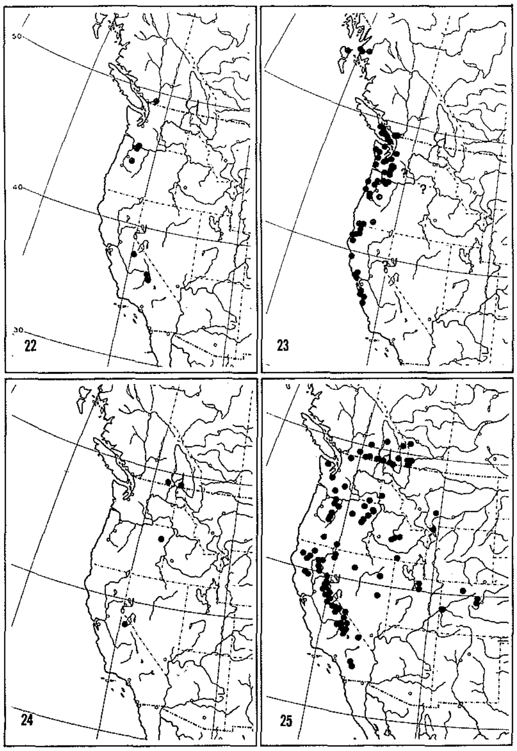
Fig. 18–21. Geographical distrtribution maps. — 18. *Bembidion carli.* — 19. The *erasum* species group. — 20. *B. osculans.* — 21. *B. pseudoerasum.*

Concordance between phylogenetic relationships and geography does express itself within

Table 3. Distribution of character states among members of the *erasum* species group for characters used in cladistic analysis

	Character																									
Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
B. osculans	–	–	–	–	–	Fa	Gc	H	–	–	–	La	M	–	–	Pc	Q	R	–	–	–	–	–	Xb	–	Za
B. pseudoerasum	–	–	–	–	–	Fc	Gc	H	–	–	–	Lb	M	–	–	Pc	–	R	S	T	–	–	–	Xa	–	Zb
B. sequoiae	–	–	C	–	–	Fa	Gc	H	–	–	–	La	M	–	–	Pc	–	R	S	T	–	–	–	Xa	–	Zb
B. castum	–	–	–	–	–	Fa	Gb	H	–	Jb	–	La	M	N	Ob	Pb	–	–	–	–	–	–	–	–	–	–
B. disjunctum	A	B	–	–	–	Fb	–	H	I	–	–	La	M	N	Oa	Pa	–	–	–	–	–	–	W	Xc,d	–	–
B. erasum	–	–	–	D	–	Fa	Ga	H	–	–	–	La	M	N	Oa	Pa	–	–	–	–	U	–	W	Xc,d	–	–
B. lindrothellus	–	–	–	–	E	Fa	–	H	–	Jb	K	La	M	N	Ob	Pa	–	–	–	–	U	V	W	Xc	Y	–
B. lummi	–	–	–	–	–	Fa	–	H	–	–	–	La	M	N	Ob	Pa	–	–	7	–	U	V	W	Xd	Y	–
B. chintimini	–	–	–	–	–	Fa	–	H	–	Ja	–	?	?	?	?	?	?	–	–	–	U	V	W	Xe	Y	–

A dash indicates plesiotypic state for taxon members; upper case letter (or combination of upper and lower case letters) indicate apotypic state for taxon members (see Tab. 2 for explanation of character states and code).



Figs. 22–25. Geographical distribution maps. — 22. *Bembidion sequoiae*. — 23. *B. castum*. — 24. *B. disjunctum*. — 25. *B. erasum*.

