Bark beetles of the genus Dryocoetes (Coleoptera: Scolytidae) in North America

Donald Edward Bright Jr.

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BARK BEETLES OF THE GENUS DRYOCOETES
(COLEOPTERA: SCOLYTIDAE) IN NORTH AMERICA

A THESIS
SUBMITTED TO
THE DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY
BRIGHAM YOUNG UNIVERSITY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF
MASTER OF SCIENCE

BY
DONALD EDWARD BRIGHT, JR.
JUNE, 1961
This Thesis by Donald Edward Bright, Jr. is accepted in its present form by the Department of Zoology and Entomology of Brigham Young University as satisfying the Thesis requirement for the degree of Master of Science.

June, 1961
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Special thanks are given to my wife, Merlene, for her help and encouragement during the course of this study.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>111</td>
</tr>
<tr>
<td>LIST OF CHARTS</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF ILLUSTRATIONS</td>
<td>vi</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>HISTORY</td>
<td>3</td>
</tr>
<tr>
<td>METHODS</td>
<td>5</td>
</tr>
<tr>
<td>INTRASPECIFIC VARIATION</td>
<td>7</td>
</tr>
<tr>
<td>Sexual Variation</td>
<td>7</td>
</tr>
<tr>
<td>Individual Variation</td>
<td>7</td>
</tr>
<tr>
<td>Geographical Variation</td>
<td>8</td>
</tr>
<tr>
<td>DISCUSSION OF CHARACTERS</td>
<td>11</td>
</tr>
<tr>
<td>PHYLOGENY</td>
<td>15</td>
</tr>
<tr>
<td>SYSTEMATIC SECTION</td>
<td>17</td>
</tr>
<tr>
<td>Genus <em>Dryocoetes</em></td>
<td>17</td>
</tr>
<tr>
<td>Key to the species of the genus <em>Dryocoetes</em></td>
<td>20</td>
</tr>
<tr>
<td><em>Dryocoetes autographus</em> (Ratzeburg)</td>
<td>23</td>
</tr>
<tr>
<td><em>Dryocoetes betulae</em> Hopkins</td>
<td>28</td>
</tr>
<tr>
<td><em>Dryocoetes confusus</em> Swaine</td>
<td>31</td>
</tr>
<tr>
<td><em>Dryocoetes granicollis</em> (Leconte)</td>
<td>34</td>
</tr>
<tr>
<td><em>Dryocoetes affaber</em> (Mannerheim)</td>
<td>37</td>
</tr>
<tr>
<td><em>Dryocoetes sechelti</em> Swaine</td>
<td>41</td>
</tr>
<tr>
<td><em>Dryocoetes caryi</em> Hopkins</td>
<td>43</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>45</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>48</td>
</tr>
<tr>
<td>Chart</td>
<td>Description</td>
</tr>
<tr>
<td>-------</td>
<td>--------------------------------------------------------</td>
</tr>
<tr>
<td>1.</td>
<td>Variations in size of <em>Dryocostes affaber</em></td>
</tr>
<tr>
<td>2.</td>
<td>Variations in size of <em>Dryocostes autographus</em></td>
</tr>
</tbody>
</table>
## LIST OF ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Illustrations</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fig. 1.</strong> Dorsal aspect of pronotum of <em>Dryocoetes granicollis.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 2.</strong> Dorsal aspect of pronotum of <em>Dryocoetes affaber.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 3.</strong> Dorsal aspect of pronotum of <em>Dryocoetes autographus.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 4.</strong> Antenna of <em>Dryocoetes affaber.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 5.</strong> Male genitalia of <em>Dryocoetes caryi.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 6.</strong> Male genitalia of <em>Dryocoetes sechelti.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 7.</strong> Male genitalia of <em>Dryocoetes granicollis</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 8.</strong> Male genitalia of <em>Dryocoetes affaber.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 9.</strong> Male genitalia of <em>Dryocoetes betulae.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 10.</strong> Male genitalia of <em>Dryocoetes confusus.</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Fig. 11.</strong> Male genitalia of <em>Dryocoetes autographus.</em></td>
<td>47</td>
</tr>
</tbody>
</table>
INTRODUCTION

The genus *Dryocoetes* is widely distributed in Europe, Asia, North America and Central America. It consists of about sixty species, seven of which occur in North America.

All seven species in North America bore in the bark of the host tree where they feed and reproduce in the phloem layer. Usually they are found in the larger part of the bole or near the ground line feeding in roots. The species generally are host specific, limiting their attacks to two or three genera of trees. Only one North American species, *etulae*, attacks broadleaf trees; the remainder feed in coniferous trees, usually *Picea* or *Abies*. Since these insects feed for the most part in dying or injured trees and windfalls, direct economic loss is generally nil. However, *confusus* may attack and kill apparently healthy trees.

As far as known all species in the genus are polygamous, ordinarily with about three or four females associated with one male. Apparently, the male begins the entrance tunnel and hollows out the nuptial chamber where he waits for the females. In the cambial layer, each female constructs an egg gallery that radiates from the nuptial chamber. Eggs are laid along the gallery in niches and then covered with frass. The female pushes her excess boring dust toward the entrance where it is expelled by the male.

Mathers (1931) states, in the case of *confusus*, that the adults
emerge from hibernation in the latter part of June and fly until late July. Soon after emerging, they attack new trees where they excavate the first brood tunnels. Eggs are laid in these tunnels until late August, the beginning of cold weather, when the adults excavate feeding and hibernating tunnels. The male gallery extends from the nuptial chamber and the female continues the egg tunnel, these portions being recognized by the absence of egg niches. The parent adults pass the winter in these galleries. At the beginning of warm weather in the spring, the female beetles continue their galleries, laying eggs in the freshly cut portions. Egg laying continues until late June or early July, after which the parent adults may emerge and attack a new tree or they may die in the galleries. The first brood of eggs hatch by late August and pass the winter as young larvae. Pupae of this brood are present in late July or early August of the following year and transform to adults in late August. These young adults remain in the trees until spring, thus giving a life cycle of two years.

The two year life cycle described above is probably true only in the northern portion of the range of *confusus*. In the western and south-western United States, the life cycle evidently may be completed in one year or less.

