

***Pterostichus lattini* LaBonte, a New Species of Carabid Beetle
(Coleoptera: Carabidae: Pterostichini) from Oregon**

James R. LaBonte¹

*Oregon Department of Agriculture, 635 Capitol Street N.E.,
Salem, OR 97301-2532; jlabonte@oda.state.or.us*

A new species of carabid beetle, *Pterostichus lattini* LaBonte, is described from Oregon (Type locality: Marys Peak, Benton Co., Oregon). Diagnostic characters include the distinctive shape of the pronotum and of the apex and shaft of the median lobe of the male genitalia. Features distinguishing *P. lattini* from species of *P. (Hypherpes)* found in Oregon are discussed. Although this species can be extremely abundant where it occurs, it is known only from north and central western Oregon. Habitat and phenological data are provided.

Species in the carabid genus *Pterostichus* Bonelli are among the most familiar beetles of forested habitats in the western United States. This is particularly true of members of the *amethystinus* species group (*sensu* Lindroth 1966 and Bousquet and Laroche 1993). Characteristics in common among these species include fused elytra, extremely brachypterous hind wings, and the absence of discal dorsal elytral setae. Most of these species (about 70) can be placed in the subgenus *Hypherpes* Chaudoir.

Adult members of typical *Pterostichus (Hypherpes)* species are rather consistent in appearance: black or brown medium-sized (circa 10–20 mm in length) beetles that are slightly flattened, with large heads and rather large and broad pronota. This uniform appearance, combined with considerable intraspecific variation, renders identification of many members of *P. (Hypherpes)* *sensu stricto* challenging. Examination of male genitalia is often necessary to confirm identification. Compounding this problem is the plethora of Casey names, many of which may be synonyms. The most recent North American species of *P. (Hypherpes)* to be described was *P. neobrunneus* Lindroth 1966 (Bousquet and Laroche 1993).

The Oregon carabid fauna, comprising roughly 500 species, is well known, due in large part to Hatch (1953) and Lindroth (1961–1969), as well as subsequent researchers, e.g., Bousquet (1985) and Kavanaugh (1984). Consequently, it was surprising to detect an undescribed, locally abundant, species of *P. (Hypherpes)* in western Oregon. The purpose of this paper is to describe the adults of this new species, to discuss features that distinguish it from other species of *P. (Hypherpes)* found in Oregon, and to provide data on the known distribution, habitat, and phenology.

MATERIALS AND METHODS

I examined the types of the *P. amethystinus* group, particularly those of *P. (Hypherpes)* species, available at the California Academy of Sciences (CAS), San Francisco, CA and the National Museum of Natural History (USNM), Washington, D.C.. Reliably determined examples of most

¹ Research Associate, Department of Entomology, California Academy of Sciences

species not represented by types were also examined where possible. Yves Bousquet and Serge Laplante (Agriculture and Agri-Food Canada) very kindly examined specimens of *P. lattini* and concluded they were not conspecific with those species for which I had not seen examples.

Specimens were examined under a stereoscopic microscope with a maximum magnification of 160 \times . Absolute and relative measurements were obtained via an ocular micrometer used with a stereomicroscope. Total length included the left elytron from apex to humerus, the midline of the pronotum, and the midline of the head from the occiput to the apices of the mandibles. Specimens in my personal collection (JRLC) and the Oregon State Arthropod Collections (OSAC) at Oregon State University (Corvallis, OR) were used for length measurements. Images of pronota and male genitalia were acquired via the Oregon Department of Agriculture's digital imaging system, comprised of a Leica MZ16 stereomicroscope, a Spot Insight digital camera (model 3.2.0, Diagnostic Instruments, Inc., Sterling Heights, MI), and Image-Pro 5.0 image acquisition and analysis software (Media Cybernetics, Silver Spring, MD).

DESCRIPTION OF NEW TAXON

Pterostichus lattini LaBonte, sp. nov.

HOLOTYPE.— Male. Label data "OR, Benton Co., Marys Peak, Elev. 1092 m, J.R. LaBonte, 14 Aug. 1996, T12S R7W Sec20, SW1/4 of NE1/4 of SE1/4, N face". Deposited at the California Academy of Sciences, CAS Type no. 18122.

