

Classification, reconstructed phylogeny,
and zoogeography of Pytho Latreille
(Coleoptera: Heteromera: Pythidae) based
on study of larval, pupal, and adult stages

by

Darren Andrew Pollock

A thesis
presented to the University of Manitoba
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Department of Entomology
University of Manitoba.

Winnipeg, Manitoba

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ISBN 0-315-47944-2

CLASSIFICATION, RECONSTRUCTED PHYLOGENY, AND ZOOGEOGRAPHY OF
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STUDY OF LARVAL, PUPAL, AND ADULT STAGES

BY

DARREN ANDREW POLLOCK

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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ACKNOWLEDGMENTS

I am very grateful for the kind assistance received from the various private collectors and curators of museum collections, whose specimens formed the basis of my study. I am especially indebted to the following curators who loaned me type material: L. Jessop (BMNH), S. Koponen (DBTU), S. Takagi (HUS), O. Merkl (TMB), S.R. Shaw (MCZ), H. Silfverberg (ZMH), F. Hieke (ZMHB), and G. Scherer (ZSM). Throughout my study, I obtained gifts of specimens and advice, both of which were invaluable. I should like to thank the following for their generous contributions: B. and J. Carr, R.C. Craw, R.A. Crowson, N. Hayashi, S. Hisamatsu, J.F. Lawrence, R. Pettersson, and D.K. Young. Dean of Agriculture R.C. McGinnis provided part of my financial support during my programme, and for his assistance I am very grateful.

I would especially like to thank R.E. Roughley, who has allowed me to explore an interesting group of beetles, and also has allowed the academic latitude needed to appreciate systematic research. Without his financial and other support, I surely would not have been able to carry out this study. To the other members of my committee, Drs. T.D. Galloway and B. J. Hann, I express my gratitude for suggestions and guidance. For obtaining many references, I should like to thank profusely, the diligent workers in the Interlibrary Loan Department of Elizabeth Dafoe Library. For help with translation, I thank Rolf Beutel, Ingolf Askevold, Germaine Léger, and Roger Pettersson. I am

grateful to Dr. B. Dronzek and B. Luit for the use of the scanning electron microscope. Finally, I thank Lisa Reichert, for helping with the illustrations and helping return loans, but especially for her understanding and patience through the past several years.

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ABSTRACT

Pollock, Darren A. 1988. Classification, reconstructed phylogeny, and zoogeography of Pytho Latreille (Coleoptera: Heteromera: Pythidae) based on study of larval, pupal, and adult stages. M.Sc. dissertation. Dr. R.E. Roughley, advisor.

The nine world species of Pytho Latreille are reviewed in detail, through an examination of adult, and reared/associated larval and pupal stages. Keys are provided for separation of species in all these three life stages. Taxonomic changes, as well as type designations, were done where necessary. Cladistic analysis, based on six larval, and 12 adult stage characters indicates four monophyletic species-groups: one species-group with a Nearctic distribution (one species), two species-groups with North American-European-Japanese distributions (three species each), and one species-group with a North American-European distribution (two species). Larval synapomorphies were relatively more useful in delimiting species-groups, than were characters of the respective adult stages. The ancestor of the northern Hemisphere Pythinae was isolated on Laurasia, and may have been associated with Coniferae as early as the Jurassic. Considering zoogeographic evidence, there was a possible Euramerican ancestor for two of the species-groups, and a trans-Beringian ancestor for another.

Chapter I

INTRODUCTION

The genus Pytho Latreille 1796 occurs in North America, Europe, including U.S.S.R., and Japan. Although considered to be a boreal insect, it occurs in more southern areas capable of supporting coniferous forest. All species have larval stages which feed on the decaying cambial-phloem layer, or inner bark of dead coniferous trees. Because Pytho feeds only on trees past economic importance, the natural history of every North American species is poorly known. Such data about the three European species is present in many scattered references. Even though the number of species is relatively small, the number of available names in Pytho is relatively high. The proliferation of names, mostly in the latter part of the eighteenth, and early part of the nineteenth centuries, was due to two species which exhibited great colour and size variations. This fact, and the scattered nature of descriptions of the various species, caused some difficulty in assigning specimens accurately to species names. This problem, again, was more prevalent in North America. Several authors, including Horn (1888) and Wickham (1899) comment on the problems encountered with the small number of North American species of Pytho.

I had several objectives in undertaking this study. Firstly, I wished to conduct a taxonomic revision of the species of Pytho in order to solve the existing nomenclatural problems. This included the

construction of accurate and useful keys and distributions of all world species. For an insect that is so common in northern coniferous forests, there is very little published information on the natural history of Pytho species. I wished to examine the natural history and life cycle of the North American species. Included in the natural history study is the rearing, association, and description of the larvae and pupae of the North American species, none of which have been dealt with in detail previously. Because of the confused nature of the classification within Heteromera, I felt that it was important to use modern methods of phylogenetic systematics to clarify the relationships within the genus Pytho, as well as of the family Pythidae. This was recently begun by Watt (1987), who restricted his study to the family/subfamily level. Finally, I wanted to examine the zoogeography of the entire subfamily Pythinae, as well as the individual clades present within Pytho. Because all world species are examined in this study, a more complete analysis of the historical events that shaped the present distribution of the genus Pytho was possible.

Chapter II

CONSTITUENTS AND SYSTEMATIC PLACEMENT OF PYTHIDAE

The taxon Pythidae has been interpreted historically as being relatively diverse and has included several groups which have eventually achieved independent family status (Crowson, 1955). Furthermore, various members of Pythidae (sensu latiore) were transferred to Oedemeridae, Salpingidae, and Pyrochroidae at various times, and vice versa. Therefore, the exact definition of the family Pythidae has long been unstable. For instance, Seidlitz (1916), Blair (1928) and Arnett (1968) have accepted and retained a broad concept of this family whereas several more recent workers have used a restricted definition of the group (e.g. Crowson 1955, 1981; Lawrence 1977, 1982; Watt 1987).

A major reason for the historically broad concept of Pythidae was the total reliance upon adult stage characters. Once larvae became available for study, and were examined for many groups, familial limits and definitions became clearer. Larval characters have been very important in establishing both the constituents and systematic placement of Pythidae. Authors who have used larval characters to classify various taxa of Heteromera, include Lawrence (1977, 1982) and Watt (1987). Watt (1987) is the first to incorporate larval analysis and cladistic technique to define the constituents and systematic placement of Pythidae. In this treatment, I accept the classification of Pythidae

given by Watt (1987) for several reasons. Larval characters are seemingly given equal weight to those of the adults. Therefore, much emphasis is placed upon the former. I believe it should. This, in turn, has increased the number of available characters for taxonomic and phylogenetic analyses. Secondly, because cladistic methods are used, it is easy to follow Watt's (1987) analysis. Because the rationale is provided for his choice of synapomorphies, the classification is "testable".

Watt's (1987) classification basically agrees with that of Lawrence (1982), in that two subfamilies, Pilipalpinae and Pythinae are proposed. The Pilipalpinae includes several genera variously assigned to Pyrochroidae (Crowson, 1955; Paulus 1971), Oedemeridae, Anthicidae (Abdullah, 1964b), and Pythidae (Watt, 1987). Recently, Nikitsky (1986) has proposed the family Pilipalpidae for these taxa, which are known from Chile, Australia, New Zealand, and eastern Palearctic.

The subfamily Pythinae (Watt, 1987) corresponds closely with Pythini of Horn and LeConte (1883) and Arnett (1968), and Pythinae of Blair (1928), except that the genera Boros and Lecontia are now placed in the family Boridae. According to Watt (1987), Pythinae includes Pytho and four monobasic genera: Priognathus monilicornis (Randall), Trimitomerus riversii Horn, Synercticus heteromerus Newman, and Sphalma quadricollis Horn. The Australian species Anaplopus tuberculatus, described by Blackburn (1890) in Pedilidae, and placed subsequently in Tenebrionidae by Abdullah (1966), belongs in the restricted definition of Pythidae (sensu Crowson, 1955) (Lawrence 1987). No specimens of this beetle were examined, however.

The genus Pytho, being the nominal genus of the subfamily, has remained relatively unaltered in family position since being described; it has always been in various authors' concepts of Pythidae. The genus Priognathus was proposed by LeConte (1850) for Dytilus monilicornis, originally placed in Oedemeridae by Randall (1838). Since LeConte's treatment, P. monilicornis has remained a member of Pythidae.

Sphalma quadricollis was originally described as a pythid by Horn (1872), contrary to Watt (1987) who states that S. quadricollis was originally placed in Melandryidae. Several subsequent authors (e.g. Hatch 1965, Arnett 1968) have included this species in the Melandryidae; Young (1976) demonstrated on the basis of larval and adult characters that S. quadricollis is a member of Pythidae. This species is known from several states in the western United States, and possibly from British Columbia.

The Australian species, Synercticus heteromerus Newman, has been assigned to Tenebrionidae, Pythidae, or Boridae (Watt, 1987). Crowson (1955) suggests that it exhibits characters of both Boridae and Pythidae. Lawrence (1982) lists Synercticus as a member of the subfamily Pythinae; this placement is used also by Watt (1987).

The true phylogenetic position of Trimitomerus riversii has never been demonstrated, although originally described in Pythidae by Horn (1888). This species, known only from Arizona, is thought to have possible affinities to Trictenotomidae (Crowson 1955). Crowson (1980; pers. comm.), like Watt (1987) believes that Trimitomerus belongs in Pythidae, while Lawrence (pers. comm.) has hypothesized a position

closer to Synchronidae, Oedemeridae (Calopodinae) or Cephaloidae (Stenotrachelinae). The larva of T. riversii is undescribed, but Lawrence (pers. comm.) has a "likely candidate." Once the larva is associated and described, the true phylogenetic position of this species will become clearer.

The concept of Pythinae used in this treatment, follows that of Watt (1987), except that I have excluded Trimitomerus. I feel that because the larva is unknown, and the adult is so aberrant structurally, inclusion of Trimitomerus in Pythinae is unsubstantiated, compared to the other pythine taxa with adequately described larvae.

Historically, Pythidae has been placed near a number of other families, including Mycteridae, Boridae, Trictenotomidae, Pyrochroidae, Salpingidae, Elacatidae and others (Böving and Craighead, 1931; Crowson, 1955, 1966, 1981; Arnett, 1968; Lawrence, 1977, 1982; Watt, 1974, 1987; Young, 1985). The reconstructed phylogeny for the salpingid group of families (Trictenotomidae, Pythidae, Boridae, and Salpingidae) provided by Watt (1987) gives evidence for the systematic placement of Pythidae, which form the sister group of Boridae. Pythidae + Boridae is the sister taxon to Salpingidae, and all three are the sister group of Trictenotomidae.

The only synapomorphy used by Watt (1987) to demonstrate monophyly of Pilipalpine + Pythinae, is an adult procoxal character. There is no larval character in support of Watt's (1987) hypothesis. Crowson (pers. comm.) states that the inclusion of Pilipalpine in Pythidae is hardly possible based on larval characters. It is probable that the taxa

included by Watt (1987) in Pilipalpinae are deserving of independent family status (Nikitsky, 1986).

Although the classification of Watt (1987) is admittedly preliminary, and places the Pythidae in relatively the same position as most previous authors, the combination of cladistic methods and interpretations, and inclusion of larval characters make Watt's (1987) scheme more useful and meaningful than most earlier efforts. I have adopted the conclusions of Watt (1987), for use in this treatment.

Chapter III

NATURAL HISTORY OF PYTHO

Virtually nothing is published concerning the natural history of Nearctic species of Pytho outside of scattered host records. The Palearctic species, comparatively, are well-studied, with very detailed natural history known for P. kolwensis (Burakowski, 1962; Pettersson, 1983). The numerous references to the natural history of all three European species may be found in Seidlitz (1916, 1917) and Blair (1928). Any important references not included in these two sources will be given in the individual species treatments.

In this section, the biology and natural history of Pytho in general, will be discussed, with the life cycle, host interrelationships, overwintering strategies, and predators and parasitoids. References to the natural history of Palearctic species were taken from the literature, while those of Nearctic species were obtained from personal field observations and specimen label data. No major differences in the natural history of Nearctic and Palearctic species are thought to exist.

All stages of Pytho species may be found under the bark of dead coniferous trees (Pinus, Larix, Picea, Tsuga, Abies, Thuja). It appears that host selection is associated more closely with stage of decay of the tree rather than with the actual host tree genus or species. This is based on numerous field observations, literature and specimen data,

and attempts at rearing larvae. Host specificity is not apparent in Nearctic species of Pytho. For instance P. seidlitzi has been collected in association with nine different hosts. Pytho planus is collected predominantly from Pinus species, but records from Picea species are also known. Pytho strictus has been collected from only Pinus strobus, however only one of the specimens examined had any host data. For the Palearctic species, P. kolwensis is considered to be associated with Picea exclusively, as is P. abieticola (Saalas 1917; Burakowski 1962; Pettersson, pers. comm., 1983). Pytho depressus is known also from Picea, as well as Pinus silvestris L. (Saalas 1917; Pettersson, pers. comm.). Detailed host records are given in the individual species treatments.