The tribe Dryocoetini is large and complex. Its systematics cannot be adequately understood until all included genera are redefined and revised. The present study, although limited to North America, is a contribution to our knowledge of *Dryocoetes* Eichhoff, the largest genus in this group. It was undertaken because no revisional study is available to assist in the identification of North American species.
HISTORY

The genus *Dryocoetes* was described by Eichhoff (1864, p. 38) to include four European species: *Bostrichus autographus* Ratzeburg, *B. cryptographus* Ratzeburg, *B. dactyliperda* Fabricius, and *B. villosus* Fabricius. Of these, *B. cryptographus* was transferred to *Xyleborus* by Eichhoff (1881, p. 276), and *B. dactyliperda* was made the type of *Coccotrypes* also by Eichhoff (1879, p. 309). Eichhoff (1864, p. 38) further stated that probably *B. alni* George, and apparently *B. bicolor* Herbst (transferred to *Taphrotychus*, Eichhoff (1879, p. 205)) should be included in *Dryocoetes*. Since then, numerous species from North America, Central America and Eurasia have been described.

In the only other division of the genus, Balachowsky (1949, p. 178) erected the genus *Dryocoetinus* for *alni* and *villosus*, based on the almost totally granulate pronotum, with punctures on the anterior portion of the disk, and the deeply impressed sutural interspace at the apical portion of the declivity of these species. This new division has not been accepted by later workers, and Schedl (date unavailable) placed this genus in synonymy.

The first North American species of *Dryocoetes* was described as *Bostrichus septentrionis* by Mannerheim (1843, p. 298). In 1852, Mannerheim described a second species, *affaber* (p. 359), also in the genus *Bostrichus*, and Leconte (1868, p. 162) a third, *granicollis* as a *Xyleborus*. The remaining North American species were described as
Dryocoetes by Hopkins and Swaine. In 1912, Swaine described pubescens (p. 350) and confusus (p. 351); in 1915, sechelti (p. 350) and pseudotsugae (p. 360) were described. Hopkins, in 1915a, described betulae (p. 50), caryi (p. 50), americanus (p. 51), liquidambaris (p. 51) and piceae (p. 51).
METHODS

Approximately four thousand specimens of Dryocoetes were examined during this study, including the allotype of caryi and one broken paratype of sechelti. Of the remaining species, specimens of betulae, piceae, and confusus which bore the same data as the type, but not designated as paratypes, were seen. Specimens of americanus determined by Hopkins and specimens of affaber, granicollis and pubescens determined by Blackman were examined. The identification of septentrionis is based on a specimen in the collection of S. L. Wood which had been compared by him to the Mannerheim specimen in the Canadian National Collection.

After dissecting the male genitalic capsule from a specimen, the capsule was placed in a cold five per cent potassium hydroxide solution until the muscle fiber had dissolved away. The capsule was then washed in water several times, and transferred to microvials containing glycerine. The dissected specimen was remounted and the vial containing its genitalia was placed on the pin for future reference. A minimum of two to four specimens per species were used for each of the above dissections.

Illustrations were prepared with the aid of an ocular grid. The antennal drawing was made from a Canada balsam slide preparation; those of the male genitalia were made while the genital capsule was immersed in glycerine; and pinned specimens were used for drawings of the pronotums.

Measurements were made by using a calibrated ocular grid. These
Measurements represent the averages of many measurements and should be used with caution since some specimens may not fall in the size range that is stated.
INTRASPECIFIC VARIATION

Sexual Variation

Sexual variation was observed in all species of North American Dryococetes. In the small species, sechelti, caryi and granicollis, the differences are slight and very difficult to detect. Generally, the female has more hair-like pubescence on the frons and somewhat larger granules on the elytral declivity.

The most striking sexual variation in this genus occurs in confusus, where the female frons is very densely, closely hairy with the short setae longer at the periphery. The male frons is convex, granulate-punctate and only sparsely hairy. The sutural interspace of the elytral declivity is more strongly elevated and more coarsely granulate in the female.

In the other large species, the frons of the female is flattened or slightly concave and usually more or less densely clothed with hairs, whereas that of the male is convex or smooth and punctured and only sparsely hairy.

Individual Variation

Variation in body length was noted in all species, but is prominent only in two. The difference in length between the largest and smallest specimens equalled about thirty percent of the smallest. Environmental factors evidently influence the size of the individuals, since host conditions, such as moisture content and temperature are important agents.
Body color generally is consistent throughout the genus, varying from reddish-brown to almost black. The immature specimens are lighter in color, and gradually acquire the mature, darker color.

The surface of the pronotum often exhibits differences between individuals of the same series. Certain specimens of autographus have the smooth median line obscured by punctures and asperities. Other specimens may show a difference in the size and abundance of punctures. The pronotal shape may also show a slight variation. For example, in most specimens of affaber the pronotum is triangular (Fig. 2), but occasionally it may be more rounded, with the widest part more toward the middle. In individuals of all species, variations in placement and depth of punctures, and in size and surface sculpture of asperities may be found.

The elytral disk and declivity also show slight variation within a series. No one species can be singled out for discussion, since the variations are observed in all species. The most prominent individual difference occurs in the size, depth and distribution of the punctures on the elytral disk and in the degree of elevation of the sutural striae on the declivity. Other characters that may vary are the amount and length of pubescence, the abundance of interstrial punctures and the size of the granules of the declivity.

Geographical Variation

Geographical variation was noted especially in the size of specimens of affaber and autographus from different areas of their ranges (Charts 1 and 2). These species exhibited a gradual increase in size from the eastern and southeastern portions of their ranges to the north-
western and northern parts. The largest average size of both species is reached between Oregon and Alaska.

<table>
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<tr>
<th>Locality</th>
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<th>Maximum</th>
<th>Minimum</th>
<th>Average</th>
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<tr>
<td>Maine</td>
<td>10</td>
<td>2.60</td>
<td>2.30</td>
<td>2.45</td>
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<tr>
<td>Michigan and Minnesota</td>
<td>10</td>
<td>2.75</td>
<td>2.35</td>
<td>2.58</td>
</tr>
<tr>
<td>Colorado</td>
<td>10</td>
<td>2.80</td>
<td>2.40</td>
<td>2.50</td>
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<tr>
<td>Utah</td>
<td>10</td>
<td>2.85</td>
<td>2.50</td>
<td>2.74</td>
</tr>
<tr>
<td>Oregon</td>
<td>10</td>
<td>3.00</td>
<td>2.25</td>
<td>2.70</td>
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<tr>
<td>British Columbia</td>
<td>10</td>
<td>3.50</td>
<td>2.50</td>
<td>2.88</td>
</tr>
<tr>
<td>Juneau, Alaska (near type locality)</td>
<td>10</td>
<td>3.25</td>
<td>2.70</td>
<td>3.10</td>
</tr>
</tbody>
</table>

Chart 1. Variations in size of *Dryococetes affaber*.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Number of Specimens</th>
<th>Maximum</th>
<th>Minimum</th>
<th>Average</th>
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<tbody>
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<tr>
<td>Juneau, Alaska (near type locality)</td>
<td>10</td>
<td>4.75</td>
<td>3.75</td>
<td>4.25</td>
</tr>
<tr>
<td>England</td>
<td>10</td>
<td>4.00</td>
<td>3.25</td>
<td>3.65</td>
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</tbody>
</table>

Chart 2. Variations in size of *Dryococetes autographus*. 
The charts on the preceding page show the range in size of series from various localities and illustrates the gradual increase in size from southeastern to northwestern areas. A series of autographus from Europe is included in Chart 2 to show the size of specimens from that area.