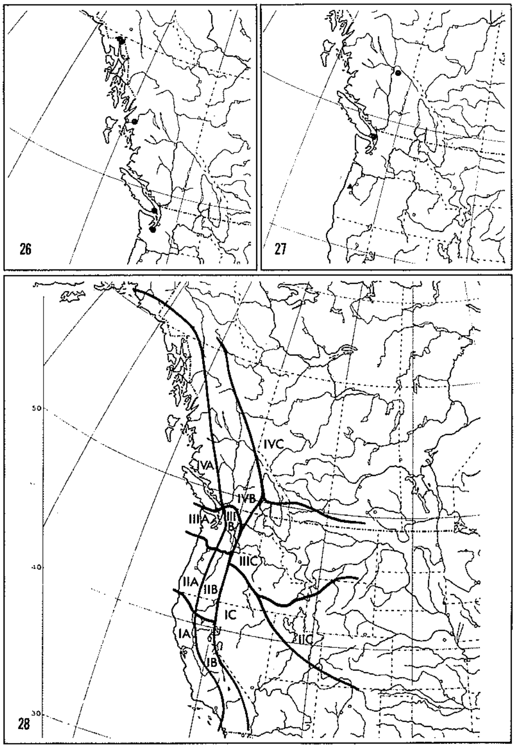
the *erasum* group, if only obscurely and in spite of much sympatry among member species and species subgroups. The discussion which follows is based on this perceived concordance which, we readily admit, is open to alternative interpretation in several instances. We present alternative hypotheses where extant evidence is equivocal and suggest what subsequent findings might potentially falsify a given hypothesis.

The *erasum* group is presently widespread in western North America (Fig. 19) and is apparently restricted to that region. At present, we cannot identify the sister group of the *erasum* group (although the *carlhi* group may eventually prove to be its closest extant relative); and without some idea of the identity and distribution of this sister, we can only begin our scenario with the common ancestor of the *erasum* group in western North America and suggest that the group arose and has had its entire evolutionary history within this region. Discovery of *erasum* group members in the Palaearctic Region would refute the last part of this hypothesis; and if such hypothetical Palaearctic representatives could be shown to have phylogenetic relationships at or near the base of the cladogram (Fig. 29) presented here, then the hypothesis would appear to be fully falsified.

Because all known *erasum* group members are cool- or cold-adapted, and in the absence of any fossil or other evidence to the contrary, we suggest that the group arose no earlier (and probably later) than early Miocene time, when the general cooling trend initiated in Late Eocene (Wolfe 1979) appears to have had a major effect on biota in western North America. Although some *erasum* group members occur outside montane areas, most group members are well represented only in such regions; and it is likely that the origin and initial spread of the group was associated with Miocene orogenic events. In the absence of data on the distribution of its unknown sister group, we cannot, however, suggest any particular climatic or physiographic event(s) with which the group's origin may have been associated.

The geographical ranges of all *erasum* group subgroups are mutually sympatric, at least in part, except apparently for the *castum* and *disjunctum* subgroups. This high incidence of subgroup range overlap is indicative of wholesale dispersal of subgroup members and/or their ancestors and serves to blur our perception of antecedent distribution patterns. However, we suggest that present geographical distributions and presumed caldistic relationships, taken together, point to the sequence of vicariant events outlined below as causally important in the evolution of the extant subgroups.

The *osculans* subgroup mainly occupies the southern portion of the range of the species group at present, while its sister group (the *castum, disjunctum,* and *erasum* subgroups) is best represented in more northern regions. The initial vicariant event appears to have been the splitting of a widespread common ancestor into northern and southern isolates, the former adapted to cooler climate than the latter. At this time, we can suggest no specific climatic or physiographic event with which this vicariance could have been associated.



Figs. 26–28. — 26–27. Geographical distribution maps. — 26. *Bembidion lindrothellus*. — 27. *B. lummi* (solid circles) and *B. chintimini* (solid triangle). — 28. Geographical subdivisions of western North America: IA = South Coast region; IIA = Oregon Coast region; IIIA = Washington Coast region; IVA = North Coast region; IB = Sierra Nevada region; IIB = Southern Cascades region; IIIB = Northern Cascades region; IVB = Central Plateau region; IC = Great Basin region; IIC = Southern Rocky Mountains region; IIIC = Middle Rocky Mountains region; and IVC = Northern Rocky Mountains region. Subdivisions are for convenience and reflect, in a general way, distribution patterns among *Bembidion* species treated in this study.

A second apparent vicariant event was the isolation of the ancestral *castum* subgroup stock, in coastal regions, from the inland stock which gave rise to the *disjunctum* and *erasum* subgroups. This vicariance may have been associated with uplift of the Cascade volcanic region in late Miocene and Pliocene time (McKee 1972).