Pytho larvae are found under the bark of trees within a fairly narrow range of decay and such trees are suitable probably only for 4 to 10 years duration (Pettersson, pers. comm.). Generally, host trees are dead for 3-4 years before being used by larvae of Pytho. Other families of Coleoptera, including Buprestidae, Cerambycidae, and Scolytidae, which are earlier colonizers of dead and dying trees, loosen the bark and allow adults of Pytho species access to this habitat. The trees must be moist, although large larvae and adults of P. niger and P. planus were collected from trees that were very dry and in a more advanced stage of decay. Most of the larvae collected in the field were taken from logs lying horizontally near or on the ground. A few were collected from inclined logs, and only very few specimens from dead, standing trees. Pettersson (pers. comm.) states that P. abieticola prefers trees leaning against other trees. As a rule, if there is a

heavy infestation of white rot or any other subcortical fungus within an otherwise suitable host tree, Pytho larvae are not found.

According to a study of P. depressus by Andersen and Nilssen (1978), larvae of this species are xylophagous and feed on the decaying cambial-phloem layer. Pytho depressus larvae were offered live Diptera larvae, and dead and live specimens of Tribolium castaneum Herbst (Coleoptera: Tenebrionidae), all of which remained untouched by the Pytho larvae. These findings, which are supported in my own rearing of larvae, contradict earlier authors' (e.g. Peterson 1951; Arnett 1968) claims that Pytho larvae are carnivorous. DeLeon (1934) states that Pytho are occasionally predaceous. Gut contents of P. niger larvae were analyzed by Smith and Sears (1982) and only finely granulated wood particles and fibres were present. Additionally, studies of larval structure suggest a xylophagous rather than predaceous life style. For instance, Pytho larvae have stout mandibles with a moderately well-developed mola, enabling them to loosen decaying woody material (Smith and Sears 1982).

An hypothetical life cycle for species of Pytho is difficult to construct because of the overlap in generations that is often present in the field. Often, in my own collecting of Nearctic species, several sizes of larvae as well as pupae and adults are found beneath the bark of one tree at the same time. One species, P. kolwensis, has a fairly well-documented life cycle (Burakowski 1962; Pettersson pers. comm.). This life cycle is given below and will be used as a general plan to which all other species, especially the Nearctic species, will be compared.

Adult P. kolwensis overwinter under bark in pupal cells, which they leave by the end of April or the beginning of May. Copulation takes place in May, with the males dying immediately following copulation. Females die after oviposition, which occurs in mid-May. Eggs are laid into tunnels in the wood formed by various members of Scolytidae. Larvae live for several years and usually pupate after three years but may extend this to five years if conditions are not optimal. The larvae build pupal cells between July and August. The pupal stage lasts two to three weeks. Emerging adults overwinter under the bark in the pupal cells. This life cycle is probably indicative of all species of Pytho but it would be valuable to examine each stage in more detail, particularly with respect to the Nearctic species.

Adults of Pytho species were collected from within pupal cells from late September through the winter to April or May. After overwintering under bark, adults leave the host tree and presumably disperse to new trees. If the old host is still suitable and not too decayed, adults may remain to mate and oviposit in the original host tree. Because the distribution of suitably useful host trees is not uniform, Pytho, as well as any other insects utilizing trees as a food source, must be able to sense their host trees (Payne 1983). It is not known how adults of Pytho discriminate among trees encountered. According to Payne (1983) many scolytids orient to vertical objects. A similar situation may exist in adult Pytho, except that perhaps horizontal objects would be preferentially sought by adults in flight. This conjecture is based upon the observation that in the field, adults and larvae are most commonly found under the bark of dead, horizontally oriented, trees.

Available flight records for several Nearctic species are from May, June and July. Mating and oviposition occur sometime during these three months. I did not observe oviposition in the field or laboratory, but it is probable that oviposition into scolytid tunnels, as found for P. kolwensis by Burakowski (1962), is widespread among adult females of the species of Pytho. DeLeon (1934) states that one female of P. planus laid 41 eggs between 29 June and 1 July, 1930. It is unfortunate, however, that the actual oviposition process is not discussed. Matings were observed in the laboratory, most of which were less than one minute duration. Males did not die immediately after copulation, as indicated by Burakowski (1962) for those of P. kolwensis.

The newly hatched larvae feed and grow until September, at which time feeding ceases and the larvae prepare for overwintering. From laboratory studies, a fairly high mortality occurs in these young larvae during winter. The next spring, larvae resume feeding and grow quickly. Under the bark, larvae maintain a spatial segregation and encroachments are minimized by larvae prodding each other with the acute urogomphal tips. Most larvae will have attained maximum size by August of the second year, but it is possible that some larvae require a third growing season. In late August or September mature larvae cease feeding and construct an oval to circular pupal cell, approximately 20-25 mm in diameter. The walls of the cell are of variable thickness, and are constructed with the decaying cambial-phloem material upon which the larva fed. Soon after completion of the cell, the larva becomes distended and almost cylindrical, the legs become non-functional, and pupal tubercles become visible beneath the larval cuticle. This

prepupal stage, which has a laboratory duration of four days, is active especially when disturbed, and moves by twisting the abdomen.

The pupal stage lasts about 10 days under laboratory conditions, but this is undoubtedly longer in the field. Pupae remain in the cells, but are fairly active, moving by abdominal twisting. Mandibles, eyes, tarsal claws, and genitalia darken first, with the elytra and the rest of the integument sclerotizing only after eclosion. Adults require at least one week to harden fully, and remain within the pupal cells to overwinter.

Because pupae are thought to be incapable of overwintering, larvae have a threshold temperature at which they will not pupate and risk death by frost. As mentioned, both adults and all stages of larvae are capable of overwintering. Cold-hardiness studies have been done for P. depressus (Zachariassen 1977, 1979, 1980) and P. planus (Ring 1981, 1982; Ring and Tesar 1980, 1981) indicating that both larvae and adults have relatively high supercooling points and overwinter in a frozen state. Both species are presumed to have nucleating agents in the haemolymph which cause the formation of ice at relatively high sub-zero temperatures (Zachariassen 1977; Ring and Tesar 1980). The fact that more than one stage (larvae and adults) is capable of overwintering, allows Pytho to be more opportunistic in host use, as well to use more than one growing season, the latter of which may be a consequence of its predominantly boreal distribution.

Subcortical, insect co-inhabitants of species of Pytho in the province of Manitoba, based on my fieldwork include members of the

families Staphylinidae, Elateridae, Cleridae, Tenebrionidae, Boridae, Cerambycidae, and Scolytidae (Coleoptera), and Sciaridae and Xylophagidae (Diptera). No actual predators of Pytho larvae were observed in the field, but probably one or more of the carnivorous genera of elaterid or clerid larvae, or the centipedes common in older logs, prey on smaller larvae of Pytho. Burakowski (1962) lists Palearctic species of the elaterid genera Harminius, Denticollis, and Melanotus as predators of P. kolwensis larvae. The only known parasitoids of Pytho are Cyanopterus flavator Fab. (Hymenoptera: Braconidae) from P. depressus and Meteorus corax Marshall (Hymenoptera: Braconidae) from P. abieticola (Pettersson, pers. comm.). No parasitoids were discovered in my numerous larval rearing trials of Nearctic species.

Adult Pytho vary considerably in size. This is certainly not unique to Pytho, and is common in other groups of insects utilizing wood as a food source (Haack and Slansky 1987; Andersen and Nilssen 1983). Generally, wood-feeding insects can complete development under adverse conditions, particularly with respect to food availability and quality. This may be one of the reasons for great size variability (Haack and Slansky 1987) among xylophagous insects. Andersen and Nilssen (1983) studied the range of variation among wood-feeding and free-living insects and found that variation in the former group is significantly higher than the latter. Two reasons are supplied in explanation of this (Andersen and Nilssen 1983: 1462): 1) populations of xylophagous insects contain a wide variety of phenotypes, each with a genetically set size; or 2) each individual within the population is flexible, and able to be either small or large, depending on nutritional availability.

Chapter IV

HISTORICAL REVIEW

This section is an historical account of the genus Pytho on a world basis. Included, are important taxonomic and natural history references, with most faunal catalogues and lists excluded. Even though there are three species in Europe and four species of Pytho in North America, literature references on the European species far outnumber those dealing with Nearctic species. Many of the European references are omitted here, and only those which offer new information are considered. The North American literature, because references to Pytho are so scarce, is covered more thoroughly. As a general observation, the genus Pytho has received little attention from entomologists, despite the fact that it is a common inhabitant in northern coniferous forests. Compared with economically important groups such as Scolytidae, the natural history and habits of Pytho are virtually unknown.

The first species ultimately to be included in the modern sense of the genus Pytho was described as Tenebrio depressus by Linnaeus (1767). Because of the variable nature of the colour of this species, several additional names were proposed by some of the eminent entomologists of the late eighteenth century. Degeer (1775) used the name Tenebrio, while Fabricius (1792) used the generic name Cucujus in which to

describe three species of "Pytho". Latreille (1796) introduced the genus Pytho, which appeared in the original publication as "Tytho" due to a printer's or typesetter's error. The vernacular "Pythe" appeared in the description, indicating that a lapsus had indeed occurred. Latreille (1796) did not include any species in his new genus, but he made reference to certain species described in Tenebrio and Cucujus by Linnaeus and Fabricius.

Fabricius (1801) first included actual species in Pytho: P. coeruleus, P. festivus, and P. castaneus, all of which had been described in the genus Cucujus by Fabricius (1792). Latreille (1804) explained the reasons behind the proposal of the new genus Pytho. Because the number of tarsal segments was not the same in Tenebrio and Cucujus, Latreille determined that the two should be separated. The genus Pytho was erected to accommodate several species previously, included in both Tenebrio and Cucujus. Latreille (1804) also includes the three species of Fabricius (1792) in his concept of Pytho. In 1810, Latreille published a list of genera and the type species of each. For Pytho, Latreille (1810) chose P. coeruleus Fabricius as the type of the genus. In all, seven different names were proposed for colour varieties of P. depressus by various authors. Most of these, as mentioned above, were published in the late 1700s, but Pic (1912) proposed two new varieties of P. depressus based on colour differences only.

Also late in the eighteenth century, the first species of Pytho from North America was described as Tenebrio planus by Olivier (1795). Apparently, this name was forgotten by subsequent authors who later redescribed it. Reasons for the obscurity of this name are not known,

however the fact that Tenebrio planus is a homonym of a synonym of P. depressus may be one cause. This fact led to the use of the name Pytho planus Herbst for Pytho planus (Olivier) in some more recent taxonomic works (Leng 1920; Brimley 1938). Horn (1886) discusses the species described by Olivier (1795) and states that "in a few instances the names proposed by Olivier seem to have been lost sight of and the species have been renamed by later authors" (Horn 1886: 143). Horn (1886) does not explain why this occurred, but it is certainly true of Tenebrio planus Olivier, with which Kirby (1837) was probably not familiar. From specimens collected during the northern land expeditions under Sir John Franklin, Kirby (1837) briefly described two new species of Pytho. Pytho niger is given as having three colour varieties, and P. americanus, five such varieties. The description of Tenebrio planus Olivier matches exactly Kirby's description of the typical variety of P. americanus, and these two names are synonymized in this study. Kirby (1837) also comments on the placement of the genus, stating that Fabricius had "better reason" to place Pytho next to Cucujus than Latreille had in placing it among his Helopians. Latreille placed greater emphasis on the number of tarsal segments, which still remains an important classificatory character of Coleoptera. Several years later, Mannerheim (1843) described a Pytho deplanatus from Alaska, which has been variously synonymized with both P. depressus and P. planus. Horn (1888) states that P. deplanatus is merely an immature, poorly developed specimen of P. americanus. The fifth name for a Pytho in North America was published by LeConte (1866), who described P. strictus on the basis of a single female specimen from Canada.

A very important European work was published by J. Sahlberg (1875), in which a new species from Finland, P. abieticola is described. More importantly, though, Sahlberg (1875) provides detailed descriptions and natural history notes for P. depressus, P. kolwensis, and P. abieticola. For the first time, the larval stages of all three European species are treated in one work.

Meanwhile, in Japan, a new species of Pytho was collected by Lewis (1888) from snow-covered mountains above Nikko. This was to be the first of two species of Pytho presently known from Japan.

Near the end of the 19th century, much attention in the literature was drawn to the faunal similarities between Europe and North America, including species of Pytho. This was begun by Horn (1886, 1888) and continued by Fauvel and Hamilton. Much of the discussion, or "controversy" deals with the three species, P. depressus, P. americanus, and P. deplanatus. Fauvel (1889), and Hamilton (1889, 1890, 1894a, 1894b) variously "synonymize" these species. Likewise, Sahlberg (1892) is said to have examined specimens of two of the North American species of Pytho. From this examination, P. americanus and P. depressus and P. strictus and P. kolwensis were thought by Sahlberg to be distinct species. However, P. niger Kirby and P. abieticola Sahlberg were deemed identical. This synonymy was used in several works such as Saalas (1917), but was not used consistently thereafter.