In the eastern part of its range, the declivital punctures of affaber are somewhat smaller than those from the west. On some individuals of this species from Colorado and Utah, the declivital punctures are larger and more coarse; this can also be seen on specimens from all parts of its range. This variation evidently is somewhat common in the intermountain region, more so than in other areas. The size of the declivital granules also varies from east to west; those with smaller granules being more common in the east.

Specimens of autographus from the eastern portion of its range also have smaller declivital granules, and somewhat smaller elytral punctures.

In specimens of confusus from Arizona, the sutural striae are comparatively more strongly elevated than in specimens from farther north.
DISCUSSION OF CHARACTERS

The classification of the genus *Dryocoetes* in North America was formerly based by Swaine (1918) on size, locality and host; morphology being used to indicate species groups. A thorough analysis of all the characters useful in the classification of the family Scolytidae is not available nor have all the possible characters been investigated. The most useful characters used in this study are briefly discussed.

The genus *Dryocoetes* belongs in the tribe Dryocoetini in the subfamily Ipinae. Other related genera in this tribe include *Taphrochus* Eichhoff (Europe), *Cryptogenius* Strohmeyer (Africa), *Ozopemon* Hagedorn (southeast Asia), and *Carposinus* Hopkins (southeast Asia). These genera are distinguished from all other acolytid genera by the evenly convex pronotum; by the obliquely truncate antennal club (or possessing a club derived from that type); by the flattened, spinose distal portion of the tibiae and by the convex or flattened, unarmed, granulate declivity.

These genera may be distinguished from one another by several characters, the most important of which are the characters of the antennal club. In *Taphrochus*, the antennal club is circular, with the thickened basal area occupying less than one-fourth the total length and margined distally by a recurved line, the female frons is concave with a dense pile of short hairs and the declivity is convex with the sutural striae more strongly convex. *Cryptogenius* may be distinguished by the circular club, as in *Taphrochus*, but the club has no basal corneous
area. It may also be distinguished by the four-segmented antenunal funicle, by the impressed elytral striae and by the scutellum being wider than long. In Ozopemon, the club is more pointed at the distal end, the corneous basal portion occupying less than half the total length, with the first suture indicated by a sclerized procurred line; the pronotum is much wider than long, with a distinct summit and acute asperities; the scutellum is V-shaped. Carpoeinus is distinguished by the sub-truncate, circular antenunal club; by the impressed elytral striae; by the indefinite pronotal summit and by the V-shaped scutellum.

Frons

The pubescence of the frons of the female is extremely valuable in the classification of the genus. It varies from densely clothed, completely hiding the surface of the frons in confusus, to only sparsely clothed in autographus. The surface may be smooth and minutely granulate, as in gramicollis, to moderately roughened, as in autographus.

In the male, frontal variations are less obvious, but nevertheless are present. For example, the frons is distinctly punctured and smooth in sechelti but roughly granulate-punctate in confusus and, to a lesser extent, in affaber. Pubescence of the male frons varies but little.

Antenna
(Fig. 4)

The antennal scape is slightly longer than the funicle, slender, and widened at the distal end. The funicle is five-segmented, longer than the club, with the pedicle enlarged and cup-shaped, with segments two to five smaller and gradually increasing in size distally. The club
is obliquely truncate with the truncate portion occupying less than half the club in all species. The shape varies from sub-oval, approximately 1.4 times wider than long in *autographus*, to slightly longer than wide in *affaber*. The distal pubescent portion of the club projects beyond the corneous apex on the posterior face in *autographus*, *betulae* and *granicollis*. In the other species, no pubescence can be seen projecting beyond the apex. This character was not included in the key, since many specimens have the antennae lying close to the body, making observation of this character impossible.

**Pronotum**

The shape of the pronotum varies from somewhat triangular in *caryi*, *sechelti* and *affaber* (Fig. 2), to more nearly circular in *betulae*, *confusus* and *autographus* (Fig. 3), and elongate with parallel sides in *granicollis* (Fig. 1). In *autographus*, the surface of the pronotum is closely, densely punctured over the posterior two-thirds, the punctures being obscured, but still visible, by small asperities on the anterior portion. The surface of the pronotum in *affaber* is asperate over the entire surface tending to become granulate on the posterior one-fourth. In some specimens of *affaber*, a few small obscure punctures may be seen. The pronotal surface of *granicollis* is also asperate with a few shallow punctures.

**Elytra**

The sutural striae on the elytral disk may be impressed as in *granicollis*, or unimpressed as in *affaber*. The striae are regularly punctured in rows, varying greatly in depth and size between individuals.
The interspaces are smooth and minutely punctured in all species, except *granicollis* where they are roughened by the large, impressed strial punctures.

As in many scolytids, the declivity offers excellent characters. In *granicollis*, the sutural striae are deeply impressed making the suture strongly and prominently elevated, and the striae are deeply punctured. In *confusus* and *betulæ*, the sutural striae are much less impressed and the suture is only moderately elevated. The remaining species have the sutural striae very slightly impressed, if at all and a feebly elevated suture.

**Tibiae**

The tibiae are slightly curved, widened at the distal end, abruptly truncate, and margined by from five to seven teeth. The number of teeth varies between individuals and even may vary in the same specimen. For this reason, the tibiae were of no value in the classification of the genus.