HABITUS.— General color black without metallic highlights; palpi, antennomeres 5–11, and tarsi brown. Overall luster shiny. Total body length 15.7 mm. **Head**: Large (typical of *P. [Hypherpes]* species). Microsculpture at center of frons isodiametric. **Pronotum** (Fig. 1a): More or less quadrate, about 0.75 times as wide as long, widest at anterior one-quarter of pronotal length; margin between anterior angles 0.75 times as wide as margin between posterior angles. Anterior margin evenly arcuate, with slightly protruding anterior angles. Lateral margins slightly obliquely convergent posterior to anterior lateral setiferous punctures, very slightly sinuate at posterior third; lateral beads distinct, broadening at posterior one-third and broadest at posterior angles, with a few crenulations present just anterior to posterior angles. Bases of anterior lateral setae within deep foveae, just mediad of and adjacent to lateral marginal grooves. Posterior margin more or less truncate, slightly concave medially; lateroposterior beads distinct to just mediad of inner boundaries of inner basal depressions and clearly connected with lateral beads at posterior angles. Posterior angles slightly obtuse and slightly denticulate. Outer basal depressions deep, elongate-oval, and approximately linear, with inscribed line at bottom, each depression terminated distinctly anterior to posterior margin, separated from posterior marginal bead by a distinct convexity, bounded externally and separated from lateral bead by distinct, obtuse linear convexity, with this convexity extended anteriorly to about the posterior one-seventh of pronotum and terminated just anterior to posterior bead. Inner posterior depressions about twice as long as outer depressions, oblong-linear, deep, incised at bottom, extended to posterior bead. Convexities between outer and inner depressions distinct, slightly flattened adjacent to inner margin of outer depressions, extended to posterior bead. Median depression and inner posterior depressions with evanescent horizontal wrinkles extended laterally. Extreme posterior of pronotum between inner depressions with faint longitudinal incisions. Meshes of microsculpture elongate-rectangular or oblong, in irregular horizontal rows. **Elytra**: Fused along suture, without dorsal setae (typical of *P. [Hypherpes]* species). Hind wings extremely brachypterous, reduced to small stubs (typical of *P. [Hypherpes]* species). Meshes of microsculpture irregularly pentagonal, in irregular horizontal rows; rows more or less imbricate, with posterior margins of meshes in a given row raised above anterior margins of meshes in the fol-

lowing row. **Legs:** Tarsomeres 1–3 of protarsi expanded, with two longitudinal rows of squamose setae ventrally; tarsomeres 4 expanded, without such setae. Fifth tarsomeres of all tarsi asetose ventrally. Dorsolateral margins of crenulae on inner faces of meso- and metatibiae only faintly tuberculate. **Venter:** Mesepisterna densely and shallowly punctate in anterior one-third, with only evanescent stria connecting the punctures (best seen in oblique light). Apical margin of last visible abdominal sternite simple, without carina, tubercle, or lobe, with one pair of long setae. **Aedeagus** (Figs. 2a, 3a, 4a): Median lobe simple: in lateral views, bend between base and shaft approximately 90°, shaft without ventral swelling or lobe, base of apex ventrally produced and apex thin and sinuate; in dorsal view, apex symmetrically narrowed toward the very slightly asymmetrically expanded tip.

PARATYPES.— Paratypes have been placed or are located in the following institutions or collections (codens follow the “Insect and Spider Collections of the World” website at the Bishop Museum <www.bishopmuseum.org/bishop/ento/codens-r-us.html> as of September 2005): CAS (64), CIDA (2), CMNH (2), CNC (2), CUIC (2), EMEC (2), JRLC (42), LACM (2), MCZ (2), MSUC (2), ODAC (2), OSAC (331), UASM (2), UCDC (2), USNM (2), WFBM (2), WSU (2).

VARIATION.— The venter of late teneral adults is brown, as are the lateral margins of the pronota and elytra. The legs are paler than in fully pigmented specimens.

Females have more pronounced microsculpture and slightly duller sheen. Protarsomeres 1–4 are not expanded and lack squamose setae ventrally. The crenulae on the inner faces of the meso- and metatibiae are extremely faint, almost absent, and the dorsolateral margins are not tuberculate. The apical margin of the last visible abdominal sternite has two pairs of long setae.

One male specimen (from the H.J. Andrews Experimental Forest) has a single pair of very short ventral setae on the fifth tarsomeres. This specimen otherwise appears to be a typical *P. lattini*.

There is considerable variation in the form of the pronotum among specimens examined. The posterior angles varied from slightly obtuse to rectangular. The lateral pronotal margins in the posterior half range from slightly sinuate, in most specimens, to completely oblique in a few individuals. Some specimens have shallower and more oviform outer posterior depressions with less pronounced lateral convexities. Such variation is most evident in a series from the H.J. Andrews Experimental Forest. In some of these specimens, the outer posterior depressions are almost entirely effaced. The medial development of the posterior bead ranges from extended just mediad of the inner posterior impressions (in most specimens) to extended across the entire posterior margin. The posterior lateral crenulations are almost absent from many specimens. The fine linear grooves at the posterior of the pronotum between the inner depressions range from evanescent to deeply incised. Some specimens with pronounced lateral convexities have the posterior area between the outer and inner depressions flattened.

There appears to be relatively little size variation in this species. Total lengths of specimens selected for a full range of size (N = 50) ranged from 13.0 to 15.5 mm, with a mean of 14.2 mm ± 0.5 mm. Males (n = 25) averaged slightly smaller than females (n = 25), with means of 14.1 mm and 14.4 mm, respectively.

ETYMOLOGY.— I take great pleasure in naming this species in honor of my friend, colleague, and mentor, John D. Lattin (Emeritus Professor, Botany and Plant Pathology Department, Oregon State University). Among his many accomplishments were his tireless efforts promoting an understanding and appreciation of the insect fauna of the H.J. Andrews Experimental Forest, where *P. lattini* is among the most commonly collected carabids. The species epithet is a noun in apposition.