Wickham (1899) provided the first key to species of Pytho which occur in Canada (the key was for species from Ontario and Quebec). Three species are included in his key: P. americanus Kirby, P. niger Kirby,

and P. strictus LeConte. Wickham (1899) comments on the difficulty in assigning correct names to the species.

The largest single work on the world fauna of Pythidae (sensu latiore) is that of Seidlitz (1916, 1917). In this treatment, Seidlitz presents a taxonomic history of the genus Pytho, including all older taxonomic references. As well, Seidlitz (1916) gives major references dealing with the morphology, anatomy and physiology, and systematic placement of the family. For Pytho, a key to adults of the world species is presented, with eight species included. From the work of Sahlberg (1875), Seidlitz (1916) constructed a key to the larval stages of the three European species of Pytho. Pytho nivalis Lewis is not treated by Seidlitz (1916), but its position within the genus was considered as a matter of speculation. A new species from North America, P. fallax, was described from eastern North America, based on the misidentification of the specimens of P. niger before him. The taxonomic information section for P. seidlitzii (below) provides more details on this.

K.G. Blair is another worker who contributed much to the world fauna of "Pythidae". Blair (1925) published an article based on Seidlitz (1916), including synonymies overlooked by Seidlitz as well as some corrections. Included is a new species of Pytho. Pytho seidlitzii Blair was based upon the description of P. niger Kirby in Seidlitz (1916). Blair (1925) discusses the relationship between P. fallax Seidlitz and P. niger Kirby, and states that the name P. fallax should be retained for only a certain form of P. niger Kirby. Three years later, Blair (1928) published the first and only catalogue of world Pythidae, in

which ten species of Pytho are included. Pytho americanus, P. deplanatus, and P. depressus are listed as separate species, as are P. fallax Seidlitz and P. niger Kirby. Several taxonomic references subsequent to Seidlitz (1916) are included in the catalogue of Blair (1928). Only one species has been described since Blair (1928), that being P. jezoensis Kôno (1936), the second known Japanese species of Pytho.

The first description and illustration of the larval stage of a Nearctic species, is that of P. niger Kirby by Böving and Craighead (1931). This treatment consisted of only several figures, but remained the most detailed description of the larval stage of any Nearctic Pytho species.

The only reference to a Nearctic species of Pytho in the pupal stage is that of Rozen (1959), who discusses the shape and pattern of abdominal tubercles in Oedemeridae and related groups. A simple figure of an abdominal tubercle of P. planus is included.

Burakowski (1962) published a detailed study of the distribution, natural history and bionomics of P. kolwensis. The egg, larval, and pupal stages of this species are described and illustrated. This is the first discussion of the egg stage of any Pytho and also the first complete description and illustration of the pupal stage. A more complete taxonomic work appeared 1976, where Burakowski dealt with the Polish species of Pytho. All three of the Polish (European) species are keyed and illustrated in larval, pupal, and adult stages.

Hatch (1965) included P. americanus, P. niger and P. seidlitzii in his key to species of the Pacific Northwest of North America. This is the first key to include the latter species.

Several important works appeared in the 1950s and 1960s dealing with larvae of Japanese insects. Many of the Coleoptera larvae were described by N. Hayashi. The larvae of P. nivalis Lewis and P. jezoensis Kôno are described fully and the Japanese species keyed in Hayashi (1969). Hayashi et al. (1959) include figures of P. nivalis, which, however, do not represent any known Pytho larva.

Iablokoff-Khnzorian (1985) examined the Palearctic species of Pythidae, which he used in a very wide sense. The key to adult stages is based on several variable characters, and the key to larval stages is based on the work of Burakowski (1962) and Hayashi (1959). This treatment is useful, but seemingly suffered from a lack of comparative material.

Chapter V

MATERIALS AND METHODS

5.1 MATERIALS

Specimens of Pytho and other related taxa examined in this study were borrowed from a number of institutions and private collections in North America, Europe, and Japan. Also, field collecting, especially of larvae, was carried out by the author from 1985 to 1988. The collections from which material was borrowed and curators of these collections are listed below in association with abbreviations used in the text. The abbreviations were taken from Heppner and Lamas (1982) whenever possible. For private collections, the name of the curator is given first; for institutional collections, the curator's name follows the address of the institution. The author's material is in DAPC; voucher specimens of larvae and of reared and associated pupae and adults are deposited in JBWM.

AMNH: Department of Entomology, American Museum of Natural History, New York, New York, U.S.A. 10024; L.H. Herman.

ANIC: Australian National Insect Collection, C.S.I.R.O. Division of Entomology, P.O. Box 1700, Canberra City, A.C.T. 2601, Australia; J.F. Lawrence.

BCPM: Entomology Division, British Columbia Provincial Museum, Victoria, British Columbia, Canada V8V 1X4; R.A. Cannings.

- BLNU:** Biological Laboratory, Nagoya Women's University, Takamiya-cho, Tenpaku-ku, Nagoya 468, Japan; M. Satô.
- BMNH:** Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD, England; L. Jessop.
- BYU:** Entomology Collection, M.L. Bean Life Science Museum, Brigham Young University, Provo, Utah, U.S.A. 84602; R. Baumann.
- CARR:** J.L. and A.F. Carr, 24 Dalrymple Green, Calgary, Alberta, Canada T3A 1Y2.
- CAS:** Department of Entomology, California Academy of Sciences, San Francisco, California, U.S.A. 94118; D.H. Kavanaugh.
- CDAS:** Canada Department of Agriculture, Research Station, 107 Science Crescent, Saskatoon, Saskatchewan, Canada S7N 0X2; P. Mason.
- CMP:** Section of Entomology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A. 15213; R. Davidson.
- CMSC:** Entomological Museum, Department of Entomology, Fisheries and Wildlife, Clemson University, Clemson, South Carolina, U.S.A 29631; M.W. Heyn.
- CNCI:** Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, Canada K1A 0C6; A. Smetana.
- CU:** Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York, U.S.A. 14853; J.K. Liebherr and E.R. Hoebeke.
- DAPC:** Darren A. Pollock, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2.
- DBTU:** Department of Biology, University of Turku, SF-20500 Turku, Finland; S. Koponen.

- DEUM:** Department of Entomology, Deering Hall, University of Maine, Orono, Maine, U.S.A. 04469; E.S. Osgood.
- DKYC:** D. K. Young, Department of Entomology, University of Wisconsin-Madison, Madison, Wisconsin, U.S.A. 53706.
- EUM:** Entomological Laboratory, College of Agriculture, Ehime University, Matsuyama 790, Japan; S. Hisamatsu.
- FEM:** Frost Museum, Department of Entomology, Pennsylvania State University, University Park, Pennsylvania, U.S.A. 16802; T.A. Miller.
- FMNH:** Division of Insects, Field Museum of Natural History, Chicago, Illinois, U.S.A. 60605; A. F. Newton, Jr.
- FPMI:** Forest Pest Management Institute, Great Lakes Forest Research Centre, P.O. Box 490, Sault Ste. Marie, Ontario, Canada P6A 5M7; P. Syme.
- FSCA:** Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, U.S.A. 32602; R.E. Woodruff.
- HUS:** Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo 060, Japan; S. Takagi.
- INHS:** Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, Champaign, Illinois, U.S.A. 61820; K. McGiffen.
- ISUI:** Insect Collection, Department of Entomology, Iowa State University, Ames, Iowa, U.S.A. 50011; R.E. Lewis.
- JBWM:** J.B. Wallis Museum, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2; R.E. Roughley.

- LACM** Los Angeles County Museum of Natural History, 900 Exposition Blvd.,
Los Angeles, California, U.S.A. 90007; R. Snelling.
- LEMC**: Lyman Entomological Museum and Research Laboratory, Macdonald
College, McGill University, Ste. Anne de Bellevue, Quebec, Canada
H9X 1C0; F. Génier.
- MAIC**: M.A. Ivie, Department of Entomology, Montana State University,
Bozeman, Montana, U.S.A. 59717.
- MCZ**: Department of Entomology, Museum of Comparative Zoology, Harvard
University, Cambridge, Massachusetts, U.S.A. 02138; S.R. Shaw.
- MNV**: Museo Civico di Storia Naturale, Lungadige Porta Vittoria 9, 37100
Verona, Italy; M. Daccordi.
- MPM**: Section of Invertebrate Zoology, Milwaukee City Public Museum,
Milwaukee, Wisconsin, U.S.A. 53233; G.R. Noonan.
- MSUC**: Entomological Museum, Department of Entomology, Montana State
University, Bozeman, Montana, U.S.A. 59717; M.A. Ivie.
- NDSU**: Department of Entomology, North Dakota State University, Fargo,
North Dakota, U.S.A. 58102; E.J. Balsbaugh, Jr.
- NFRC**: Newfoundland Forest Research Centre, P.O. Box 6028, St. John's,
Newfoundland, Canada A1C 5X8; A.G. Raske.
- NMDC**: N.M. Downie, 505 Lingle Terrace, Lafayette, Indiana, U.S.A. 47901.
- NMNH**: National Museum of Natural History, Smithsonian Institution,
Washington, D.C., U.S.A. 20560; D. Anderson.
- NSMC**: Nova Scotia Museum, Halifax, Nova Scotia, Canada, B3H 3A6; B.
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5.2 METHODS

5.2.1 Generalized methods - all stages

Line drawings were prepared by first pencil sketching the figure using a Wild M-5 stereomicroscope fitted with a Wild camera lucida. The pencil drawing was then enlarged, after which it was inked on acetate film. Scanning electron micrographs were taken with a Cambridge Stereo Scan MK IIA. Specimens were first coated with gold in a Balzer Spatter Coater.

Characteristics of larvae, pupae, and adults of all species of Pytho, are given in the generic description below. For each individual species, the following are provided: citation of the valid species epithet, and original description; taxonomic and natural history references for all life stages; information on the type specimens and other taxonomic notes; a diagnosis, consisting of distinctive characters for each known life stage; description of all known life stages; number of specimens examined for each stage (for adult specimens, sexes are not indicated because of the inability of determining the sex of individuals

glued to cardboard plates); association methods for larvae and pupae; natural history notes; distribution. To avoid repetition, the first author in all lists of synonyms is Blair (1928), who compiled all previous references. Some references were omitted by Blair (1928); these are listed after Blair (1928) in the list of taxonomic and synonymical references. Included in the list of references for each species, are those dealing with all aspects of the species in question. Because the references to Palearctic species such as P. depressus are so much more numerous in the literature than are those for Nearctic species, emphasis is placed on references to the latter. There may be several references to Palearctic species which are omitted here; hopefully, all important references to Nearctic species are included. Those references which are not taxonomic, are annotated as such.

Distribution and locality records were obtained both from the literature and actual specimens. Locality data for Nearctic species were taken only from label data. For most of the Palearctic species, label data were the sole sources of locality records. However, for the two Japanese species, of which I examined few specimens, additional locality records were obtained from the literature. For the European species, anecdotal accounts of the distributions are mentioned in my treatment of the distribution for each species; no localities from the literature are included on the distribution maps for any European species. Records from the literature are included on the maps of the two Japanese species.

In the list of localities (Appendix A), larvae, pupae and adults are dealt with separately under the state, province, or equivalent

geopolitical area. The following information is listed: country, state or province (or equivalent), county (or equivalent), locality, date, collector, other label information, number of specimens from that locality, and the acronym of the collection from which the specimens were borrowed. In most cases, the information was recorded as it appeared on the label. Where the information concerning date of collection was unambiguous, the months were converted to Roman numerals, with the days in Arabic numerals.

5.2.2 Generalized methods - immature stages

Because one of the objectives of this study was to rear and associate the larval and pupal stages for all species where this was not previously done (i.e. all Nearctic species) field collecting of larvae was essential to supplement the small number of larvae obtained in loans. Initially, areas of coniferous forest in Manitoba were investigated for possible Pytho habitat. Once a suitable site was found, that is one with a number of large, felled, dead coniferous trees, trees were sampled for larvae, pupae and/or adults. A large, flat-bladed screwdriver was a very effective tool for stripping the bark from dead trees. This instrument was used exclusively throughout my field collecting. I could determine the condition of a tree, or if it was of suitable stage of decay for Pytho by plunging the screwdriver into the bark at a right angle. If the blade barely penetrated the outer bark, I was fairly certain that the tree was too recently killed to be colonized by Pytho. The presence of large numbers of Scolytidae, and dead needles still on the branches, were also indications that the

tree was too recently dead. On the other hand, if the screwdriver blade penetrated more than about 5 cm into the tree, or into the heartwood, I knew that the log was probably too advanced in decay to contain specimens of Pytho. I often checked under the bark of such older logs, because large larvae, pupae or adults were occasionally present. The optimum host tree has the outer bark loosened, but more or less intact. The heartwood is not greatly decayed, and a large amount of cambium-phloem (inner bark) is still present.