**Male Genitalia**

Excellent characters were found on the endophallic portion of the male genitalia (figs. 5-11). This structure varies from a large, flat, sac-like form, as in *autographus*, *confusus*, *betulæ*, and *affaber*, to moderately lobed in *caryl* and *sechelti* and deeply lobed in *granicollis*. The remainder of the genitalic capsule displays no characters useful in the determination of species. For this reason, the various structures are not named and no attempt is made in this study to homologize the structures with those of other species.
Since the present study only includes a small fraction of the species of the genus Dryocoetes, a thorough discussion of the phylogeny of the group is not possible. A few general statements can be made, however.

Sexual dimorphism of the same general type is present to varying degrees in all the genera related to Dryocoetes. Any extreme development of these characters may be considered a specialization since they do not occur generally in other scolytids. The larviform male of Ozopemon brownei, (Browne, 1957), is certainly a specialization. The reduction in number and size of stria! and interstrial punctures and the reduction in number of pronotal asperities in Ozopemon are other specialized characters. Since reduction in number or size of parts is indicative of specialization, the four-segmented antennal funicle of Cryptogenius may be considered specialized. The antennal club of related genera is obliquely truncate, except in Cryptogenius, where the club has no basal corneous portion and is not obliquely truncate.

From the above line of reasoning, it is thought that Ozopemon and Cryptogenius represent the more specialized genera in this discussion. Dryocoetes, because of the low degree of sexual dimorphism (except in three species), its obliquely truncate antennal club, moderate to large stria! punctures and only a slight reduction in number of tibial spines, is considered to be a comparatively unspecialized genus.

These genera appear to have evolved from a common ancestral stock.
which probably had its center of distribution in Eurasia. In order to
determine this hypothetical parent, approximately fifteen species in the
five genera mentioned above were studied and analyzed. The author's
concept of the hypothetical ancestor is most nearly fulfilled in the
genus Dolurgus, which some authors place in the Dryocoetini. Dolurgus
superficially resembles Dryocoetes and shows many of the same characters
in a more primitive form. Sexual dimorphism is not evident, the antennal
club shows a primitive obliquely truncate form, pronotal asperities are
not developed and the anterior tibiae have six or more spines.

Among North American Dryocoetes, two lines of specialization are
apparent. Along one line, the extreme advanced characters are the deeply
impressed sutural striae of the declivity, the enlarged pronotum with
parallel sides and the peculiar male genitalia shown by granicollis. Along
the same line but less specialized are caryi and sechelti. The second
line of specialization is illustrated by the sexual dimorphism, the
reduced elytral punctures and the host specificity of betulæ and
confusus. The least specialized characters such as a convex, not
impressed declivity, low degree of sexual dimorphism and unspecialized
male genitalia are found in autographus. The position of affaber is
uncertain, but it appears to be intermediate between the betulæ-confusus
group and autographus.

The above discussion, unfortunately, must be largely speculation.
Since the tribe Dryocoetini is very large and occurs throughout the world,
a thorough consideration of phylogeny is impossible at this time.
SYSTEMATIC SECTION

Genus Dryocoetes Eichhoff

Dryocoetes Eichhoff, 1864, Berliner Ent. Zeitschr., 8: 38; ___, 1879,
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europäischen Borkenkäfer, p. 261; Leconte, 1876, Amer. Philos. Soc.,
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Hopkins, 1914, U. S. Nat. Mus., Proc. 48: 121; Blatchley and Leng,
1916, Rhynchopora of North Eastern America, p. 610; Swaine, 1918,
54; Chamberlin, 1939, The Bark and Timber Beetles of North America,
p. 462; Beal and Massey, 1945, Duke Univ. School of Forest., Bull.
10: 159; Balachowsky, 1949, Fauna de France 50: 177; Stark, 1952,
Fauna U. S. S. R. 31: 323; Chamberlin, 1958, Scolytidae of the Northwest, p. 188.

**Dryocoetinus** Balachowsky, 1949, Fauna de France 50: 188.

This genus is distinguished from related genera by the granulate to punctate, evenly convex pronotum, with low, indistinct asperities; by the obliquely truncate antennal club with the basal portion reaching beyond the middle in the central area; by the short, steep, unarmed, granulate declivity; by the scutellum being longer than wide and by the rather slender, flattened, armed tibiae.

**Description.**—Body cylindrical, 2.0 - 4.8 mm. Color of mature specimens black to reddish-brown.

Frons convex, granulate over much of the surface and often densely hairy in the female. Antennal scape but little longer than funicle, widened on distal half; funicle five-segmented, pedicle larger and cup-shaped, segments two to five smaller, gradually increasing in size toward the club; club obliquely truncate with one or two recurved sutures on the pubescent anterior face, basal corneous portion occupying more than half the total length.

Pronotum evenly convex with anterior margin unarmed; dorsal surface usually granulate to finely asperate, more strongly in anterior portion, sometimes punctured in posterior portion. Scutellum longer than wide.

Elytra with striae feebly or not impressed, strial punctures large, usually impressed in regular rows; interspaces slightly wider than striae, smooth; interstrial punctures much smaller and somewhat more abundant than those of the striae, armed with long hair-like setae. Declivity steep, convex or flattened, unarmed; sutrial striae impressed;
interspaces feebly granulate.

Middle and hind tibiae rather slender, somewhat flattened distally, runcate at distal end, armed with three to seven teeth (variable within individuals).

Vestiture abundant, hair-like.

*Type species.*— *Bostrichus autographus* Ratzeburg, subsequent designation by Hopkins (1914: 121).
Key to North American species of Dryocosmus.

1. Pronotum widest at or near the middle, sides rather strongly arcuate (Fig. 3); proepimeron usually with large, shallow punctures; larger species, usually over 3 mm. __________________________ 2

-- Pronotum widest at base or sides parallel, sides weakly arcuate (Figs. 1 and 2); proepimeron indistinctly if at all punctured except in a few afarber; smaller species, usually under 3 mm. __ 4

2. Female frons with a dense brush of short, yellowish, hair-like setae; declivity of both sexes steep, flattened, with sutural interspace distinctly, sometimes slightly, elevated; disk of pronotum finely densely asperate. _________________________________ 3

-- Female frons with sparsely placed hair-like setae, granulate-punctate with an impunctate smooth median space; male frons more sparsely clothed with setae and distinctly granulate; declivity evenly convex, not steep, with sutural interspace feebly raised; disk of pronotum distinctly punctured with an impunctate or slightly raised median line, asperities small and low on anterior and lateral portions. ___________________________ autographus (Ratzeburg)