Subsequently, the range of the common ancestor of the *disjunctum* and *erasum* subgroups was split, probably again into eastern and western isolates. Because neither *disjunctum* nor *erasum* subgroup members occupy far-northern areas of the interior at present, it seems probable that this vicariant event was associated with a severe cooling trend in the region, which isolated parts of the ancestral stock on opposite side of the Great Basin (including the Columbia Plateau) region. The present disjunct distribution of *B. disjunctum* suggests that the ancestor of the *disjunctum* subgroup differentiated on the western flank of the Great Basin while the ancestor of the *erasum* subgroup did so on the eastern flank, perhaps in the middle or southern Rocky Mountain region. The *erasum* subgroup then adapted to a more extreme continental climate (subject to greater fluctuations and extremes in temperature and moisture), while the *disjunctum* subgroup remained adapted to more moderate climate toward the west. Based on the sequence and timing of subsequent events required for the differentiation of extant species of various subgroups (see below), it appears likely that this vicariant event was associated with the Illinoian Glaciation, which had a profound effect on the northern Great Basin region (McKee 1972; Richmond et al. 1965).

The evolution of extant species of the *osculans* subgroup appears to have begun with an east/west split of the ancestral subgroup stock, just as with its sister group (ie. the *castum/disjunctum/erasum* stock) and perhaps contemporary with initial vicariance in the latter. *Bembidion osculans* became isolated in coastal regions of California and Oregon while the common ancestor of *B. pseudoerasum* and *B. sequoiae* was restricted to the Sierra Nevada. Present sympatry of the last two species indicates that their differentiation occurred before Recent time. The present distribution (including a northern extension) of *B. sequoiae* was probably attained during a cooler period, presumably no later than the Late Wisconsinan. We therefore suggest that the range of the common ancestor of *B. pseudoerasum* and *B. sequoiae* became dissected (probably into north/south isolates) during an interglacial period (perhaps as early as the Sangamon Interglacial) and that differentiation of these two forms occurred prior to the Late Wisconsinan. Kavanaugh (MS in preparation) has found the same distributional pattern for a pair of *Nebria* sister species (*N. ovipennis* LeConte and *N. spa-*

tulata Van Dyke) and invokes the same scenario to explain it.

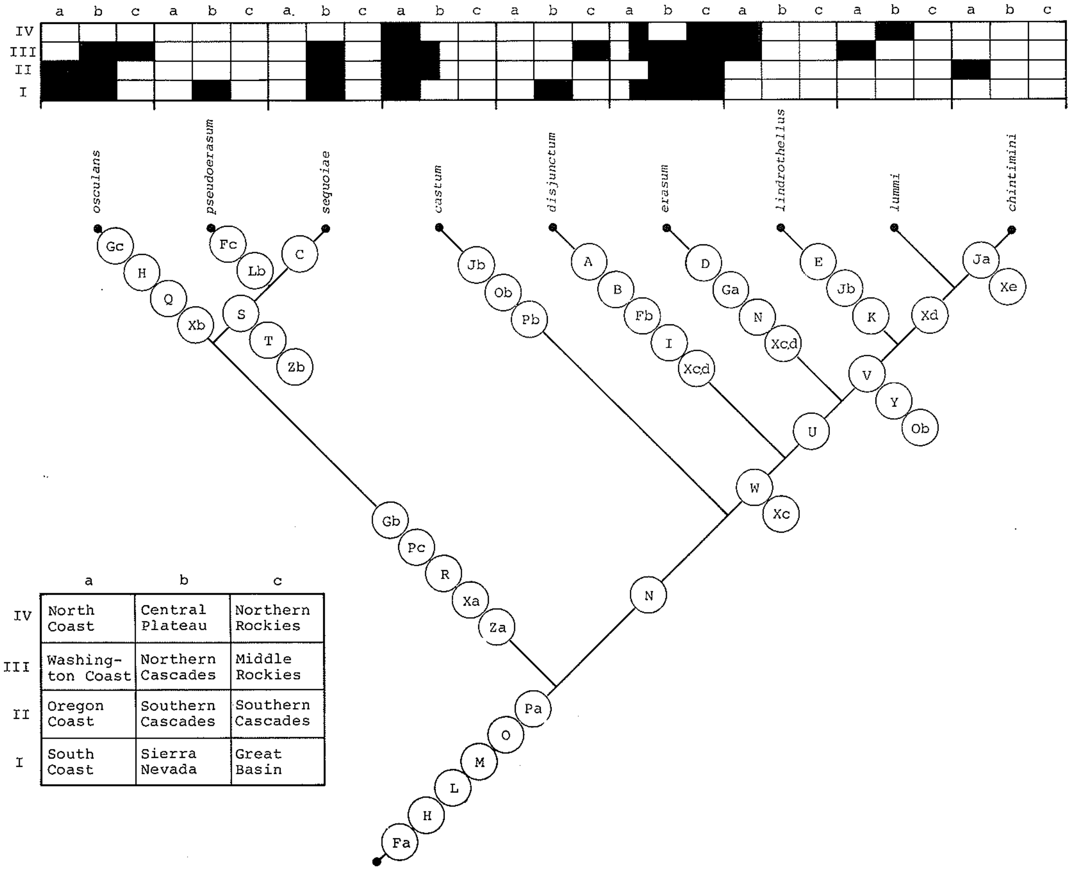
We judge the present range of *B. osculans* to have been attained recently—in Late Wisconsinan or post-glacial time. Like the ranges of many other carabid taxa (e.g. *Zacotus matthewsi* LeConte, *Nebria virescens* Horn, and *N. eschscholtzii* Ménétriés), this particular distribution pattern (i.e. mainly southern and coastal but with a narrow incursion up the lower Columbia River drainage and east across the Columbia Plateau to the western flank of the Rocky Mountains in Idaho) corresponds to present climatic patterns (Kavanaugh 1979b) and involves species whose members exhibit little or no geographical variation throughout their respective ranges. The extensive sympatry of *B. osculans* and its sister species pair in the Sierra Nevada similarly dates to late- or post-glacial time.