Larvae were often present in large numbers, and a number of them was immediately preserved in 70 per cent ethanol. If the larvae were fairly large, or presumably mature, a number were often placed into a container along with a supply of the decaying cambial-phloem material in which the larvae were collected. These were brought back into the lab for rearing, which was carried out as described in Chapter VI. Careful records of the dates of prepupation, pupation, and eclosion were kept for each vial. Those individuals to be terminated in the pupal stage were immersed in near boiling water for several minutes. Pupae were then stored in 70 per cent ethanol along with the last instar larval exuvium, including normal label data supplemented with dates of prepupation, pupation and termination. It was noted that if pupae which have only recently (less than two or three days) become pupae are killed and preserved by the above method, they turn dark within a day of being placed in the 70 per cent ethanol. Therefore, pupae were given a minimum of three days before being killed and preserved. Several methods have been published for the preservation and/or storage of Coleoptera larvae and pupae (e.g. Perkins 1980). I found that larvae

first killed in recently boiling water and then stored in ethanol tended to be straighter and easier to manipulate. These larvae also tended to be more opaque than larvae killed in ethanol. Often, in ethanol-killed larvae, the layers of cuticle separated, with the outer layer becoming almost transparent.

A large sample of pupae was collected into 70 per cent ethanol, with mixed results. In life, the pupae have the wings folded ventrally against the body. When preserved, many of the pupae in the sample had the wings filled with the ethanol, and extended out from the body. However, the wings of several of the pupae were still in their original positions. Perkins (1980) describes a method by which pupae are preserved in a 35 per cent ethanol solution saturated with salt. This method is apparently effective in preventing the distended wings in pupae. This system was attempted with one mature pupa, but the specimen turned black after two days in the solution. It is true, as Perkins (1980) suggests, that pupae with distended wings are unnatural in appearance, but I found that such specimens remain useful for analysis and description. The taxonomic usefulness of such pupae is not diminished.

Those specimens which were to be reared through to the adult stage were allowed up to two weeks to harden fully, once they had eclosed. The new adults were then placed into a vial filled with wood chips charged with a small amount of ethyl acetate. The genitalia were dissected from some of these adults while they were still fresh and relaxed. The reared adults were stored in two different ways. The adult, along with the associated exuviae, was placed in 70 per cent

ethanol in a 3-dram, glass, allergy vial. Some of the reared adults were pinned, with the larval exuvium placed into a small plastic microvial, pinned beneath the specimen. In both methods, data on dates of collection, prepupation, pupation and eclosion were included with the specimen.

For the storage of ethanol-preserved material, I found that wood vial racks and 3-dram, glass, allergy vials were the most efficient combination. Large storage jars containing small shell vials of specimens, as illustrated in Martin (1977: 100) are quite cumbersome and impractical. This method would only be useful for long-term storage of alcohol-preserved material, and is the system currently used by a variety of museums. Neoprene stoppers are preferred over corks or screw caps, for prevention of evaporation, although certain types of rubber stoppers tended to swell greatly within the vial. Once removed from the vials, these enlarged stoppers were very difficult to reinsert.

Taxonomically, the larvae were treated in much the same way as were the adult stages. Taxonomic complexes of more or less closely related "species" were assembled by an examination of two major characters, the parabasal ridge processes, and the urogomphal plate. The individual larvae of each species were correlated with their respective adults stages. In this way, the taxonomic congruence of both life stage arrangements could be evaluated.

Mouthparts and spiracles were dissected from larvae, cleared in hot KOH, and mounted in glycerin on slides for examination. Representative whole larvae were glycerinated using the technique of Goulet (1977).

5.2.3 Generalized methods - adult stage

Adult Pytho were borrowed from the above collections, and field-collected. Adults were also obtained by rearing larvae and pupae collected in the field. The taxonomic procedures followed are similar to those used by Whitehead (1972). Specimens were initially sorted into groups of apparently more or less closely related forms, based on overall morphological similarity. These complexes were further refined by separating specimens according to geographic area. When these groups contained presumably conspecific individuals, species concepts were invoked to delimit the "species" present in the samples. Names were applied to the species according to the original descriptions, as well as an examination of the type specimens. For the Nearctic and Japanese species, all of which are less well known taxonomically, compared to the European species, types were seen for all species. Lectotypes were designated where required. Based on analysis of the original descriptions and on examination of types, synonymies were established.

For in depth taxonomic study, adult male and female specimens of the individual taxa were selected from widely separated localities within their respective ranges in order to analyze any geographic variation. For examination of genitalia, dried specimens were first relaxed for several hours in warm water, to which was added a small amount of detergent. Not only did this relax the beetles, but the detergent also dissolved the oils which tended to accumulate on the cuticle of many individuals. Once sufficiently relaxed, the elytra were spread slightly, and a hooked insect pin was used to extract the genitalia through an incision in the last visible tergite (as in Lindroth 1969:

xxx-xxxi). Both male and female genitalia were macerated for several minutes in hot KOH, rinsed in water and then stored in glycerin within plastic microvials pinned beneath each specimen.

A number of measurements were made on adult specimens, selected from as widely separated localities as sample size permitted. The first measurement included in the description of each species is the range of total length (TL). Seven other measurements are included in Tables 1-9, including list the ranges, means, and standard deviations for these various body measurements. The ranges and means were rounded off to one decimal place, and the standard deviations were taken to two decimal places. Where possible, at least 10 specimens from each locality were chosen, with as equal as possible representation of either sex. When this was not practical, data from a larger geographical area were pooled. No laboratory-reared specimens were used in any of the measurements due to possible effects of rearing on size. The measurements are meant to be a supplement to the descriptions; it was found that only TL and GPW/PL could be used more or less confidently for separation of certain taxa. These measurements and their abbreviations are:

HL = head length (length from anterior margin of pronotum to anterior margin of labrum, along midline),

GHW = greatest width across head, excluding eyes,

PL = pronotal length (length from anterior to posterior margins of pronotum, along midline),

GPW = greatest width across pronotum,

EL = elytral length (length from posterior tip of scutellum to apex of elytron),

GEW = greatest width across both elytra,

TL = total length (HL + PL + EL),

GPW/PL = ratio of greatest pronotal width to pronotal length.

Measurements were taken with a measuring ocular on a Wild M-5 stereomicroscope. All measurements are presented in millimetres. Care was taken to select only intact specimens, to ensure accurate values.

5.3 SPECIES AND SPECIES-GROUP CONCEPTS

5.3.1 Species Concepts

The species concept which a researcher employs obviously has far-reaching implications on the results of a study of organisms. Not only will the actual number of species vary with different species concepts, but the perceived origin of, and proposed evolutionary patterns exhibited by the species will be affected. It is important for authors to state the criteria by which their species are recognized, so that the results obtained are more easily understood by others.

The most popular species concept in the literature, both to proponents and opponents, is the biological species concept (BSC) of Mayr (1969) and others. Much has been written of the apparent weaknesses and limitations of the BSC, and it is not my point to provide a review of these arguments. It is obvious though, that there are potential flaws in the BSC and that it is not universally applicable to all organisms. Häuser (1987) has reviewed the controversy regarding the BSC and concludes that it should be neither changed nor rejected.

Sokal and Crovello (1970) provide evidence showing that the BSC is essentially a phenetic concept, and that it is impossible to recognize a biological species in nature, or from preserved specimens. Wiley (1978, 1981) provides an evolutionary species concept as an alternative to the BSC. Both the evolutionary and biological species concepts in that both systems require species to be reproductively isolated at least as much is needed for maintenance of species identity. Donoghue (1985) also has difficulties accepting the BSC, and suggests that a species concept that "incorporates the observation that breeding, morphology, and ecology are not necessarily linked" (Donoghue 1985: 175). Donoghue's (1985) phylogenetic species concept is based on the assumption that nature is hierarchical in construction, with more and less inclusive monophyletic groups. Hence, only monophyletic groups are acceptable in this concept. According to Donoghue (1985) and Rosen (1978), "every one of the smallest units that can be identified be given species rank" (Donoghue 1985: 179). In the phylogenetic species concept, no reliance upon breeding knowledge is mentioned, although it is important to the underlying evolutionary foundation of the concept.

As Donoghue (1985: 174) mentions, "modern species delimitation is, in almost all cases, still based upon morphology and geography and not upon direct knowledge of breeding behaviour." The species concept used in my study is no exception to this generalization. In similar recent studies, morphology is used in species discrimination, but in many cases, it is the morphology of the male aedeagus or components thereof, that are deemed most important (e.g. Roughley 1982; Roughley and Pengelly 1981, Askevold 1988). Differences in these structures, and

particularly if correlated with other character sets, may be indicative of reproductive isolation in nature, and fulfill the requirements of the BSC (Roughley and Pengelly 1981). In Pytho, no consistent, diagnostic features of the male genitalia were found for all species. Therefore, presumably, reproductive isolation exists, but cannot be demonstrated by differences in male copulatory structures. There is in nature, much potential for interbreeding among sympatric species of Pytho. In eastern North America, for example, all four species are sympatric on a large scale, but also micro-sympatric on a habitat level. Two or three species may be present under the bark of one host tree. Consistent differences in host tree preferences, or life cycle leading to reproductive isolation were not noted. Therefore, it is impossible to provide hard evidence that Pytho would be a candidate for implementation of the BSC. Obviously, species separated by oceans or other impassible barriers would be essentially reproductively isolated. I believe Pytho to be a poor disperser, at least from one area of coniferous forest to another such area across a barrier without such forest.

The species concept applied to Pytho is a combination of several of the modern concepts in the literature. A biological species can also be an evolutionary species, or a phylogenetic species, or vice versa. This combination of species concepts has been used by Askevold (1988) who invokes both the BSC and evolutionary species concept to delimit species of Neohaemonia (Coleoptera: Chrysomelidae). By using a morphological, or phenetic species concept, four species-groups (later proven to be monophyletic) based on mostly larval, but also on some adult characters, were recognized. The forms included in these species-groups were

separated based on geographic barriers, which in essence dictates reproductive isolation based on the hypothesized low vagility of Pytho. These final, or smallest recognizable units were given species rank as in the phylogenetic species concept of Donoghue (1985). These units eventually represented the terminal taxa on the cladogram depicting the reconstructed phylogeny.

5.3.2 Species-group Concept

Species-groups in Pytho are recognized on the basis of structure of the larval urogomphal plate (figure 12), and parabasal ridge processes (figure 11). These characters delimit four discrete groups, all except one of which is corroborated with at least one adult synapomorphy. The names of the species-groups are those of the oldest published valid names in each group. The four recognized species-groups with their included species are as follows:

Checklist of world species of Pytho Latreille,
arranged by species-group.

P. seidlitzii-Group

P. seidlitzii Blair 1925

P. kolwensis-Group

P. strictus LeConte 1866

P. kolwensis C. Sahlberg 1833

P. nivalis Lewis 1888

P. niger-Group

P. niger Kirby 1837

P. fallax Seidlitz 1916

P. abieticola J. Sahlberg 1875

P. jezoensis Kôno 1936

P. depressus-Group

P. planus (Olivier 1795)

P. americanus Kirby 1837

P. deplanatus Mannerheim 1843

P. depressus (Linnaeus 1767)

Species Incertae Sedis

P. erotis Gistel 1857

Chapter VI

REARING METHODS

To have accurately associated larvae, pupae, and adults of Pytho for this study, larvae of all Nearctic species were reared to pupal or adult stages. Such effort was undertaken because of a general lack of knowledge regarding the taxonomy of the larval and pupal stages of all four Nearctic species of Pytho. Palearctic larvae and pupae were studied sufficiently to enable identification from the literature. By far the most convenient rearing method was that of ex evolutione imago, or from larva to adult (van Emden 1942). Association ex ovipositione, from adult to larva (van Emden 1942) was attempted, but adult females could not be induced to oviposit in the laboratory. Rearing was done not only to associate the immature stages, but also to obtain more adult specimens, which are more rarely encountered in the course of field collecting.

When investigating the details of an appropriate rearing system, little information was available in the literature. Andersen and Nilssen (1978) reared a larva of P. depressus to the adult stage by placing it beneath a layer of absorbent cellulose paper, on top of which was placed a piece of bark. A somewhat similar method was suggested to me by Pettersson (pers. comm.) in which larvae are placed between bark pieces attached with several rubber bands. This assembly is placed in a

large jar or similar vessel upon a layer of moistened moss. Using his method, Pettersson successfully reared adults of P. kolwensis, P. abieticola, and P. depressus. I was able to rear a number of P. planus larvae to pupal and adult stages using the above method, but I found it impractical in several respects: 1) larvae became very active when the bark pieces were separated, and often crawled out once the pieces of bark were refastened; 2) because the bark pieces must be held together tightly, several larvae were damaged when refastening the elastic bands; 3) Pettersson's system required a large amount of space to rear only a few larvae; 4) it was difficult to associate mixed series of larvae with specific adults.