3. Female frons very densely clothed by hair-like setae, concealing the surface of the frons, setae shorter in center, longer and incurved at periphery; pronotum finely asperate over entire surface,
clothed by long, yellow setae; declivity flattened with sutural interspace distinctly raised; from Abies. __________ confusus Swaine

--- Female frons less densely hairy, not concealing the surface of the frons; disk of pronotum sparsely punctured in median area of posterior half, distinctly asperate on lateral and anterior portions; interspaces of declivity less strongly impressed than confusus; from Betula and Pyrus. __________ betulae Hopkins

4. Declivity with the sutural striae deeply impressed, the punctures large, deep; sutural interspace strongly elevated with median row of granules; pronotum about 1.3 times as long as wide, the sides subparallel on posterior two-thirds; elytral punctures large, close and deep; interspaces narrow on disk, wider on declivity. __________ granicollis (Leconte)

--- Declivity with sutural striae feebly if at all impressed; sutural interspace slightly raised; pronotum less than 1.2 times as long as wide, widest behind middle; elytral punctures smaller, slightly impressed; interspaces as wide or wider than striae on disk and declivity. __________ affaber (Mannerheim)

5. Female frons closely pubescent, setae long and uneven, those on upper margin longer and incurved; male frons with fewer setae; declivity more strongly flattened, with first and second striae slightly impressed; pronotum less strongly convex; larger, 2.6 - 3.2 mm.; in Picea. __________ affaber (Mannerheim)

--- Female frons only slightly more pubescent than male; declivity
evenly convex; pronotum strongly convex, disk appearing granulate; smaller, 1.5 - 2.5 mm.

Sutural striae very slightly impressed, the punctures on declivity reduced in size or indistinct; frons granulate-punctate with slightly raised, impunctate, longitudinal median line; in Abies ________________ sechelti Swaine

Sutural striae distinctly impressed, their punctures not reduced on declivity; median line of frons wider and more distinctly raised; in Picea. __________________________ caryi Hopkins
Dryocoetes autographus (Ratzeburg)

Bostrichus autographus Ratzeburg, 1837, Die Forst-insecten 1: 160.

Dryocoetes autographus, Eichhoff, 1864, Berliner Ent. Zeitschr. 8: 39;


This species is distinguished from all other North American **Dryocoetes** by the distinctly punctured pronotal disk, by the convex
declivity with the sutural interspace only slightly raised, and by the absence of a dense mat of hair on the female frons.

**Female.**-- Length 3.4 - 5.0 mm. Mature color reddish-brown to black.

Frons broad, strongly convex, flattened just above the epistomal margin; surface granulate-punctate, clothed with a few long yellow hairs, with impunctate median smooth space about the size of, or smaller than, antennal club. Antennal club as long as wide, basal corneous portion occupying half the total length. Eyes coarsely granulate and shallowly emarginate.

Pronotum as wide as long, widest at or near middle, sides strongly arcuate and anterior margin broadly rounded; lateral areas and anterior third roughened by small, low confused asperities, disk strongly punctured with median line impunctate or slightly raised. Pubescence consisting of moderately abundant long yellow hair.

Elytra 1.7 times as long as wide; sides parallel, posterior outline broadly rounded; strial punctures large, deep and in regular rows; interstriae usually as wide as striae, punctures as numerous as striae except on declivity, and much smaller, each armed by a moderately long yellow hair-like seta about as long as width of an interspace. Declivity convex, first and third interspaces slightly elevated, second interspace flattened, slightly depressed; interspaces with a median row of small granules armed by moderately long yellow hair.

**Male.**-- Similar to female except frons more sparsely hairy, somewhat broader; declivity more strongly flattened with sutural and third interspaces less elevated; the interstrial granules much reduced or obsolete. Male genitalia as illustrated (Fig. 11).
Type Locality.— Europe, exact locality not know.

Hosts.— Picea, Tsuga and Pseudotsuga, also recorded from Abies
frazeri, Lirodendron tulipifera and Pinus spp.

Distribution.— Throughout the coniferous forests of Europe and
Asia and in North America north of North Carolina and New Mexico.

Specimens examined from: Alaska: Anchorage, Chichagof Island,
Eagle, Juneau, Kasilof, Ketchikan, Matanuska, Ruby, Shagluk, Tolstoi and
Colorado: Alma, Craig, Durango and Kenoske Pass. Maine: Beaver Pond,
Brunswick, Camp Caribou, Meadows, Crono, Paris and Portland.
Minnesota: Duluth and Itasca. Montana: McDonald Lake. New Hampshire:
New Mexico: Capitan. New York: Cicero Swamp, Cranberry Lake, Dundee,
Herkimer Co., Ithaca, Mt. Whiteface and Wells. North Carolina: Black
Mountain and Pisgah Ridge. Oregon: Astoria, Forest Grove, Santiam and
Yarnhill Co. Pennsylvania: North Mountain and Pocono Park. South Dakota:
Black Hills and Elmore. Tennessee: Gatlingburg. Utah: Beaver and
Uinta National Forest. Vermont: Braintree. Washington: Carson, Easton,
Hoquiam, Junction City, Lake Quinault, London, Olympic National Forest
and Rock Creek. West Virginia: Bayard, Cranesville, Davis, Delslow,
Grant Co., Monogalia Co., Morgantown, Randolph and Tucker Co. Wisconsin:
Bayfield Co. Alberta: Banff, Calgary, Edmonton, Jasper, Ledue, Lesser
Slave Lake, Nordegg and Olds. British Columbia: Avola, "Chilliwack
River", Glacier, Inverness, Lorna, Metlakatla, Mission, Pender Harbor,
Queen Charlotte Islands, Steelhead, Trinity Valley, Vancouver and
Wycliffe. Labrador: Goose Bay. Manitoba: "Piquitenay River".

The heretofore European species, autographus, was described by Ratzeburg in 1837. Since that time this species has been recorded from England, Europe and across Asia to Japan. When Hopkins described americana in 1915, he stated that his new species was closely related and doubtfully distinct from the European autographus. Swaine (1918) also stated that septentrionis was related to autographus. The type of pseudotsuga has been compared to a Mannerheim specimen of septentrionis by Wood and found to be identical. After a thorough and fruitless search during this study for characters to distinguish these four species, it was concluded that only one variable Holarctic species is represented and that the earliest name, autographus, must be used.

Details of the geographical variation in size found in this species is illustrated on page 7.

This species is commonly found in the base and roots of dying or injured standing trees, and in felled or windthrown trees.