The *castum* subgroup appears to have been restricted to the Coast Ranges and adjacent lowlands throughout its history. The present range of *B. castum* extends from central British Columbia to central California; and there is no evidence to support a history involving other than minor contractions, expansions, and/or north/south displacements of its range in response to changing climate throughout the Quaternary.

The *disjunctum* subgroup, which we suggest arose on the western flank of the northern Great Basin during Illinoian time, appears to have extended its distribution during a subsequent cool (but not cold) period to attain a range extended north and east across the northern edge of the Columbia Plateau to southeastern British Columbia and eastern Oregon and Washington and south into the eastern Sierra Nevada. *Bembidion disjunctum* is presently known from a few widely disjunct populations, among members of which there is remarkably little differentiation. This minimal differentiation may be due to a relatively recent continuity of populations (i.e. in Late Wisconsinan time, just prior to major post-glacial warming in the northern Great Basin). Alternatively, the present distribution of the species is not as disjunct as is apparent (see above).

The ancestral stock of the *erasum* subgroup arose on the eastern flank of the Great Basin during Illinoian time. During some subsequent warm period (probably the Sangamon Interglacial), this ancestral stock extended its range north and west across the Columbia and Fraser Plateaus to coastal British Columbia, and perhaps southern Alaska and northwestern Washington. Subsequent cooling and advance of the ice sheet and valley glaciers across the area from the Okanagan Highland to the Blue Mountains of Oregon effectively cut off the ancestral stock of *B. lindrothellus, B. lummi,* and *B. chintimini,* on the west coast, from the ancestral stock of *B. erasum,* which became isolated and differentiated in the Rocky Mountain region. During late or post-glacial time, *B. erasum* extended its range into the central and northern Great Basin region, the Sierra Nevada, the eastern slope of the Cascade Range, into the Cowlitz Valley and Puget lowland of western Washington, and to the eastern flank of the Olympic Mountains.