DISTINGUISHING *P. LATTINI* FROM OTHER PACIFIC NORTHWESTERN SPECIES OF *PTEROSTICHUS*.— There are several Pacific Northwestern *P. (Hypherpes)* species whose adults are somewhat similar externally to those of *P. lattini*. The species most apt to be confused with *P. lat-*

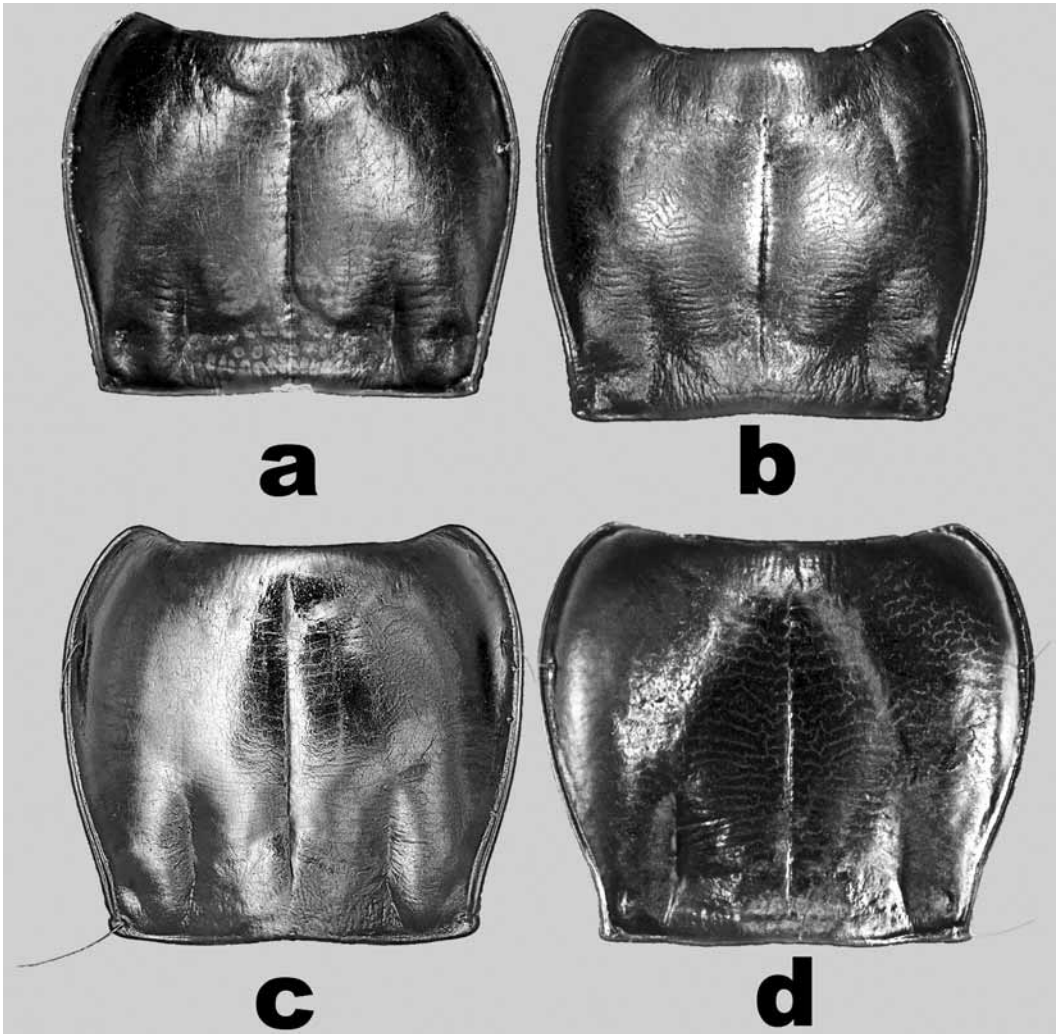


FIGURE 1. Dorsal aspect of pronotum (a. *Pterostichus lattini* LaBonte; b. *P. herculeanus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

tini, at least based on existing keys, is *P. herculeanus* Mannerheim. These two species often occur sympatrically, increasing the opportunity for confusing them. I have seen specimens of *P. herculeanus* from most *P. lattini* sites.

The pronotum of *P. herculeanus* (Fig. 1b) has distinct linear convexities that form the lateral boundaries of the outer posterior depressions, as in *P. lattini* adults. However, the pronotum of *P. herculeanus* differs in the following characters: the anterior angles are very strongly produced, forming distinct obtuse angles with the medioanterior margin; the outer posterior depressions extend to the posterior margin; the outer and inner posterior depressions are indistinctly separate, forming a flattened area between the posteriolateral convexities and the inner margins of the inner depressions; the posteriolateral convexities are generally more sharply delineated medially and are continuous posteriorly with the posterior marginal bead; strong horizontal wrinkles extend laterally from the median depression and laterally and medially from the inner posterior depressions;