Chamberlin (1939) states that in Douglas fir, the galleries are short and irregular. The winter hibernation galleries are in the inner bark and are larger than the egg galleries.
Dryocoetes betulae Hopkins

Dryocoetes eichhoffi Hopkins, 1894 (nec. Ferrarie, 1867), Canadian Ent. 26: 279; _____, 1904, Yearbook of Agric. 1903: 320; Hagedorn, 1910,
Coleoptorum Catalogus 4: 67.

Blatchley and Leng, 1916, Rhynchophora of North Eastern America,
273: 169; Chamberlin, 1939, The Bark and Timber Beetles of North 
America, p. 466; Beal and Massey, 1945, Duke Univ. School of 
Forest., Bull. 10: 159.

14(2): 131.

This species and confusus form a rather sharply defined group
characterized by the dense brush of hair on the female frons. It may be
separated from confusus by the presence of shallow punctures on the disk
of the pronotum, by the flatter, and less strongly impressed declivity
and by the host.

Female.— Length 2.8 - 4.5 mm. Mature color reddish-brown.

Frons broad, convex; surface granulate, rather densely clothed with
yellow hairs, (less dense than *confusus*), not entirely hiding the surface beneath, with a smooth, glabrous, median smooth space, sometimes reaching epistomial margin. Antennal club as long as wide, basal corneous part occupying half or slightly more of the total length. Eye emarginate and granulate.

Pronotum as long as wide, widest at or about middle, anterior margin broadly rounded, sides strongly arcuate; asperate over entire surface except on posterior portion near median line; punctures shallow, obscure and closely placed in median posterior area.

Elytra 1.7 times as long as wide, sides parallel, broadly rounded behind; striae punctured in regular rows, slightly or not at all impressed, the punctures large, impressed; interspaces twice as wide as striae, with numerous, small punctures each bearing a moderately long yellow hair. Declivity flat, sutural and third interspace slightly elevated with a median row of small, prominent granules, second interspace flattened, depressed and granulate, other interspaces granulate toward declivity.

**Male.**— Similar to female except frons less strongly granulate and pubescence less abundant; declivity steeper, the sutural and third interspaces more strongly raised, second interspace more strongly depressed, and the granules larger. Male genitalia as illustrated (Fig. 9).

**Type Locality.**— Grant County, West Virginia.

**Hosts.**— Betula species. Also recorded from Fagus, Pryus and Liquidamber.

**Distribution.**— British Columbia to Newfoundland; south in the eastern United States to Mississippi and Florida.

This is the only North American member of the genus that normally attacks broadleaf trees. It generally attacks trees that are injured or dying and is of no economic importance.

The galleries are irregular with transverse, longitudinal or diagonal branches, according to Beal and Massey, 1945.
Dryocoetes confusus Swaine


This species is closely related to betulae, but may be separated by the absence of punctures on the pronotal disk, by the very dense mat of hair on the female frons, by the more strongly impressed elytral declivity and by the host.

Female.—Length 3.4 - 4.3 mm. Color of mature specimens reddish-brown to black.

Frons flat; surface granulate, with a shallowly impressed post-epistomal impression, clothed on a circular area by a very dense brush of reddish-brown to yellow hair-like setae, longer at margin; epistomal margin fringed by closely placed yellow hair. Antennal club wider than long, basal corneous part occupying little more than half the total length. Eyes coarsely granulate, shallowly emarginate.

Pronotum 1.1 times wider than long, widest at or near middle;
anterior margin broadly rounded, sides strongly angulate; anterior and lateral portions finely asperate, asperities low, confused, the disk granulate-asperate, clothed by erect reddish hair.

Elytra 1.6 times longer than wide, sides parallel, broadly rounded posteriorly; strial punctures smaller than in other species, weakly impressed in regular rows, sutural striae more impressed; interspaces at least twice as wide as striae, the punctures much smaller and more numerous, each armed by an erect yellowish hair. Declivity convex; strial punctures smaller, obsolete in some specimens; sutural interspace raised and granulate-setose, granules prominent, uniseriate; second interspace impressed, less granulate-setose; third interspace raised.

Male.— Similar to female except frons only sparsely clothed by yellowish hair, surface granulate-punctate, with an impunctate, smooth, median space and a transverse impression just above epistomal margin; elytral declivity with the sutural interspace more strongly elevated and second one more strongly impressed, granules larger. Male genitalia as illustrated (Fig. 10).

Type Locality.— Colorado, exact locality not known.

Hosts.— Abies lasiocarpa, less commonly from other species of Abies and Picea engelmannii.

Distribution.— Throughout the range of its host in western North America from British Columbia to New Mexico.


This species attacks Abies lasiocarpa and less commonly other trees in the genus Abies. It is the most aggressive North American member of the genus and has been known to attack green trees. According to Swaine (1918), it attacks and kills healthy balsam in eastern British Columbia and northern Alberta. It has also been observed to kill overmature alpine fir in Utah.

The gallery consists of a small, circular nuptial chamber entirely in the phloem, with several radiating egg galleries which may score the sapwood (Keen, 1938).
Dryocoetes granicollis (Leconte)

Xyleborus granicollis Leconte, 1868, American Ent. Soc., Trans. 2: 162.


This species is not closely allied to any other species in the North American fauna. Its closest known relative evidently is the European villosus.

It may be distinguished from other North American representatives of the genus by the strongly punctured elytra, by the strongly elevated sutural interspace on the declivity, by the strongly impressed first striae and by the elongate pronotum with its parallel sides.

Female.— Length 2.3 - 3.0 mm. Mature color reddish-brown.

Frons flattened or slightly concave with indistinctly raised longitudinal median line just above epistomal margin, occasionally absent; smooth and minutely granulate, punctured near vertex; lateral areas of epistomal margin slightly raised and granulate. Pubescence consisting of sparsely placed hairs. Eye moderately granulate and
slightly emarginate. Antennal club as long as wide, basal corneous part occupying about half the total length.

Pronotum 1.3 times longer than wide, sides subparallel on posterior two-thirds, anterior margin broadly rounded; basal angles strongly incurved; anterior and lateral portions finely asperate-granulate, indistinctly subgranulate and punctured on disk; clothed by abundant, moderately long yellow hair.

Elytra 1.32 times as long as wide; sides parallel; striae strongly punctured in regular rows, sutural striae impressed, punctures large and deep; interspaces narrower than striae, the punctures much smaller, each armed by a moderately long, yellow hair. Declivity convex; sutural striae deeply impressed, the punctures large, coarse and close; sutural interspace very strongly elevated and distinctly granulate; other pleclival interspaces elevated and granulate.