During pre-Wisconsinan time, the western vicar of the *erasum* subgroup expanded its range along the Pacific Coast from Alaska to central Oregon. In Wisconsinan time, two subunits of this stock became isolated. The ancestral stock of *B. lindrothellus* became isolated in some northern, coastal refuge, in which it subsequently differentiated. These beetles, like many restricted to mountain tops and other habitat islands (including glacial refugia; see Lindroth 1979), became wing dimorphic. In post-glacial time, the winged forms have extended the range of the species south along the coast to central Washington. The ancestral stock of *B. lummi* and *B. chintimini* became isolated and differentiated south of the Cordilleran ice sheet in western Washington and Oregon. Post-glacial warming of the region resulted in the isolation and differentiation of the ancestral stock of *B. chintimini* at Mary's Peak, Oregon, or at least in the surrounding uplands. The ancestral stock of *B. lummi* subsequently differentiated and extended its range, in the wake of the retreating Puget Lobe of the Cordilleran ice sheet, up the Fraser River system into central British Columbia. Although now known only from disjunct populations at San Juan Island, Washington and Barkerville, British Columbia, we predict that other populations of this species will be found to occur in the yet poorly sampled intervening area.



	a	b	c
IV	North Coast	Central Plateau	Northern Rockies
III	Washington Coast	Northern Cascades	Middle Rockies
II	Oregon Coast	Southern Cascades	Southern Cascades
I	South Coast	Sierra Nevada	Great Basin

Fig. 29. Cladogram illustrating hypothetical phylogenetic relationships among and geographical distributions of members of the *erasum* species group of *Bembidion* (relationships based on cladistic analysis of data as presented in Tab. 3); see Fig. 28 for names and illustration of geographical areas schematically presented here.

Literature cited

Andrewes, H. E. 1935. The fauna of British India, including Ceylon and Burma. Coleoptera. Carabidae Vol. II. Harpalinae I. Taylor and Francis Publishers, London, 323 pp.

Ball, G. E. 1972. Classification of the *Harpalus* subgenus *Glanodes* Casey (Carabidae: Coleoptera). — Coleopts Bull. 26: 179–204.

Casey, T. L. 1918. A review of the North American Bembidiinae. — Memoirs on the Coleoptera 8: 1–223.

Corwin, D., Clifford, C. M. & Keirans, J. E. 1979. An improved method for cleaning and preparing ticks for examination with scanning electron microscope. — Jour. med. Ent. 16: 352–353.

Darlington, P. J., Jr. 1965. Biogeography of the southern end of the World: distribution and history of far-southern life and land, with an assessment of continental drift. Harvard University Press, Cambridge, Massachusetts, x + 236 pp.

Erwin, T. L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). — Quaest. ent. 6: 4–215.

— 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: a revision of the New World-Australian genus *Pericompsus* Le Conte. — Smithsonian Contributions to Zoology No. 162, 96 pp.

— 1978. Techniques. — Coleopts. Bull. 32: 372.

— 1979. The American connection, past and present, as a model blending dispersal and vicariance in the study of biogeography. [pp. 357–367]. *In:* Erwin, T. L., Ball, G. E., Whitehead, D. R. & Halpern, A. L. (editors), Carabid beetles: their evolution, natural history, and classification (Proc. First Intern. Symp. of Carabidology, Smithsonian Institution, Washington, D. C., August 21, 23, and 25, 1976). W. Junk b.v., Publishers, The Hague, 635 pp.

— & Kavanaugh, D. H. 1980. On the identity of *Bembidion puritanum* Hayward (Coleoptera: Carabidae: Bembidiini). — Coleopts Bull. 34: 241–242.

Hayward, R. 1897. On the species of *Bembidium* of America north of Mexico. — Trans. Am. ent. Soc. 24: 32–143.

Jeannel, R. 1941. Faune de France, 39. Coléoptères Carabiques. Première partie. P. Lechevalier et Fils, Paris 571 pp.

Kavanaugh, D. H. 1978. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Unpublished Ph.D. Dissertation, Department of Entomology, University of Alberta, xlviii + 1041 pp.

— 1979a. Rates of taxonomically significant differentiation in relation to geographical isolation and habitat: examples from a study of the Nearctic *Nebria* fauna. [pp. 35–57]. *In:* Erwin, T. L., Ball, G. E., Whitehead, D. R. & Halpern, A. L. (editors), Carabid beetles: their evolution, natural history, and classification (Proc. First Intern. Symp. of Carabidology, Smithsonian Institution, Washington, D. C., August 21, 23, and 25, 1976). W. Junk b.v., Publishers, The Hague, 635 pp.

— 1979b. Investigations on present climatic refugia in North America through studies on the distributions of carabid beetles: concepts, methodology, and prospectus. [pp. 369–381]. — Ibid.