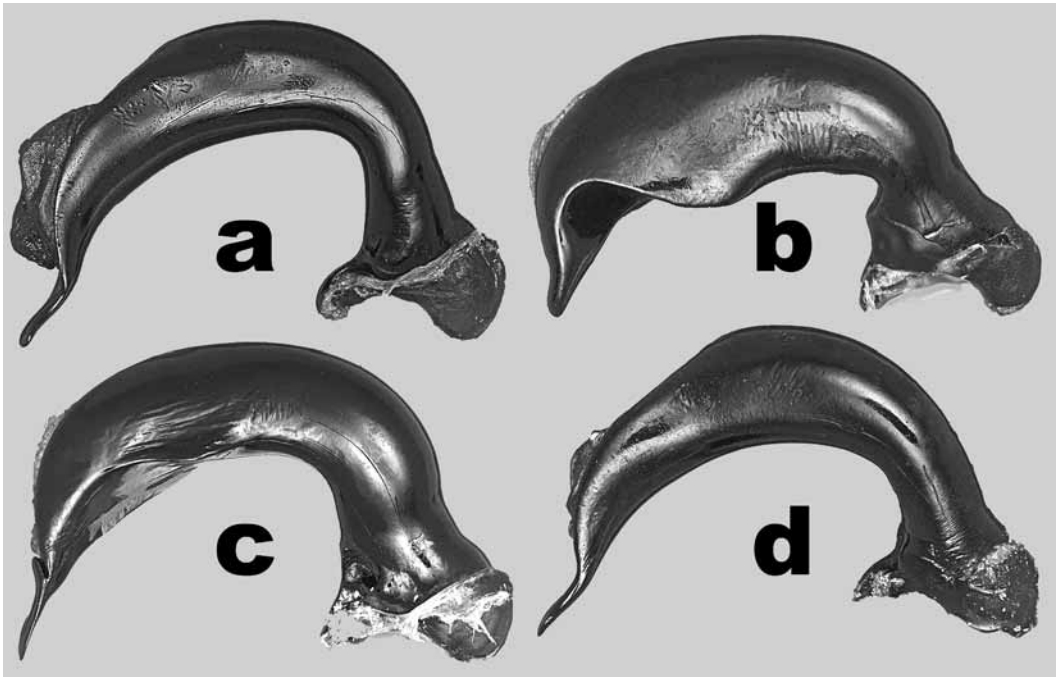


FIGURE 2. Right lateral aspect of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

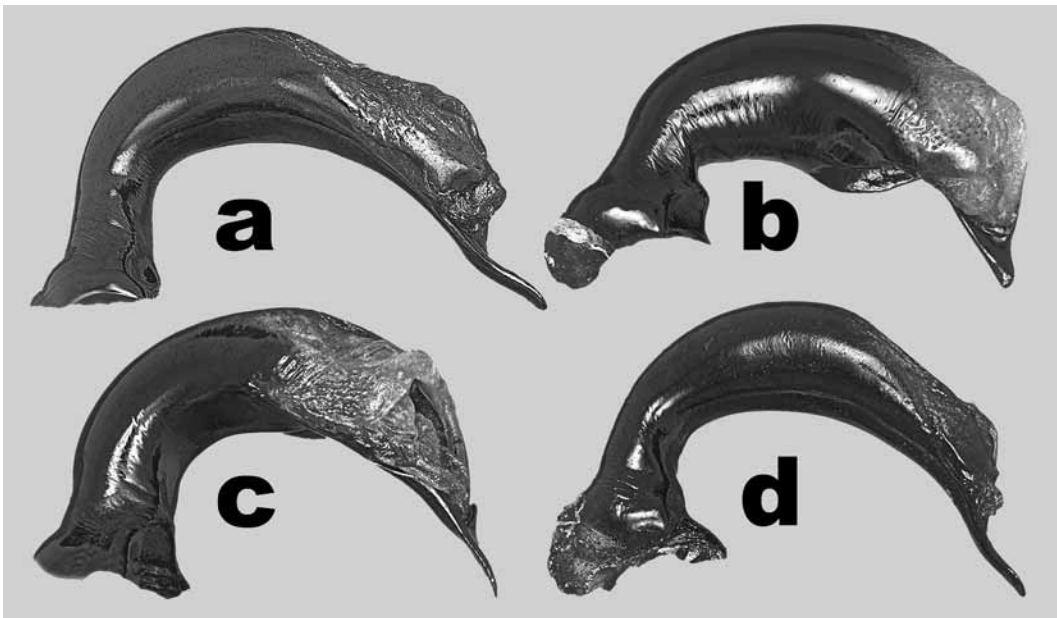


FIGURE 3. Left lateral aspect of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculaneus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

strong longitudinal incisions along the medioposterior margin between the inner depressions extend