Often, in my own collecting, larvae of two species were "microsympatric" under bark of the same log. Because of this, I sought a larval rearing method in which individual specimens could be monitored for moulting, pupation, etc. with a minimum of disturbance and space required. This system is described in Pollock (1988), and involves the use of 3-dram, glass allergy vials, into which 1 cm depth of moistened, compacted, paper towelling was placed. Above this, was placed a 1 cm layer of the cambial-phloem material that was collected from the host tree. Larvae were placed into individual vials where they constructed feeding tunnels soon thereafter. The paper towelling and tree material were fed upon indiscriminantly and I have used solely one or the other food source, with equal success. The tops of the vials were usually loosely stoppered with a piece of paper towelling; water was added to the medium when needed. Larvae collected late in the season, i.e. past their developmental threshold temperature, had to be exposed to several months of cold before they pupated.

I found the above method to be both practical and effective with a number of advantages: 1) larvae are kept individually, and moults, pupations and eclosions can be monitored very accurately; 2) 3-dram vials are conveniently stored in large number; 3) vial boxes are portable in the field. This enables larvae to be placed immediately into the rearing medium, thus reducing the risk of mortality between the field and the laboratory (desiccation, cannibalism [which does occasionally occur if larvae are overcrowded], etc.); 4) vials are easier to keep properly moist than are large pieces of bark; 5) the bottom layer of paper towelling acts both as a food source, and as a moisture retainer; 6) individuals need not be greatly disturbed during routine examination. Using this scheme, I successfully reared larvae to pupal and adult stages of P. seidlitzii, P. strictus, P. niger, and P. planus. No parasitoids were observed during these trials. Once I had reared and associated all four North American species, larvae and pupae collected in the field or present in borrowed material, were readily identified.

Chapter VII

TAXONOMIC CHARACTERS AND TERMS

7.1 ADULT STAGE

Sexual dimorphism

Adults of Pytho spp. possess several secondary sexual characters. Females are consistently larger than males. This character is of little value in determining the sex of few to several specimens; in large series, males and females can be separated by size alone, with a high degree of accuracy. There is also an oval to circular pit on the mentum of males (figure 5 C,D). Females possess no such pit. Extending ventrally from the base of the pit, are a number of setae, twisted together (figure 5 D). This structure is mentioned by Seidlitz (1916: 117), but no function is suggested. The sexes of Pytho spp. are dimorphic in form of antennae. Horn (1888: 46) states that male antennae have antennomeres "1-6 obviously longer than wide, and 7-10 as wide as long. Females have antennomeres 1-5 longer, and 6-10 wider than long." This was true in specimens examined in this study. Another sexually dimorphic character is the ventral pubescence on the tarsi. Males have ventral, pro- and mesotarsal pubescence composed of setae different in structure from those on the metatarsi. The ventral setae on the metatarsus of the male are bristlelike, and are similar to those on all tarsi of the female. Stork (1980) discusses the terminology of

tarsal setae in Coleoptera. Normal, adhesive setae are defined as those used by the beetle in holding on to surfaces of the substrate on which it walks. This name may be applied to the ventral setae on the metatarsi of males, and all tarsi of females. "Male setae" are defined by Stork (1980) as those present only on males of the species, which are used to grasp the female before or during mating. This term may be used for the ventral pro- and mesotarsal setae of male Pytho.

Head

Head shape is uniform among adult specimens of Pytho. In the majority of species, the lateral margin of the mandible is evenly arcuate to apex. In two species, P. nivalis and P. kolwensis, the mandible is abruptly bent subapically. Differences in dorsal head punctation may be diagnostic, but since this character is variable, it was not used in the key. There is a ring-like area of sensilla on the last 4 to 5 antennomeres, excluding the ultimate antennomere, which is covered with sensilla (figure 5 A). Adults of three species have these sensilla on antennomeres 8-10, while those of the other six species have sensilla on antennomeres 7-10. Occasionally, antennomere 7 and 6 in the two groups of species may have a few of these sensilla, but they are not in a well-delimited sensillar area, and these antennomeres are not included in the above counts.

Pronotum

Overall pronotal shape is a good diagnostic character, and four types of pronotal shape are used: sides subparallel or slightly convergent anteriorly (P. seidlitzii) (figure 2 A); sides slightly arcuate, not

constricted anteriorly, widest anterad of middle (P. planus and P. depressus) (figure 2 H,I); sides arcuate, constricted anteriorly, widest near middle (P. niger, P. abieticola, and P. jezoensis) (figure 2 E,F,G); and, collared basally with angulate lateral margins near middle (P. kolwensis, P. strictus, P. nivalis) (figure 2, B,C,D). Form of the dorsal pronotal depressions, which is a feature characteristic of all species of Pytho may be used as a taxonomic character, although they are variable intraspecifically. They vary among species from shallow, oval, and poorly defined, to deep, linear and distinctly engraved. Historically, authors such as Wickham (1899) and Hatch (1965) have used the interruption of the anterior pronotal margin by the depressions, as a key character. This character was found to be too vague and variable and is not used here. The pronotal depressions may extend onto the lateral areas in the form of transverse grooves, as in some specimens of P. kolwensis and P. nivalis. In the remaining species, the swollen lateral areas are uninterrupted. Dorsal punctation is used to separate specimens of P. niger and P. jezoensis, but this character varies intraspecifically to a degree. All species except P. seidlitzi (figure 2 A) possess a posterior pronotal bead, and only three, P. kolwensis, P. strictus, and P. nivalis, consistently have the anterior bead.

Prosternum

The only character of diagnostic value on the prosternum is the intercoxal process, which is weakly developed in all species of Pytho. Shape and length of the process do not significantly vary intraspecifically. The posterior bead of the prosternum delimits the intercoxal process. In all species except one, this bead is uniform in

width on the process, with only the apex of the process level with bead. Adult P. niger, however, have the entire apex of the process incorporated into, and elevated to the same level as, the posterior prosternal bead (figure 6 A).

Mesoscutellum

In most species, punctation of the scutellum is variable, while in the seven specimens of P. nivalis examined, it is impunctate. This character is tentatively included in the key.

Mesepimeron

In all species except one, and in few specimens of a second, this sclerite is uniformly, and densely punctate. All specimens of P. seidlitzii examined, exhibit a marked reduction in the degree of punctation, which is much less than that of the mesepisternum. Some specimens have impunctate mesepimera, or with punctation restricted to lateral margin only (figure 6 D). Several individuals of P. abieticola also have reduced punctation on the mesepimeron (figure 7 D).

Mesosternum

There are several mesosternal characters used to separate adults of various Pytho spp. The posterior bead, present medially in all species, is distinct almost to the lateral mesosternal edge only in P. niger (figure 7 B). The bead is visible in some species laterally only to the anterior mesocoxal margin, and in others to the inner edge of the mesotrochantin (figure 7 A). The posterior intercoxal process is variable in length among species. In P. kolwensis, P. strictus, and P.

nivalis, the process is long and acute and almost, or does, reach the metasternal process. In the remainder of species, the mesosternal process is acute, but somewhat shorter in P. planus and P. depressus. Although variable, the mesosternal punctation is consistently reduced in P. abieticola (figure 7 C).

Elytron

One character which is used by most authors publishing keys to species of adult Pytho is the number of elytral striae (e.g. Seidlitz, 1916; Wickham, 1899; Hatch, 1965). Because of the variable nature of the elytral punctation, it is very difficult to distinguish striae, especially near the lateral margin of the elytron. Other authors, such as Iablokoff-Khnzorian (1985) use the number of carinae (intervals) as an important character of the elytron. Four species, P. kolwensis, P. strictus, P. nivalis, and P. seidlitzii have 10 distinct, carinate intervals (including the sutural), with the outer (10th) visible posterior of mid-length. In the remaining four species, the 10th interval is barely apparent and the other intervals are only feebly to moderately carinate. Overall convexity of the elytra can be used to separate adults of the P. kolwensis group, while those of other species have dorsally depressed or slightly convex elytra. The region lateral to the 9th interval has increased pubescence in adults of two species (figure 8 C).

Metasternum

The metasternum has little taxonomic value, but one character which may be of some use is the metasternal, intercoxal process.

Intraspecifically, this structure is somewhat variable, but it seems to be characteristic. In most species, the process is more or less acute, with the apex rounded or sharp. In adults of P. planus and P. depressus, it is quite short and broadly rounded apically, and in those of P. jezoensis, the process is broadly truncate at its apex.

Abdomen

The abdominal sterna are quite uniform among species and no important identifying characters (except colour) could be found. The genitalia of adult male Pytho, (figure 3) and of all Pythidae were discussed and illustrated by Sharp and Muir (1912), Spilman (1952), and Watt (1987). There is a discrepancy in terms in the literature. Sharp and Muir (1912) do not provide specific terms for the two parts of the tegmen or the dorsal articulating lobes. Spilman (1952) calls these two portions, respectively, the basal piece and the fused paramere. Together, these are equivalent to the tegmen of Sharp and Muir (1912). Spilman uses the term "lateral lobes" for the two structures projecting from near the base of the paramere. Lindroth (1957) homologizes "lateral lobes" with his "parameres". Lawrence (1982: 544) uses the terms of Spilman, except that he uses the term "accessory lobes" for "lateral lobes". Watt (1987) uses the term "basale" for the basal piece of Spilman (1952) and "apicale" to denote the entire apical piece of the tegmen. The term fused parameres, in the sense of Watt (1987) refers only to the apex of the apicale. Watt (1987) uses the term "accessory lobes" in the same sense as Lawrence (1982). The terms of Watt (1987) are used throughout this paper.

Genitalia are of limited use in distinguishing among adult males, due to the overall similarity among them, and because of intraspecific variation in shape of apex of fused paramere, shape of median lobe, and relative lengths of accessory lobes. Most species have basale and apicale subequal in length, except for males of P. seidlitzii (figure 3 B) and P. depressus (figure 3 F), in which the basale is relatively shorter than the apicale. This character is the only consistent one found thus far for the separation of adult males of P. planus and P. depressus. The general form of the apicale is widest basally, and gradually tapering towards the apex, with the lateral margins straight. In male P. seidlitzii, the lateral margins are sinuate and the apex of the fused paramere is broadly expanded (figure 3 C).

Female genitalia (figure 4 A) were quite variable within species, and no taxonomically useful characters were found. Watt (1987) states that female Pytho have no separate non-glandular spermatheca, but only a spermathecal gland. Once the limits of variation are known, the female reproductive tract may provide important data.

Colour

Overall colour has some use as a taxonomic character, even though it is quite variable. There are varying degrees of metallic lustre developed in P. nivalis, P. planus and P. depressus. The remaining species have nonmetallic brown to black elytra. Colour of the venter and of the appendages may be used also with some reliability to separate adults of certain species. Because of its variability, colour characters have been avoided whenever possible.

7.2 LARVAL STAGE

Sexual dimorphism

No sexually dimorphic characters were found among larvae.

Head

Overall head shape is quite similar among larvae of Pytho species as are the individual mouthparts and setae. However, the shape of the lyriform frontal arms of the epicranial suture, which are usually V-shaped posteriorly, are U-shaped in some larvae of P. planus (figure 9 A).

Abdomen

Several taxonomically important characters are found on the abdomen of Pytho larvae. Most of these are found on the urogomphal plate, but others are found on the tergites. Pytho larvae have terga with well-developed, raised, sclerotized lines near their anterior margins. These are similar and homologous to those structures in pyrochroid larvae. Young (1975) terms these structures the parabasal ridges (figure 9 A). In Pytho, these lines are bent posteriorly and raised, where they reach the medial portion of the tergite. These posterior projections are herein termed the parabasal ridge processes (figure 9 A). These processes vary from being small, triangular structures, to being very slender and parallel-sided (figure 11).

Despite the lack of full chaetotaxal analysis, the area immediately surrounding the parabasal ridge processes is important with respect to

setal arrangement. In most species, these parabasal setae are several to many in number, and variably sized. In larvae of P. kolwensis, P. strictus, and P. nivalis, four large setae are arranged linearly, posterior to the parabasal ridge processes (figure 11 B).