Male.— Similar to female except frons less densely hairy and declivity steeper with sutural striae more impressed. Male genitalia as illustrated (Fig. 7.).

Type Locality.— Sullivan County, Pennsylvania.

Hosts.— Picea species. There are also records from Juglandes, Castanea and Abies, but these probably are accidental hosts, misidentifications or errors in labelling of the host.

Distribution.— An uncommon species in northeastern North America, from Quebec to North Carolina.

Randolph Co. New Brunswick: "Pisiquil Br.". Quebec: Chelsea and Gaspe.

This species is one of the rarest species in this genus in North America. Nothing of the biology is known.
Dryocotes affaber (Mannerheim)


eborus affaber, Leconte, 1868, American Ent. Soc., Trans. 2: 162.

Dryocetes affaber, Leconte, 1876, American Philos. Soc., Proc. 15: 361;

Eichhoff, 1879, Roy. sci. soc. Liége, Mem., Série 2, 8: 286;

Schwarz, 1888, Ent. Soc. Washington, Proc. 1: 80; Hopkins, 1893,
West Virginia Agric. Expt. Sta., Bull. 32: 212; Schwarz, 1895,
Mem. 8(2): 752; Swaine, 1909, New York St. Mus. Bull. 134, In
Rept. of St. Ent. for 1908, Appendix B, p. 101; Hagedorn, 1910,
Coleopterorum Catalogus, p. 65; Blatchley and Leng, 1916,
Rhynchopora of North Eastern America, p. 613; Swaine, 1918, Dom.
Minnesota Agric. Expt. Sta., Tech. Bull. 132: 55; Chamberlin, 1939,
The Bark and Timber Beetles of North America, p. 467; $$\ldots$$ 1958,
The Scolytidae of the Northwest, p. 189.

ocostes pubescens Swaine, 1912, Canadian Ent. 44: 350; $$\ldots$$ 1912,
Chamberlin, 1939, The Bark and Timber Beetles of North America,
p. 468.

This species does not appear to be related to any North American species. It may easily be recognized by the pronotum being widest behind the middle, by the flattened, steep, slightly impressed declivity, by the pubescent female frons and by its size.

It is apparently the most common *Dryococetes* in North America.

**Female.**—Length 2.5 – 3.3 mm. Mature color dark reddish-brown to almost black.

Frons flattened; surface granulate-punctate, clothed by moderately dense long hair, not hiding the surface beneath, hairs longer and incurved above; epistomal margin fringed with closely placed yellow hair. Intennal club as long as wide, basal corneous part occupying half the total length.

Pronotum 1.1 times as long as wide, widest well behind middle; interior margin narrowly rounded; sides strongly arcuate; asperate over the lateral areas and anterior half, moderately granulate on disk behind. Pubescence composed of abundant long yellow hair, shorter on disk.

Elytra 1.5 times as long as wide, sides parallel, broadly rounded behind; strial punctures large, smaller toward declivity, impressed in regular rows; interstriae smooth, occasionally roughened, at least twice as wide as striae; the punctures irregular and much smaller than those of striae, somewhat less numerous, each puncture armed by a long yellow hair; sutural interspace elevated slightly on posterior half of disk. Declivity
flat, sutural interspace and third interspace slightly elevated with a
median row of prominent granules. Second interspace flattened, impressed,
with a median row of prominent granules, less numerous than the strial
punctures; other interspaces uniseriately granulate-setose.

Male.—Similar to female except frons with hair less abundant;
decivity with first and third interspaces more strongly elevated and
with their granules smaller. Male genitalia as illustrated (Fig. 8).

Type Locality.—Alaska, the exact location not given.

Hosts.—Picea species; also recorded from Abies, Larix and Pinus.

Distribution.—The spruce forests of North America from Canada
and Alaska south to North Carolina and New Mexico.

Specimens examined from: Alaska: Andreafsky, Eagle, Fairbanks,
Fort Yukon, Homer, Juneau, Kenai, Matanuska, McGrath, Naknek Lake,
Patterson Bay, Rampert House, Tolstoi and Yakutat. Colorado: Craig,
Grand Lake, Gunnison National Forest, Jackson Co., Longmont, Newcastle and
Snowmass. Idaho: Coeur d’Alene, Collins, Kaniksu National Forest and
Lakeview. Maine: Allagash, Beaver Pond, Camp Caribou, Cupsuptic and
Lake Moxie. Michigan: Grand Island and Marquette. Montana: Bozeman,
Columbia Falls, Glacier National Park, Lake McDonald and Lincoln Co.
New Hampshire: Coos Co., Dixville, Waterville and Wonalancet. New
North Carolina: "Pink Beds", Pisgah Ridge and Silver Mountains. Oregon:
Ahlers, Cable Cove, Push, Saint Helens and Seaside. Pennsylvania: North
Mountain. South Dakota: Black Hills and Elmore. Utah: Beaver, La Sal
Mountains, Logan Canyon, Mammoth Mountain and Wolf Creek Pass (Duchesne
Co.). Washington: Hoquiam and Lake Quinault. West Virginia: Burbin,
Cranesville, Davis, Grant Co., Pocahontas Co., Randolph Co., and Shavers

Hopkins (1915a) described *piceae* on its smaller size and eastern distribution and Swaine (1912) described *pubescens* on its apparently larger declivital punctures. From the discussion of characters presented previously it is seen that these characters are merely variations within the population. Therefore, in the absence of consistent morphological differences, only one species is represented.

Keen (1938) states that this species attacks the top of felled and dying spruce in the western United States. It has been observed attacking both the upper and lower bole and stumps of standing and felled spruce in Utah, Colorado, eastern Canada and Alaska.

The adults construct a central nuptial chamber from which the egg galleries, usually three in number, radiate (Chamberlin, 1958).
Dryocoetes sechelti Swaine


This species is one of the smallest species in the genus. It is said to, but may be separated from caryi by the smaller declivital 
structures on the sutural striae, by the obsolete median line of the frons by the host. It may be distinguished from other members of the genus 
its small size, by the more strongly precipitous anterior portion of 
pronotum and by the steep, flat declivity.

Female.—Length 2.0—2.5 mm. Mature color reddish-brown, legs 
antenna sometimes lighter.