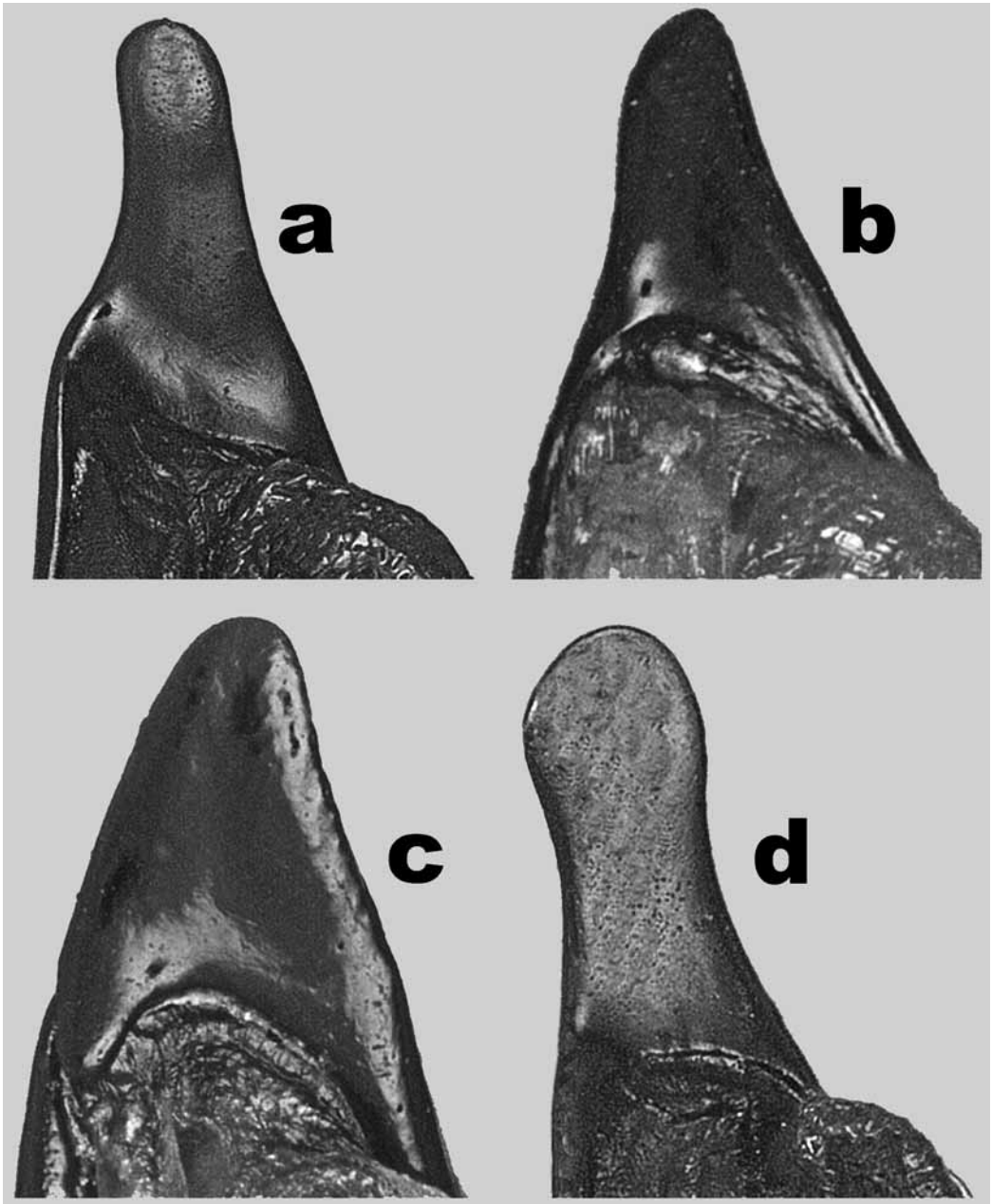


FIGURE 4. Dorsal aspect of apex of median lobe of aedeagus (a. *Pterostichus lattini* LaBonte; b. *P. herculeanus* Mannerheim; c. *P. algidus* LeConte; d. *P. setosus* Hatch).

anteriorly to about half the length of those depressions.

There are also several non-pronotal characters distinguishing the two species. The mesepisterna of *P. herculeanus* are densely, deeply punctate over at least the anterior one-third to one-half, with distinct striae between the punctures (best seen with oblique lighting). The dorsolateral margins of the crenulae on the inner faces of the meso- and metatibiae of *P. herculeanus* males are dis-

tinctly tuberculate. The median lobe of the aedeagus of *P. herculaneus* bears no resemblance to that of *P. lattini* as it is much broader overall and has a blunt, broad apex in dorsal view (Figs. 2b, 3b, 4b).

Pterostichus lattini specimens with poorly developed posteriolateral pronotal convexities could be confused with adults of *P. algidus* LeConte. The following characters easily distinguish *P. algidus* from *P. lattini*: the outer posterior pronotal depressions are shallow and round, with the outer margins in contact with the lateral beads (Fig. 1c), not separated from the margins by the lateral convexities, as in *P. lattini*; three pairs of long ventral setae on the fifth tarsomeres; males have dorsolateral tubercles on the inner faces of the meso- and metatibiae, although these are less pronounced than in *P. herculaneus* males; the median lobe of the aedeagus bears no resemblance to that of *P. lattini*—among other differences, a large right ventrolateral lobe extends from about the middle of the shaft and the apex in dorsal view is broad and triangular (Figs. 2c, 3c, 4c). *Pterostichus algidus* is widespread and eurytopic in Oregon, but is known to be sympatric with *P. lattini* only at Marys Peak.

Pterostichus lattini specimens with poorly developed posteriolateral pronotal convexities could conceivably be confused with *P. setosus* Hatch. The following characters most easily distinguish *P. setosus* adults from those of *P. lattini*: two pairs of short, ventral, setae on the fifth tarsomeres; males have two pairs of long setae on the apical margin of the last abdominal sternite; males have dorsolateral tubercles on the inner faces of the meso- and metatibiae, although these are less pronounced than in *P. herculaneus* males. The general conformation of the pronotum is also quite different (Fig. 1d): the pronotum is not quadrate; appears distinctly broader at the anterior margin than at the posterior margin; the lateral margins are strongly and evenly arcuate from the anterior angles to just before the hind angles; the outer posterior depressions are small and round. The elytra are elongate-oviform, narrowest at the humeri, and the humeri are evenly arcuate in dorsal view (versus obtusely angulate in *P. lattini*). The overall habitus of *P. setosus* is also more gracile than that of *P. lattini*. *Pterostichus setosus* is known only from southwestern Oregon (Hatch 1953; LaBonte, unpublished data), where *P. lattini* is not known to occur.