In larval Pyrochroidae, the entire ninth abdominal segment has been termed the urogomphal plate by Young (1975). I have used the same term for the homologous structure in Pytho. The urogomphal plate possesses the most important diagnostic features for species separation. Pytho larvae possess well-separated, moderately long, immovable paired urogomphi (figure 9). On each urogomphus, there are two to three small teeth, which either project inwardly, or (in particular the apical tooth) ventrally. These teeth are herein called the inner urogomphal teeth (figure 9 B). Young (1976), in his description of the larva of Sphalma quadricollis Horn, states that the third inner urogomphal tooth is one of two parts of a divided urogomphus. This interpretation may also be valid for the urogomphus of Pytho larvae. In two species, P. planus and P. depressus, the larvae have the basal, inner urogomphal tooth smaller than the middle tooth (figures 9; 12 D), while in those of the remainder of species, the reverse is true. Larvae of some species have the third, or apical inner tooth well-developed, while in others, it is absent. At the base of, and between, the urogomphi is the urogomphal lip (figure 9 A), which is a heavily pigmented, shelf-like structure. This feature has some taxonomic value. The urogomphal lip may be narrow and protruding (figure 12 A) or wide and not protruding (figure 12 C,D); the posterior margin may be almost truncate, quite arcuate, or trapezoidal (figure 12 B). On the dorsal surface of the

urogomphal plate, there are a variable number of heavily pigmented protuberances which are here called tubercles (figures 9 A; 12) [as in Lawrence (1982)]. The pattern formed by these tubercles is characteristic and they usually extend transversely across segment 9 and are prolonged onto the urogomphi. In addition to the arrangement, the actual number of tubercles, although variable to a certain degree, is diagnostic of at least the major groups of species in Pytho as larvae (figure 12). The setal arrangement on the apical tubercle can be used to separate larvae of the P. kolwensis-group (figure 12 B). In this group, there are at least two very long setae (at least as long as the tubercle) on the apical urogomphal tubercle. In all other species, either one, or no long seta is present. In larvae of all species except P. planus and P. depressus, the apices of the urogomphal tubercles are directed posteriorly. In the larvae of the two above species, the medial tubercles are distinctly directed anteriorly (figure 12 D). Ventrally, the double arch of asperities (figure 9 B) may be taxonomically important. Again, this character exhibits some intraspecific variation, but is useful. The number, relative size, and degree of longitudinal furrowing of the asperities may be of diagnostic use, but are not considered to be important here due to the variation noted.

7.3 PUPAL STAGE

Sexual dimorphism

The sex of Pytho pupae may be determined by the genitalia, visible externally on the venter of the abdominal apex. Males possess paired appendages which do not project ventrally. Female pupae, have paired processes which project ventrally, and laterally at their apices. Since size is sexually dimorphic in adults, the same is probably also true for pupae, although this was not measured.

Head

The head of Pytho pupae has little taxonomic value. The tubercles near the eye may be diagnostic, but intraspecific variation precludes their use. The denticles on the antennal segments may be taxonomically important and are especially well-developed in pupae of P. seidlitzii and P. strictus. However, this character is difficult to quantify. The labrum of P. strictus pupae is deeply incised anteromedially, while in those of the remaining species, the anterior margin is truncate, or only slightly emarginate (figure 13 A).

Pronotum

The pronotum has the basic shape of the adult and may be used to separate species into major groups. In all species except P. seidlitzii, the dorsal pronotal tubercles (figure 13 A, B) of pupae are more or less uniform in size and restricted to the margins. Normally, there are less than 20. In pupae of P. seidlitzii, the tubercles range in size from large (on anterior margin) to small (on disc). In this species, the

tubercles have extended onto the disc and swollen lateral areas of the pronotum.

Abdomen

The terms used for the dorsal abdominal tubercles on segments 1-6 follow that of Rozen (1959) and Young (1975). Among Pytho pupae, the abdominal tubercle pattern is present on segments 2-6 only. On segment 1, the pattern is recognizable, but with fewer tubercles, i.e. incomplete. On 7-9, the segment shape has changed along with the tubercle arrangement. In the key to pupae, and in the diagnoses and descriptions, the number of tubercles or setae given for a certain structure is the number on one side of that structure.

There are four or five lateral marginal tubercles (figure 13 C), and the number is species specific. The posterior marginal tubercles (figure 13 C) are separated laterally from the lateral marginal tubercles by a distinct gap. The number of posterior marginal tubercles varies from one to three, but there are usually two per side, with the outer tubercle larger. The small discal tubercles (figure 13 C) are, in most species, two per side, while in pupae of P. seidlitzii there may be up to six per side. Pupae of all species except three have only one large, pleural tubercle (figure 13 D). Pupae of P. planus, P. depressus, and P. seidlitzii have an additional, smaller anterior tubercle. Overall, the abdominal tubercle shape of pupae of most species of Pytho is consistent and is evenly tapering to apex and not swollen basally. However, those of pupae of P. strictus and P. kolwensis are distinct in that all dorsal abdominal tubercles are spade-shaped with a swollen basal portion.

The tubercles on the abdominal sterna of pupae (figure 13 D) are quite uniform among species, with two posterior marginal tubercles per side, and with the outside tubercle much smaller than the inner. A difference is noted between pupae of P. planus and P. depressus, the former of which has the outer posterior marginal tubercle absent or smaller than the inner, large tubercle. The outer tubercle is smaller than the large, posterior, pleural tubercle. Pupae of P. depressus have two well-developed posterior marginal tubercles which are subequal in length, and each is subequal in length to the posterior pleural tubercle.

Chapter VIII

CLASSIFICATION

Pytho Latreille

Latreille 1796:23 (justified emendation of Tytho, Pythe); Blair 1928: 5; Hansen 1945: 20, 174; Hatch 1965: 85; Arnett 1968: 717; Kaszab 1969: 94; Burakowski 1976: 12; Arnett 1985: 351; Iablokoff-Khnzorian 1985: 202. Type species: Cucujus coeruleus Fabricius 1792 [= Cucujus coeruleus Herbst in Füssly 1782 (Blair 1928: 6)]. Fixation: Latreille (1810: 429) by subsequent designation. Synonyms: Pytholus Rafinesque 1815: 114; Enoptes Gistel 1848 (as cited in Spilman 1954).

Incorrect subsequent spellings: Pitho (Emmons 1854: 98, Matsumura 1931: 204); Phytho (Kôno 1936: 36; Kiefer and Moosbrugger 1942: 494; Phyto (Seidlitz 1916: 344; Zachariassen 1977: 27, 29).

Blackwelder (1946) states that Fabricius was the first designator of "genotypes" and according to a theory of the system by which Fabricius designated these type species, Blackwelder (1947) cites Pytho castaneus (Fabricius) as the type species of Pytho Latreille. Latreille (1796) did not include any species in his Pytho but made references to species previously included in the genera Cucujus and Tenebrio by other authors, which fit Latreille's concept of Pytho. Therefore, Pytho is not a nomen nudum according to Article 12 (b) (5) of the International Code of Zoological Nomenclature (1985). Latreille (1810) provides a table of

genera with an indication of the "type" for each. For Pytho, the type species is given as P. coeruleus Fabricius. Since P. coeruleus was one of the originally included species of Pytho (Fabricius 1801), and Latreille (1810) was the first author to subsequently designate it as type species, P. coeruleus is the valid type species. This is in agreement with Spilman (1954), and contradicts Blackwelder (1946, 1947).

Derivation of generic epithet: The genus name Pytho is derived from the Greek word meaning "to cause rot, to decay" (Jaeger 1966). This name probably refers to the habitat of the larvae and adults of the genus, that of rotting trees.

8.1 ADULT STAGE

Diagnostic combination

Pythinae (as in Lawrence 1982; Watt 1987) with the following combination of characters: pronotum with smooth lateral margin, and paired, longitudinal discal depressions (figure 2); elytra with variably convex intervals, separating linear rows of punctures (figure 8 B).

Description

Body form (figure 1) elongate, flattened to moderately convex dorsally; TL 5.6 - 16.2 mm; GEW 1.9 - 5.9 mm; body evenly and lightly sclerotized, with setiferous punctures covering body and appendages; colour of mature specimens ranging from light testaceous to black, with or without metallic lustre; elytra often contrasting in colour to head and prothorax. **Cranium** (figure 1) subquadrate, slightly longer than

wide, not significantly narrowed behind eyes; lateral frontal areas inclined and elevated above medial portion of frons; head more or less uniformly punctate dorsally, punctures with inconspicuous setae; ventrally, punctures with long, conspicuous setae; antennal insertions visible dorsally; gula well-developed and transversely ridged or wrinkled; gular sutures arcuate and divergent posteriorly from deep posterior tentorial pits; eyes protruding, coarsely faceted. **Antennae** (figure 1) slender, 11-segmented; approximately twice the length of cranium; setose from robust scape; third antennomere longest; antennomeres 2-7 subfiliform, 8-11 submoniliform; extra fine, sensory hairs present, distally, on apical 5-6 antennomeres, (figure 5 A) which are feebly clavate. **Labrum** dorsally punctate, with short discal setae; anterodorsal margin with six to eight long setae, twice length of labrum; two long discal setae also. **Mandibles** large, extending beyond labrum by almost half their lengths; lateral margins evenly arcuate to apex, or abruptly bent subapically (two species); incisor lobe apically bicusate with three or four smaller, inner marginal teeth; ventral surface with oblique row of setae arising near inner margin; ventral surface with oblique row of setae arising near inner margin; mandibles punctate and pubescent on dorsolateral surface; left mandible slightly longer with apex extending anterior of apex of right mandible; mandibles only moderately asymmetrical. **Maxillary region.** Cardo reduced in size, $1/5$ length of stipes; stipes elongate, triangular; lacinia apparently without digitus; galea and lacinia fringed with long, dense setae at apex; galea feebly widened distally; lacinia with setae along medial margin; palpifer present; palpus 4-segmented; palpomere 1 small, only slightly widened apically; approximately subequal in length to palpifer;

palpomeres 2-4 longer, about three times length of palpomere 1; palpomeres 2-3 approximately twice as wide apically as basally; apical palpomere flattened and moderately to strongly securiform (figure 5 B); apex hollow, with sensilla; all four segments with moderately long setae; long setae do not extend to apex of palpomere 4. **Labium and hypopharyngeal region.** Mentum (figure 5 C) trapezoidal, widest basally with slightly sinuate lateral margins; posteromedial area of mentum of male with subcircular pit (figure 5 C,D), approximately $1/4$ width of mentum; margin of pit feebly to strongly elevated above mentum surface; pit with ventrally protruding group of setae (figure 5 D); in both sexes, mentum with moderately long setae, densest medially; premental membrane present; prementum not visibly delimited from ligula; ligula widest apically with anterior margin deeply emarginate; fringe of fine setae on lateral lobes; medial area of ligula with several long setae; palpiger reduced; palpi 3-segmented; apical palpomere widest apically, concave, with sensilla; palpi with scattered, moderately long setae; medial area of ligula with several long setae. **Pronotum** (figure 2) subquadrate or trapezoidal, dorsal surface flattened with two longitudinal, discal depressions; lateral margins smooth and subparallel, evenly arcuate, or somewhat angulate near middle; pronotum uniformly punctate, each puncture with inconspicuous seta; punctation usually sparser down medial line, and on swollen dorsolateral areas; posterior bead present in all but one species; anterior bead present in three species; dorsal surface with no or slight microreticulation; hind angles at most suggested; anterior margin ringed with long setae anteriorly projecting around head; posterior margin with similar row of setae; ventrolateral margin of pronotum sparsely punctate with areas

impunctate; bead strongly developed along ventrolateral margin.

Prosternum trapezoidal, narrowest posteriorly, surface transversely wrinkled; anterior margin with long setae, projecting anteriorly around head; prosternal surface with setiferous punctures, either uniformly distributed or reduced; posterior prosternal margin delimiting procoxal cavities with bead; prosternal process short, not extending posterior of procoxae; apex blunt to acute, elevated as part of bead (figure 6 A), or not; lateral margins variably sinuate. **Mesosternum** (figures 6 C; 7 B,C) subtriangular in shape with moderately well-developed mesosternal intercoxal process surrounded by bead; bead widened posterolaterally (figure 7 B), or indistinct (figure 7 A); if indistinct, then marked by absence of microreticulation; apex of process with anterior bead; lateral margins of mesosternum straight to slightly sinuate; punctation reduced on lateral areas, heaviest medially; impunctate in one species; transverse microreticulation more pronounced laterally. **Mesepisternum** subtriangular with anterior bead, uniformly punctate, with long setae (two to three times width of punctures); punctures separated by about their own diameters; transverse carina near anterior margin.

Mesepimeron usually uniformly punctate, similar to that of mesepisternum; in one species, impunctate or with few punctures only (figure 6 D); lateral bead present; posterior margin extending past medial margin of metepisternum. **Mesonotum** with scutum completely divided by longitudinal mesothoracic suture; completely delimited from mesoscutellum; scutum with dense setae on posterolateral regions; posterior margin below level of scutellum. **Mesoscutellum** visible, subquadrate to rounded posteriorly, with variable number of small, setiferous punctures; impunctate in some specimens; length approximately

1/3 length of pronotum, usually slightly longer than wide. **Elytra** (figure 1) elongate, covering all but perhaps last abdominal tergite (in mature specimens); widest near or slightly posterad of midlength; elytra often with longitudinal depression near humeral angle; shoulders more or less prominent, truncate; lateral margin with bead extended completely along anterolateral margin, delimiting anterior region of epipleuron; each elytron with nine or ten carinate intervals, absent basally and at most only traceable to apex; carinae separated by rows of punctures; punctures confused or in vague single or double row; lateral margin sharply sloping with or without extra pubescence; epipleuron poorly developed, extended posteriorly to first abdominal sternite.