— 1979c. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. — Proc. Calif. Acad. Sci. 42: 87–133.

Latreille, P. A. 1802. Histoire naturelle, générale et particulière des Crustacés etr Insectes. 3. F. Dufait, Paris, 467 pp.

LeConte, J. L. 1859. Catalogue of the Coleoptera of Fort Tejon, California. — Proc. Acad. nat. Sci. Philad. 11: 69–90.

Lindroth, C. H. 1939. Zur Systematik fennoskandischer Carabiden. 2–3. — Ent. Tidskr. 60: 54–68.

— 1940. Zur Systematik fennoskandischer Carabiden. 4–12. *Bembidion*-Studien. — Notul. ent. 19: 63–99.

— 1945. Die fennoskandischen Carabiden, eine tiergeographische Studie. I. Allgemeiner Teil. — Göteborgs K Vetensk. -o. Vitterh. Samh. Handl., Sjätte Följden (Ser. B). 4: 1–709.

— 1957. The faunal connections between Europe and North America. John Wiley & Sons, New York, 344 pp.

— 1961. Sandjägare och Jordlöpare. Fam. Carabidae. Second Edition. — Svensk Insektfauna 35. Stockholm, 209 pp.

— 1962. Revision of the subgenus *Chrysobracteon* Net., genus *Bembidion* Latr. (Col. Carabidae). — Opusc. ent. 27: 1–18.

— 1963a. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 3. — Opusc. ent. Suppl. 24: 201–408.

— 1963b. The faunal history of Newfoundland illustrated by carabid beetles. — Opusc. ent. Suppl. 23, 112 pp.

— 1970. Survival of animals and plants on ice-free refugia during the Pleistocene glaciations. — Endeavor, 29: 129–134.

— 1974a. Handbook for the identification of British insects, 4(2). Coleoptera, Carabidae. — Roy. Ent. Soc. Lond., London, 148 pp.

— 1974b. On the elytral microsculpture of carabid beetles (Col. Carbidae). — Ent. scand. 5: 251–264.

— 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. — The Coleopts Bull. 29: 109–147.

— 1979. The theory of glacial refugia. [pp. 385–394]. *In:* Erwin, T. L., Ball, G. E., Whitehead, D. R. & Halpern, A. L. (editors), Carabid beetles: their evolution, natural history, and classification (Proc. First Intern. Symp. of Carabidology, Smithsonian Institution, Washington, D. C., August 21, 23, and 25, 1976). W. Junk b.v., Publishers, The Hague, 635 pp.

McKee, B. 1972. Cascadia — the geologic evolution of the Pacific Northwest. McGraw Hill Book Company, New York, xiv + 394 pp.

Merriam, C. H. 1892. The geographical distribution of life in North America with special reference to mammals. — Proc. Biol. Soc. Wash. 7: 1–64.

— 1894. The geographical distribution of animals and plants in North America. — 46. U. S. Dep. Agric. 1894: 203–214.

Netolitzky, F. 1935. Die *Bembidion*-Arten der Sammlung Motschulsky im Museum der Universität zu Moskau. — Vereinsschr. Gesellschaft Luxemburger Naturfreunde 29: 18–37.

— 1942. Bestimmung-stabelle der *Bembidion*-Arten des paläarktischen Gebites. — Koleopt. Rdsch. 28: 29–124.

— 1943. Bestimmung-stabelle der *Bembidion*-Arten des paläarktischen Gebites. — Koleopt. Rdsch. 29: 1–70.

Richmond, G. M., Fryxell, R., Neff, G. E. & Weis, P. L. 1965. The Cordilleran ice sheet of the northern Rocky Mountains, and related Quaternary history of the Columbia Plateau. [pp. 231–242]. *In:* Wright, H. E., Jr. & Frey D. G. (editors), The Quaternary of the United States. Princeton University Press, Princeton, New Jersey, x + 922 pp.

Wolfe, J. A. 1979. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. — Am. Scient. 66: 694–703.

Manuscript received June 1980.

Journal and subscription to reprints of particular groups
to be ordered from:
NFR, Editorial Service
P.O. Box 23136, S-104 35 Stockholm, Sweden.

Reprints from

Entomologica scandinavica Supplement

[redacted]

19