Whereas most Pacific Northwestern species of *P. (Hypherpes)* can be readily distinguished by the form of the male genitalia alone, this is not true for *P. setosus* and *P. lattini*. The median lobe of the aedeagus of *P. setosus* males, in either left or right lateral views, is remarkably similar to that of *P. lattini* males (Figs. 2d, 3d); however, the tip of the apex in dorsal view is symmetrically and more apically expanded (Fig. 4d) and the base of the apex is symmetrical in dorsal view in *P. setosus* males (Fig. 4d), whereas it is more swollen on the left side than on the right in *P. lattini* (Fig. 4a).

DISTRIBUTION.— Despite being one of the most commonly collected carabids on Marys Peak and at the H.J. Andrews Experimental Forest, I have seen specimens of *P. lattini* from only a limited portion of the north-central Oregon Cascades and two sites in the northern Oregon Coast Range (Fig. 5). All the Cascadian sites are on the western slope of the range, although several are near the Cascade Crest. The Coast Range sites are along the eastern flank of that range. I have examined specimens, most of which are paratypes (some specimens examined earlier were not available for paratype designation), from the following localities: OREGON: **Benton County:** Grass Mountain, 44.426°N, 123.664°W, elev. 951 m; Marys Peak (many localities, e.g., 44.497°N, 123.543°W, elev. 796 m; 44.512°N, 123.543°W, elev. 845 m; 44.512°N, 123.563°W, elev. 1,002 m; 44.513°N, 123.550°W, elev. 1,130 m). **Clackamas County:** 24 km NE Mills City, 44.918°N, 122.202°W, elev. 885 m. **Douglas County:** Dog Prairie, 43.187°N, 122.300°W, elev. 1,483 m; Watson Falls, 48.242°N, 122.389°W, elev. 842 m. **Lane County:** 29 km N Oakridge, Christy Flats, 43.911°N, 122.333°W, elev. 900 m; H.J. Andrews Experimental Forest, ~3 km N Mackenzie Bridge (many

localities, e.g., 44.212°N, 122.237°W, elev. 631 m; 44.218°N, 122.157°W, elev. 1,109 m; 44.218°N, 122.177°W, elev. 950 m; 44.218°N, 122.217°W, elev. 838 m; 44.218°N, 122.257°W, elev. 593 m; 44.233°N, 122.197°W, elev. 610 m; 44.247°N, 122.157°W, elev. 1,083 m; 44.262°N, 122.177°W, elev. 884 m; 44.277°N, 122.137°W, elev. 1,348 m; 44.277°N, 122.157°W, elev. 1,400 m); Twin Springs Campground, 43.962°N, 122.112°W, elev. 792 m. **Linn County:** ~16 km ESE Cascadia (44.326°N, 122.259°W, elev. 1,269 m; 44.351°N, 122.304°W, elev. 1,147 m; 44.367°N, 122.293°W, elev. 1,147 m); Green Peter Mountain, 44.501°N, 121.301°W, elev. 821 m; Iron Mountain, 44.395°N, 122.157°W, elev. 1,266 m; Marion Forks Guard Station, 44.604°N, 121.961°W, elev. 773 m; 2.4 km NE Middle Santiam Wilderness, 44.564°N, 122.163°W, elev. 1074 m; 1.6 km NE Upper Soda, 44.411°N, 122.258°W, elev. 638 m.

The known distribution of *P. lattini* extends over only about 210 km north to south and 145 km east to west (Fig. 5). The only species of Oregon *P. (Hypherpes) sensu stricto* with a smaller known range is *P. setosus*, with a known distribution limited to southernmost Oregon and extending 16 km north to south and 68 km east to west (LaBonte, unpublished data). There are no obvious biogeographical factors to account for such limited ranges for either species. I am confident that *P. setosus* is present in the Siskiyou region of northern California adjacent to the Oregon border. With regard to *P. lattini*, I would be surprised if it is not found to be more widely distributed along the western flanks of the Oregon Cascades. In both cases, it seems most likely that these very small overall ranges are at least in part artifacts of collecting or confusion with other species.

The apparently disjunct Coast Range populations of *P. lattini* are on the highest peaks of that range. However, this species is not restricted to the summits but has been found at lower elevations as well, as low as *circa* 730 m. Thus, there appears to be no reason to expect this species to be found in the Coast Range only in the vicinity of the highest peaks. For example, another presumably predominantly Cascadian species of *P. (Hypherpes) s. str.*, *P. tuberculofemoratus* Hatch, is not only abundant on Marys Peak but also has been collected at sea level along the Oregon Coast (LaBonte, unpublished data).

Whether *P. lattini* will be found in northern California or southern Washington remains uncertain. There are several species of *Pterostichus* known only from northwestern Oregon or with reliable records only from that area. These include *P. campbelli* Bousquet (Bousquet 1985), as well as *P. lanei* Hatch and *P. rothi* Hatch (LaBonte 1994 and unpublished data). Of course, inadequate collecting or misidentification can always be invoked as possible explanations for such distributions. However, these are all flightless species found in cool and moist habitats (Bousquet 1985, LaBonte 1994 and unpublished data). Dispersal of such species could have been constrained by the Columbia River to the north, while past or present climatic conditions further south could either have limited expansion from the north or caused range contraction. Further collecting or examination of museum material could help ascertain whether this may be the case for *P. lattini*.