Metepisternum subrectangular, elongate; length approximately four times width at anterior margin; widest apically; uniformly punctate and pubescent. **Metasternum** large, weakly convex, and trapezoidal, widest posteriorly; width at posterior margin approximately 1.5 times length along midline; anterolaterally, almost attaining anterior edge of mesocoxae; anterior bead present; sides straight or feebly sinuate; antecoxal groove prominent; antecoxal piece narrower medially; median groove visible in posterior 1/4 to 1/5 of basisternum; intercoxal process short. **Metepimeron** elongate and very narrow, thinner anteriorly; subequal in length to metepisternum; entire length fringed with setae; posterior epimeral process bulbous, densely pubescent.

Hindwing normally developed; venation as shown in figure 4 B.

Metendosternite (figure 4 C) with stalk subparallel-sided, laminae well-developed. **Legs** slender and elongate; all surfaces except dorsum of femora with setae; apicoventral margin of femora not setose and slightly concave for reception of tibiae; femora slightly enlarged

medially, with concave dorsal, and convex ventral surfaces; tibiae slender, slightly arcuate, subequal in length to femora; distal, inner margins of tibiae pubescent; tibial spurs 2-2-2, weakly arcuate, and blunt apically; tarsi heteromerous, 5-5-4; tarsomeres not expanded or lobed laterally, densely pubescent ventrally; in males, pro- and mesotarsi with ventral setae of different structure than those of metatarsi; female tarsi with ventral setae of similar structure to those on male metatarsi; procoxae conical and projecting, widest dorsally; procoxal cavities open posteriorly; mesocoxae globose, with exposed trochantins; mesocoxal cavities open laterally; metacoxae transverse; trochanters obliquely fused to femora. **Abdomen** with five visible sternites; tergites weakly sclerotized; sternite 8 and tergite 9 densely covered with setae; male (figure 3): sternite 9 with anteriorly-extending lateral sclerites articulating with tergite 9; aedeagus of typical heteromeroid type; tegmen elongate, oriented dorsally, divided into two pieces; apicale grooved ventrally for reception of elongate median lobe (figure 3 E); median lobe with no discernible internal sac armature; accessory lobes arising near base of apicale, extending near or beyond apex of fused paramere; female (figure 4 A): ovipositor elongate, with four elongate baculi; coxites densely covered with setae; styli elongate, cylindrical.

8.2 LARVAL STAGE

Diagnostic combination

Pythinae (as in Lawrence 1982; Watt 1987) with the following combination of characters: meso- and metathoracic, and abdominal tergites 1-8 with well-developed parabasal ridges (figure 9); abdominal tergites 1-8 mesally with paired, raised, parabasal ridge processes (figure 9); urogomphal plate (figure 12) with at least four tubercles per side; urogomphal lip (figure 12) well-developed.

Description

Body form (figure 9) elongate, parallel-sided; body greatly to slightly flattened dorsoventrally; mature larvae with lengths of 20 to 40 mm, and maximum widths of 3 to 5 mm; body lightly sclerotized, heaviest on urogomphal plate, parabasal ridges, and parabasal ridge processes; colour in life ranging from light yellow to dark rufous, nearly black in areas of heaviest sclerotization; body with pattern of scattered setae of variable lengths; body surface smooth except on urogomphal plate, and parabasal ridge processes. **Head** (figure 9) prognathous, posterolateral angles rounded; lateral margins arcuate to subparallel; epicranial suture with stem absent; frontal arms of epicranial suture lyriform, U- to V-shaped basally; endocarinae absent; labrum symmetrical, with convex anterior margin; labrum with eight to ten marginal, and two or four discal setae; frons fused with clypeus; five pigmented stemmata per side, three in anterior, vertical column, two in posterior column; antennae elongate, three-segmented, with exposed insertions; antennomere 1 longest, antennomere 2 slightly

shorter, antennomere 3 shortest; antennomere 1 subcylindrical, with outside margin variably sinuate; antennomeres 2 and 3 cylindrical; antennomere 2 with small, dome-shaped sensory process at apex; mandibles (figure 10 E, F) retracted, heavily sclerotized, distinctly asymmetrical; apex of left mandible extending anterad of apex of right mandible; left mandible with large molar tooth; left and right mandibles with mola, more extensive on right mandible; mandibles with two or three apical teeth and several teeth on inner, subapical margin; lateral margin of mandible evenly arcuate to apex; maxilla (figure 10 D) with cardo appearing two-segmented due to internal fold. **Thorax** with lateral margins subparallel; cervicosternum (figure 9 B) divided into three sections; thoracic nota wider than long, pronotum longer than mesonotum, mesonotum subequal in length to metanotum; anterior margins of meso- and metanotum with parabasal ridge, bearing mesal, posteriorly directed, slightly raised parabasal ridge processes; parabasal ridge processes shorter than those found on abdominal tergites 2 to 8; thoracic spiracle between pro- and mesothorax, large, annular; legs (figure 10 A, B, C) with five segments, well-developed; all leg segments with many short, stout spine-like setae in addition to several more slender setae; all three pairs of legs subequal in size and similar in shape; single tarsungulus well-developed. **Abdomen** ten-segmented, elongate, with lateral margins subparallel; abdominal tergites 1 to 9 with transverse parabasal ridges near anterior margin (figure 9 A); parabasal ridges on tergites 1 to 8 with mesal, posteriorly directed, slightly raised parabasal ridge processes; parabasal ridge processes on tergite 1 shorter than those on tergites 2 to 8; tergite 9 more heavily sclerotized than remainder of abdomen, extending ventrally to form

urogomphal plate; urogomphal plate (figure 12) dorsally with transverse truncate, to semicircular row of seven to 28, uniform or variably sized tubercles; row of tubercles near, and outlining posterior margin of urogomphal plate; bases of tubercles marked by small circular, darkly pigmented area; tips of tubercles directed posteriorly or anteriorly (in two species); immoveable, paired urogomphi (figure 9; 12) with outer margins subparallel, slightly angulate above level of tergite 9; tips of urogomphi acute, upturned; urogomphi with two or three inner teeth per side; urogomphi with single, well-developed pit medially, marked posteriorly by variably protruding urogomphal lip (figure 12); posterior margin of urogomphal lip truncate to strongly arcuate; sternite 9 with 13 to 30 small, dentiform asperities in double arch arrangement (figure 9 B); asperities uniform or greatly variable in size, with or without conspicuous longitudinal ridges; sternite 9 divided into six peripheral plates; segment 10 small, surrounding opening of anus.

8.3 PUPAL STAGE

Diagnostic combination

A generic pupal diagnosis is not included here because at present I have not examined, or pupae are not known for, Priognathus monilicornis, and Synercticus heteromerus. Also, the closely related families, and subfamilies Boridae and Pilipalpinae have no described pupae. However, the presence of the paired, longitudinal depressions on the pronotum on pupae of Pytho should probably serve as a diagnostic character. The arrangement and number of the difference sets of tubercles may also be diagnostic; an investigation of this was not done in the absence of material.

Description

General form (figure 13 A,B) similar to adults; milky-white, almost pure white at pupation and darkening with development; length variable, 12 mm to 25 mm from anterior pronotal margin to apex of abdomen; maximum widths 3 to 5 mm across pronotum. **Head** deflexed ventrally, almost completely concealed dorsally by pronotum (figure 13 B); tubercles present as follows: one conspicuous pair near inner margin of each eye; one smaller pair medially and towards vertex; setae present as follows: one small pair on sides of vertex; large seta on each eye; one seta near each antennal insertion; four setae on labrum; antennae extended dorsally over meso- and metafemur and laterad of wings and elytra (in well-preserved pupae); mandibles apically bifurcate; antennae with several minute denticles on each of antennomeres 3 to apex at widest point of each antennomere. **Pronotum** (figure 13 B) similar in shape to adults, with paired, longitudinal depressions visible; tubercles as follows: variable number of large tubercles around dorsal pronotal margin; several pairs of small tubercles on pronotal disc. **Mesonotum** rectangular, much wider than long; one or more pairs of small setae near posterior margin. **Metanotum** rectangular, almost as long as wide; pair of large setae near posterior margin. **Elytra and wings** extended ventrally over metafemora and tibiae, attaining anterior margin of abdominal segment 2; wings and elytra closely against body (in poorly preserved specimens, wings and elytra become filled with fluid and distended laterally). **Legs** as in adult; femora laterally extended with tarsi parallel to length of body; small patch of setae on dorsal apex of femora. **Abdomen** (figure 13 C,D) with segments wider than long;

tubercles as follows: posterolateral margins of tergites with four or five tubercles; posterior margins of tergites with two or three tubercles; discal area of tergites with variable number of tubercles; pleural region with one or two tubercles; posterolateral margins of sternites with one or two tubercles; abdominal tubercles roughly triangular, with single seta arising subapically.

8.4 KEYS TO WORLD SPECIES OF THE GENUS PYTHO

8.4.1 Key to adults

- 1 Pronotum with lateral margins subparallel or slightly convergent anteriorly, without well-developed anterior or posterior beads (figure 2 A); mesepimeron impunctate or at least markedly less punctate than mes- and metepisternum (figure 6 D); aedeagus of male with fused paramere (apex of apicale) broadly expanded subapically (figure 3 C) P. seidlitzii Blair
- 1' Pronotum with lateral margins variably arcuate, with posterior and in some species, anterior beads (figure 2 B-I); mesepimeron as densely punctate as mes- and metepisternum; aedeagus of male with fused paramere (apex of apicale) gradually narrowed subapically (as in figure 3 D)
..... 2
- 2 (1') Pronotum with lateral margins weakly to strongly angulate at greatest width (figure 2 B,C,D); anterior pronotal bead present, at least medially; mesocoxae almost separated by long, acute mesosternal process and anterior metasternal process; elytron markedly convex dorsally
.....3
- 2' Pronotum with lateral margins evenly arcuate at greatest width (figure 2 E-I); anterior pronotal bead absent medially, in most specimens; mesocoxae not separated by mesosternal process and anterior metasternal process; elytron flattened, to slightly convex dorsally
.....5

- 3 (2) Pronotum in most specimens with lateral margins interrupted by transverse grooves near middle, and elevated above level of pronotal disc; mandibles abruptly bent near apex; prosternal process long and slender, extending almost to posterior margin of procoxae; distribution: Palearctic
.....4
- 3' Pronotum with lateral margins complete, without transverse grooves near middle, and at same level as pronotal disc; mandibles evenly arcuate to apex; prosternal process blunt, extending only half the length of the procoxae; distribution: eastern Nearctic P. strictus LeConte
- 4 (3) Elytra piceous, with distinct brassy or violaceous metallic lustre, lighter in colour than head and pronotum; mesoscutellum impunctate; labrum longer (ratio of labrum width:length 1.6-2.2; appendages rufous; distribution: eastern Palearctic (Japan)
..... P. nivalis Lewis
- 4' Elytra piceous to black, without distinct metallic lustre, not significantly lighter in colour than head and pronotum; mesoscutellum with several setigerous punctures in most specimens; labrum shorter (ratio of labrum width:length 1.9-2.7); appendages piceous to black; distribution: Palearctic
..... P. kolwensis C. Sahlberg
- 5 (2') Elytron variable in colour from light testaceous to dark piceous, with slight to strong metallic lustre; pronotum widest anterad of middle, with sides not constricted anteriorly (figure 2 H, I)6

- 5' Elytra constant in colour from piceous to black, with no metallic lustre; pronotum widest near middle, with sides constricted anteriorly (figure 2 E,F,G)
.....7
- 6 (5) Male aedeagus with apicale and basale subequal in length (figure 3 D); distribution: Nearctic ... P. planus (Olivier)
- 6' Male aedeagus with apicale approximately 1.5 times length of basale (figure 3 F); distribution: Palearctic
..... P. depressus (Linnaeus)
- 7 (5') Ratio of pronotal width:length less than 1.5 in most specimens; body length less (TL 5.60-10.64 mm); mesosternum impunctate or with few punctures; legs (at least tibiae) rufous; distribution: western Palearctic P. abieticola J. Sahlberg
- 7' Ratio of pronotal width:length greater than 1.5 in most specimens; body length greater (TL 7.20-13.68 mm); mesosternum coarsely punctate in most specimens; legs (excluding tarsi) dark piceus or black; distribution: Nearctic and eastern Palearctic (Japan)8
- 8 (7') Prosternum with bead of posterior margin thickened near apex of prosternal process (medial portion of process elevated) (figure 6 A); pronotum coarsely and uniformly punctate; mesosternum with posterior bead expanded, visible to lateral margin of mesosternum (figure 7 B); antennomeres 8-10 with sensillar region on apices; metasternum with intercoxal process acute apically; distribution: Nearctic P. niger Kirby
- 8' Prosternum with bead of posterior margin of uniform thickness around apex of prosternal process (medial portion of process not

elevated) (as in figure 6 B); pronotum finely and sparsely punctate; mesosternum with posterior bead not expanded, visible only to inner margin of mesotrochantin; antennomeres 7-10 with sensillar region at apices; metasternum with intercoxal process truncate apically; distribution: eastern Palearctic (Japan)

..... *P. jezoensis* Kôno

8.4.2 Key to mature larvae

This key has been constructed to discriminate among mature larvae only. The criteria for a mature larva are as follows: well-developed (visible) parabasal ridge processes and urogomphal tubercles; length greater than 15 mm. This last requirement is somewhat arbitrary, and if the important characters are visible, this key can be used for smaller larvae.