Frons convex above; surface densely granulate-punctate, clothed by 
laterally long yellow hair, with slight transverse impression above 
stomal margin, also with longitudinal, scarcely raised, impunctate 
ian line from epistomal margin to vertex; epistomal margin with 
.;age of closely placed, long yellow hair in median area. Antennal club 
ong as wide, corneous basal part occupying very slightly less than 
of the total length. Eye granulate; shallowly emarginate.

Pronotum widest behind middle; sides slightly rounded, basal 
gles strongly arcuate, anterior margin moderately rounded; granulate 
or disk, asperate on anterior and lateral areas, asperities low

41
confused and closely placed. Pubescence consisting of moderately long yellow hair on sides, shorter on disk.

Elytra 1.4 times as long as wide; sides parallel; strial punctures large, impressed, in regular rows, each puncture usually with a very short hair, sutural striae slightly impressed, others slightly or not at all impressed; interstriae smooth, at least twice as wide as striae, interstial punctures much smaller and more numerous, armed by yellow hair shorter than width of an interspace. Declivity convex above, somewhat flattened below with sutural interspace slightly raised; strial punctures reduced usually becoming obsolete toward apex; interspaces with median row of very small granules each bearing a short yellow hair.

**Male.** — Similar to female except frons less densely hairy and declival granules smaller or obsolete. Male genitalia as illustrated (Fig. 6).

**Type Locality.** — Sechelt, British Columbia.

**Host.** — Abies lasiocarpa.

**Distribution.** — Uncommon in western coniferous forests from British Columbia to Colorado.


This species breeds in the lower portion of the bole in small suppressed trees less than eight inches in diameter (Wood, personal communication).
Dryocoetes caryi Hopkins


This species is very closely related to sechelti Swaine, but differs in the more prominent, impunctate, longitudinal median line of the frons, and by the large, impressed punctures of the sutural striae which are not reduced on the declivity.

Female.—Length 2.1 – 2.7 mm. Mature color reddish-brown.
Frons convex above, flattened below; surface moderately granulate-punctate, with a prominent, impunctate median line, narrower toward epistomal margin; epistomal margin slightly sinuate, lateral margins not raised. Pubescence short, moderately abundant. Antennal scape about 1.5 times longer than the funicle, widened at the distal end; club round, as long as wide, basal corneous portion occupying half the total length.

Pronotum 1.07 times longer than wide, widest behind middle; sides and anterior margin moderately narrowly rounded, basal angles more broadly rounded; strongly convex in profile, anterior portion steeper and asperite, summit behind middle, uniformly granulate in posterior and lateral portions.

Elytra 1.4 times longer than wide, sides parallel, apex subtruncate with angles broadly rounded; sutural striae slightly impressed, others not impressed, the punctures moderately large and impressed; interspaces
smooth, about one and one-half times wider than striae, punctures minute and more numerous than those of striae. Declivity somewhat flattened; sutural striae slightly impressed with punctures not reduced, second, third and fourth striae with punctures often much reduced to obsolete; interspaces with small, acute granules.

**Male.**— Similar to female except pubescence of frons shorter and less abundant; declivital granules somewhat larger. Male genitalia as illustrated (Fig. 5).

**Type Locality.**— Camp Caribou, Maine.

**Hosts.**— *Picea angustissima*, *P. rubra* and *P. glauca*.

**Distribution.**— The northern coniferous forests of North America from British Columbia to Maine, south to North Carolina and Wyoming.

Specimens examined from: **Maine:** Camp Caribou. **North Carolina:** Cherokee. **Wyoming:** Laramie. **Alberta:** Crownest. **British Columbia:** Lorna. **Quebec:** Chelsea and Gaspe.

This species evidently is quite rare; only a very few collections having been made since the type was collected. It breeds in the bole of small, weakened, shaded-out, suppressed spruce. In Quebec it was taken in association with *Xylechinus americanus* Blackman (Wood, personal communication).
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LEGEND

Fig. 1. Dorsal aspect of pronotum of *Dryococetes granicollis*.

Fig. 2. Dorsal aspect of pronotum of *Dryococetes affaber*.

Fig. 3. Dorsal aspect of pronotum of *Dryococetes autographus*.

Fig. 4. Antenna of *Dryococetes affaber*, posterior aspect.

Fig. 5. Male genitalia of *Dryococetes caryi*, lateral aspect.

Fig. 6. Male genitalia of *Dryococetes sechelti*, lateral aspect.

Fig. 7. Male genitalia of *Dryococetes granicollis*, lateral aspect.

Fig. 8. Male genitalia of *Dryococetes affaber*, lateral aspect.

Fig. 9. Male genitalia of *Dryococetes betulae*, lateral aspect.

Fig. 10. Male genitalia of *Dryococetes confusus*, lateral aspect.

Fig. 11. Male genitalia of *Dryococetes autographus*, lateral aspect.
BARK BEETLES OF THE GENUS DRYOCOETES
(COLEOPTERA: SCOLYTIDAE) IN NORTH AMERICA

AN ABSTRACT
SUBMITTED TO
THE DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY
BRIGHAM YOUNG UNIVERSITY

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BY
DONALD EDWARD BRIGHT, JR.
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This abstract by Donald Edward Bright, Jr. is accepted in its present form by the Department of Zoology and Entomology of Brigham Young University as satisfying the abstract requirement for the degree of Master of Science.

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ABSTRACT

Approximately 1,000 specimens of the North American species of the
k beetle genus Dryocoetes was examined during this taxonomic study.
Complete descriptions and a key were prepared for the seven North
american species. Distributional data, biological notes and a
bibliography for each species are presented. The morphological characters
useful in this classification are discussed and utilized to establish an
parent phylogeny.

The important external characters used in this classification include
the shape and sculpture of the pronotum, the pubescence of the female
ons, the degree of impression of the sutural striae on the declivity
d the shape of the declivity. The most significant characters were
and in the shape of the endophallic portion of the male genitalia
ich are illustrated.

Of the twelve species previously described from North America, five
was placed in synonymy. The new synonymy included follows: Dryocoetes
rigraphus (Ratzeburg) (=D. septentrionalis (Mannerheim), D. americanus
phins and D. pseudotsugae Swaine) and D. affaber (Mannerheim) (=D.
.cea Hopkins and D. pubescens Swaine).

Dryocoetes autographus (Ratzeburg), a Eurasian species, is recognized
r the first time in North American fauna. Significant extensions of
e distributions of sechelti Swaine and caryi Hopkins are included.