HABITAT DATA.— This species has been found at elevations ranging from 593–1,483 meters. Specimens examined were all from coniferous forests and forest margins, or clear cuts therein. Stands ranged in age from new plantings to old growth. Dominant conifers, depending upon the specific site, aspect, and elevation, included Douglas fir (*Pseudotsuga menziesii* Franco), noble fir (*Abies procera* Lindl.), and western hemlock (*Tsuga heterophylla* Sargent). Understory development and composition varied among sites.

Associated species of Carabidae and Trachypachidae at elevations above 1,000 m on Marys Peak in the Coast Range included *Harpalus cordifer* Notman, *Leistus ferruginosus* Mannerheim, *Notiophilus sylvaticus* Eschscholtz, *Pterostichus algidus*, *P. lanei*, *P. infernalis* Hatch, *P. lama* (Menetries), *P. rothi*, *P. tuberculofemoratus*, *Scaphinotus angulatus* (Harris), *S. angusticollis* (Fischer), *S. marginatus* (Fischer), *S. rugiceps* (Horn), *S. velutinus* (Menetries), *Tanystoma sulcata*

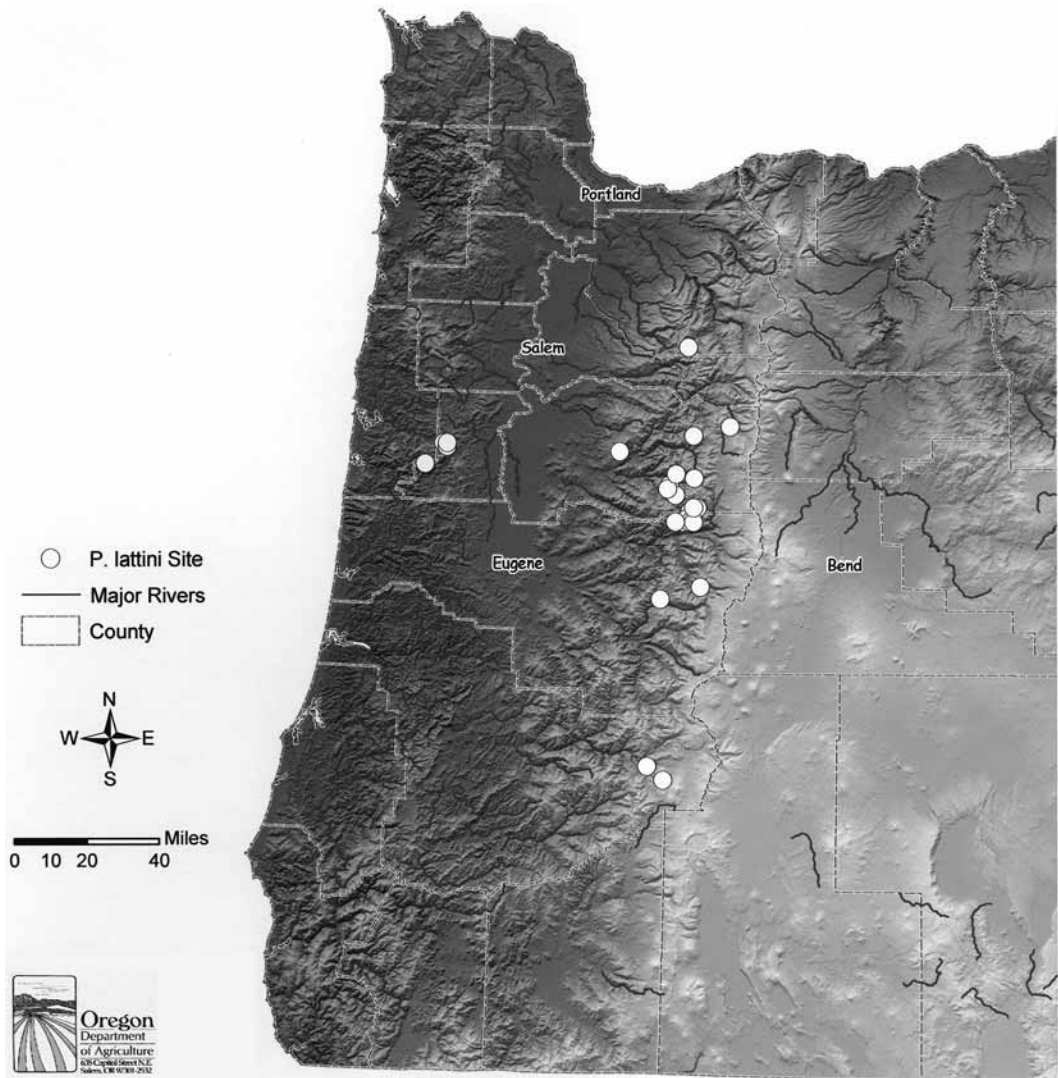


FIGURE 5. Known distribution of *Pterostichus lattini* LaBonte. Map prepared by the Oregon Department of Agriculture. Data source(s): Oregon Geospatial Data Clearinghouse, USGS, ESRI, Oregon Department of Agriculture.

(Dejean), *Trachypachus holmbergi* Motschulsky, and *Zacotus matthewsii* LeConte. Species found with *P. lattini* at a moderate elevation (885 m) Cascade site included *Amara sinuosa* (Casey), *Bembidion farrarae* Hatch, *Cychrus tuberculatus* Harris, *Harpalus cordifer*, *H. somnulentus* Dejean, *Omus dejeani* Reiche, *Promecognathus crassus* LeConte, *Pterostichus crenicollis* LeConte, *P. herculeanus*, *P. lama*, *P. neobrunneus*, *Scaphinotus angulatus*, *S. angusticollis*, *S. marginatus*, and *Trachypachus holmbergi* (LaBonte 1996). Most of these species are typical elements of mid-elevation coniferous forests west of the Cascade Crest in Oregon.

PHENOLOGICAL OBSERVATIONS.— Specimens of *P. lattini* were collected during every month from April through October. Adults no doubt can be found throughout the year, as is true for some related species. The majority of specimens examined were collected in May or June. This pattern

may not reflect the true abundance phenology of this species because available (i.e., collected, mounted, and curated) specimens represent only a subset of the total number of individuals present at a given site at the time of collection.

I have seen late teneral adults, recognized by their soft or pale aedeagi, collected in May and from July through September. I have seen early teneral adults, recognized by their entirely pale bodies, only from July and August. Although summer teneral adults suggest that *P. lattini* is a “spring-breeder” with new generation adults breeding after eclosion and with overwintering larvae (Thiele 1977), more data are needed to verify the reproductive pattern of this species.

PHYLOGENETIC CONSIDERATIONS.— Although *P. lattini* superficially resembles several other Oregon species of *Pterostichus*, it is not clear as to which of the Oregon species it is most closely related. The phylogenetic position of this species relative to species of *P. (Hypherpes)* s. str. in general is also uncertain on the basis of morphological features. Recent analyses of molecular data, based on nearly 100 terminal taxa and three different DNA markers, suggest that *P. lattini* is sister to a clade including *P. herculaneus*, *P. protractus* Le Conte, *P. neobrunneus* Lindroth, and an undescribed species near *P. parens* Casey (K.W. Will, pers. commun.)

ACKNOWLEDGEMENTS

The following institutions and individuals generously enabled me to examine holotypes and other North American material for comparative purposes: David H. Kavanaugh and the California Academy of Sciences; Terry L. Erwin, Gloria House, and Warren Steiner and the National Museum of Natural History, Smithsonian Institution. A generous loan of material from Oregon State University’s Oregon State Arthropod Collections enabled me to examine large series of *P. lattini* from the H.J. Andrews Experimental Forest. Jessica Rykken and Hoonbok Yi graciously allowed me to examine specimens of *P. lattini* and provided locality data from their studies while at Oregon State University. Yves Bousquet and Serge LaPlante of Agriculture and Agri-Food Canada (Ottawa, Ontario, Canada) kindly examined several specimens and confirmed my diagnosis that they represent an undescribed species. Special thanks are due two of my colleagues at the ODA: Kerri A. Schwarz prepared the distribution map for *P. lattini* and Steven A. Valley acquired the excellent images of *Pterostichus* spp. genitalia and pronota. My appreciation is also due the ODA for use of the imaging acquisition equipment for this project. The manuscript was significantly improved by the recommendations of several reviewers.

LITERATURE CITED

- BOUSQUET, Y. 1985. The subgenus *Pseudoferonina* Ball (Coleoptera: Carabidae: *Pterostichus*): description of three new species, with a key to all known species. *The Pan-Pacific Entomologist* 61:253–260.
- BOUSQUET, Y., AND A. LAROCHELLE. 1993. *Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America north of Mexico*. Memoirs of the Entomological Society of Canada No. 167. 397 pp.
- HATCH, M.H. 1953. *The Beetles of the Pacific Northwest. Part I: Introduction and Adephaga*. University of Washington Publications in Biology 16. 340 pp.
- KAVANAUGH, D.H. 1984. Studies on Nebriini (Coleoptera: Carabidae), V. New Nearctic *Nebria* taxa and changes in nomenclature. *Proceedings of the California Academy of Sciences*, ser. 4, 43:159–177.
- LABONTE, J.R. 1994. *Roth’s Blind Carabid Beetle (Coleoptera: Carabidae: Pterostichus rothi Hatch): Habitat, Survey, Threatened and Endangered Status*. Unpublished report to the Bureau of Land Management and the Nature Conservancy. 49 pp. [Copy available on request from the Department of Entomology, California Academy of Sciences.]

- LABONTE, J.R. 1996. *Biology of Carabid Beetles (Coleoptera: Carabidae) from the Northern Oregon Demonstration Project (Demo Project) Pitfall Traps*. Unpublished report to the National Biological Service. 33 pp. [Copy available on request from the Department of Entomology, California Academy of Sciences.]
- LINDROTH, C.H. 1961. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 2. *Opuscula Entomologica, Supplementum* 20:1–200.
- LINDROTH, C.H. 1963. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 3. *Opuscula Entomologica, Supplementum* 24:201–408.
- LINDROTH, C.H. 1966. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 4. *Opuscula Entomologica, Supplementum* 29:409–648.
- LINDROTH, C.H. 1968. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 5. *Opuscula Entomologica, Supplementum* 33:649–944.
- LINDROTH, C.H. 1969. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 6. *Opuscula Entomologica, Supplementum* 34:945–1192.
- LINDROTH, C.H. 1969. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 1. *Opuscula Entomologica, Supplementum* 35:i–xlviii.
- THIELE, H.U. 1977. *Carabid Beetles in their Environments: A Study on Habitat Selection by Adaptations in Physiology and Behavior*. Springer-Verlag, Berlin, Germany. xvii + 369 pp.