- 1 Urogomphal plate with 12 to 28 variably sized tubercles, arranged in a semicircular pattern (figure 12 A); tergites 2-7 with parabasal processes short, and inwardly curved (figure 11 A), each process with six or more medial setae; sternite 9 with 13 to 17 asperities P. seidlitzii Blair
- 1' Urogomphal plate with 7 to 16 more uniformly sized tubercles, arranged in an elliptical to semicircular pattern (figure 12 B,C,D); tergites 2-7 with parabasal processes variable in length (figure 11 B,C,D), each process with less than 6 medial setae; sternite 9 with 18 to 30 asperities 2
- 2 (1') Urogomphal plate (figure 12 D) with 11 to 16 small tubercles with the tips anteriorly directed; urogomphus with middle, inner tooth larger than or subequal in size to, the basal, inner tooth; tergites 2-7 with parabasal processes long, length of tergites 3 to 4 times length of processes (figure 11 D) P. planus (Olivier) (Nearctic) and P. depressus (Linnaeus) (Palearctic)

2' Urogomphal plate with 7 to 13 larger tubercles with the tips posteriorly directed; urogomphus (figure 12 B,C,D) with middle, inner tooth smaller than the basal, inner tooth; tergites 2-7 with parbasal processes shorter, length of tergites at least 5 times length of processes (figure 11 C,D)

..... 3

- 3 (2') Urogomphal plate (figure 12 B) with 10 to 13 large tubercles, varying in size on some specimens; apical urogomphal tubercle with more than 2 setae of equal or greater length as the apical tubercle; urogomphal lip with trapezoidal or strongly arcuate posterior margin; tergites 2-7 with parbasal processes short, length of tergites at least 7 times length of processes (figure 11 B); tergites 2-7 with four medial setae, subequal in size, in most specimens arranged linearly.....

. P. kolwensis C. Sahlberg (Palearctic), P. strictus LeConte (Nearctic) and P. nivalis Lewis (eastern Palearctic, Japan)

- 3' Urogomphal plate (figure 12 C) with 7 to 9 smaller tubercles, uniform in size on most specimens; apical urogomphal tubercle with 1 seta of equal or greater length as the apical tubercle; urogomphal lip with weakly arcuate posterior margin; tergites 2-7 with parbasal processes long, length of tergites 5 to 6 times length of processes (figure 11 C); tergites 2-7 with more than 4 medial setae, varying in size, with no distinct pattern of arrangement.....

P. niger Kirby (Nearctic), P. abieticola J. Sahlberg (Palearctic) and P. jezoensis Kôno (Japan)

8.4.3 Key to known pupae

The nomenclature of the various tubercles important in the identification of the pupal stage of Pytho is illustrated in figure 13. Pupae of the two Japanese species, P. nivalis, and P. jezoensis, are not known.

- 1 Abdominal tergites 2-6 with 5 lateral, marginal tubercles; dorsal abdominal tubercles not markedly dilated basally, evenly tapering to their apices2
- 1' Abdominal tergites 2-6 with 4 lateral, marginal, tubercles; dorsal abdominal tubercles markedly dilated basally, or evenly tapering to their apices3
- 2 (1) Abdominal sternites 2-6 with 2 large, lateral, marginal tubercles subequal in size; distribution: Palearctic P. depressus (Linnaeus)
- 2' Abdominal sternites 2-6 with 1 large, lateral, marginal tubercle (on some specimens, a second lateral marginal tubercle present, but much smaller); distribution: Nearctic P. planus (Olivier)
- 3 (1') Abdominal tergites 2-6 with more than 3 discal tubercles on most specimens; labrum with anterior margin truncate; pronotum with lateral margins parallel-sided ... P. seidlitzi Blair
- 3' Abdominal tergites 2-6 with 2 discal tubercles on most specimens; labrum with anterior margin variably emarginate; pronotum with lateral margins arcuate

-4
- 4 (3') Abdominal tergites 2-6 with tubercles spade-shaped, dilated basally; most abdominal segments with 1 large, pleural tubercle; labrum with anterior margin deeply emarginate
.....5
- 4' Abdominal tergites 2-6 with tubercles evenly tapered to their apices; most abdominal segments with 2, unequally sized pleural tubercles; labrum with anterior margin only slightly emarginate
P. niger Kirby (Nearctic) and P. abieticola J. Sahlberg (Palearctic)
- 5 (4) Most of abdominal tergites 2-6 with 5 lateral, marginal tubercles; abdominal sternites 2-6 with 3 posterior, marginal tubercles; pronotum with more than 20 tubercles per side
..... P. kolwensis C. Sahlberg
- 5' Most of abdominal tergites 2-6 with 4 lateral, marginal tubercles; abdominal sternites 2-6 with 1 posterior, marginal tubercle; pronotum with 7 or 8 tubercles per side
..... P. strictus LeConte

Chapter IX
INDIVIDUAL SPECIES TREATMENTS

9.1 PYTHO SEIDLITZI Blair 1925

(figures 1; 2 A; 3 A,B,C; 4 C; 5 A; 6 B,C,D; 8 B; 10 D,E,F; 11 A; 12 A; 13 C,D; 15)

Pytho seidlitz Blair 1925: 211 [**Type area** - Hudson's Bay. **Type repository** - BMNH]; Blair 1928: 7; Hatch 1965: 86.

Pytho niger: Seidlitz 1916: 408 (nec Kirby 1837).

9.1.1 Adult Stage

Derivation of specific epithet: Blair (1925) named this species in honour of G. von Seidlitz, who first examined specimens of this species, but mistook them for P. niger Kirby (see below).

Type information and taxonomic notes

Seidlitz (1916) presented a key to adults of the world species of Pytho, in which he treated what he called P. niger Kirby. However, Blair (1925) upon examination of the type specimens of P. niger Kirby, stated that P. niger of Seidlitz (1916) is not the true P. niger of Kirby. Therefore, the material examined by Seidlitz was that of an undescribed species, of which Blair located a single female specimen

from Hudson's Bay in BMNH. According to Article 72 (ii) of the ICZN (1985) both the specimens identified as P. niger Kirby by Seidlitz and the single female specimen seen by Blair constitute the type material of P. seidlitzii. Preference for lectotype designation should be given to specimens seen by the author, and not to those known to the author only from descriptions or illustrations in the literature [recommendation 73B, ICZN (1985)]. For this reason, the specimen from Hudson's Bay I hereby designate as lectotype. I was unable to locate the material on which Seidlitz (1916) based his concept of P. niger Kirby. If the specimens are found, they should be labelled as paralectotypes. The female lectotype has the following label information: [round label] above: "Hudson's Bay"; below: "44 17" (the 44 is above the 17)/[rectangular label 16 x 7 mm] "147 or 546 Pytho niger"/[rectangular det. label] "P. niger Seidl. (nec Kirby) det K.G. Blair"/[small det. label] "Pytho seidlitzii Blr"/[large red label] "LECTOTYPE Pytho seidlitzii Blair 1925 design. D.A. Pollock 1987". The lectotype, which is in poor condition has the following identifying structural characteristics: left antenna with four basal antennomeres only, right with three only; left protarsomeres 3-5 missing; middle left leg missing; all tarsi missing; pronotum fractured adjacent to pin hole; pronotum glued to elytral bases and mesothorax; specimen with short pin (through prothorax) into cardboard plate.

Diagnostic Combination

This species can be separated from the others in this genus by the following combination of characters: pronotum (figure 2 A) with lateral margins subparallel or slightly convergent anteriorly, and without

anterior or posterior beads; mesepimeron (figure 6 D) impunctate or with few punctures along lateral margin; male aedeagus (figure 3 C) with apex of fused paramere broadly expanded; distribution: trans - Nearctic.

Description

TL 9.3-14.8 mm; GEW 3.5-5.8 mm; other measurements given in Table 1. **Head** with lateral, frontal areas abruptly elevated above level of disc of frons; clypeus not significantly elevated above level of frons; area on frons between eyes elevated on some specimens; apical maxillomere securiform; mandibles with lateral margins evenly arcuate to apices; pit on male mentum with slightly elevated margin; posterior limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 8-10; punctation uniform and coarse, less dense on elevated, lateral, frontal areas. **Pronotum** (figure 2 A) with lateral margins subparallel through their entire lengths; in some specimens, lateral margins convergent anteriorly and/or slightly arcuate; areas laterad of depressions at same level or slightly below disc; anterior bead absent; posterior bead suggested only; pronotal depressions shallow and oval, with inner margins divergent anteriorly; median line absent to weakly impressed, in most specimens deepened anteriorly and posteriorly into subcircular depressions; punctation uniform, punctures separated by one to two times their own diameters; punctation slightly finer and sparser laterad of depressions. **Prosternum** with intercoxal process short, extending to at most, half length of procoxae; process (figure 6 B) with strong bead; bead complete apically and laterally on process. **Mesoscutellum** with 15-25 setigerous punctures. **Mesepisternum** uniformly, coarsely punctate; punctures

TABLE 1

Measurements of selected features of samples of P. seidlitzii from Ghost Dam, Alberta, and Laniel, Quebec. The samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	ALBERTA		QUEBEC	
	M (6)	F (5)	M (11)	F (8)
EL	6.8-7.9 7.4 \pm .46	7.6-8.9 8.4 \pm .56	6.6-8.8 7.6 \pm .65	6.5-8.7 8.0 \pm .75
GEW	3.7-4.6 4.2 \pm .37	3.9-4.8 4.5 \pm .34	3.7-4.7 4.2 \pm .38	3.5-4.8 4.3 \pm .45
PL	1.5-1.8 1.7 \pm .11	1.76-1.84 1.8 \pm .04	1.5-2.0 1.8 \pm .16	1.4-1.8 1.7 \pm .20
GPW	2.1-2.7 2.4 \pm .25	2.5-2.7 2.6 \pm .09	2.2-2.8 2.5 \pm .20	1.9-2.6 2.4 \pm .32
HL	1.4-1.9 1.8 \pm .17	1.8-1.9 1.8 \pm .07	1.6-2.2 1.9 \pm .16	1.4-1.9 1.6 \pm .17
GHW	1.3-1.6 1.5 \pm .14	1.4-1.6 1.5 \pm .07	1.4-1.8 1.6 \pm .13	1.3-1.5 1.4 \pm .12
TL	9.8-11.4 10.9 \pm .73	11.1-12.6 12.0 \pm .61	9.8-13.0 11.3 \pm .94	9.3-12.3 11.3 \pm .99
GPW/PL	1.3-1.6 1.4 \pm .09	1.4-1.5 1.5 \pm .04	1.3-1.5 1.4 \pm .04	1.3-1.5 1.4 \pm .06

separated by their own diameter or less. **Mesepimeron** impunctate in most specimens; in some specimens, with several punctures along lateral margin only (figure 6 D). **Mesosternum** (figure 6 C) with long, acute intercoxal process, extending nearly to half length of mesocoxae; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation coarse anteromedially, reduced posteriorly, and absent laterally. **Elytron** slightly convex dorsally, with nine moderately to strongly convex intervals; tenth interval visible posterad of midlength of elytron; striae with confused double row of punctures; posterolateral elytral flange without extra pubescence. **Metasternum** with short, triangular intercoxal process, not extending to half length of mesocoxae. **Male aedeagus** (figure 3 A,B,C) with apicale approximately 2.3 times the length of the basale; apicale expanded, spatulate apically; apicale narrowest near middle with sinuate lateral margins; accessory lobes attaining apex of fused paramere, or slightly beyond. **Colour** with no significant variation among specimens examined; uniformly non-metallic piceous to black dorsally and ventrally; elytra with same colouration as head and pronotum; lateral areas of frons, mouthparts, antennae, coxae, and tarsi rufopiceous (lighter than dorsal colouration).

Material examined: I examined 185 adults of this species.

9.1.2 Larval Stage

The larva of P. seidlitzii was previously undescribed.

Diagnostic Combination

Parabasal ridge processes (figure 11 A) short, convergent anteriorly; basal, inner urogomphal tooth larger than middle tooth (figure 12 A); apical urogomphal tooth absent; urogomphal plate gradually sloping posteriorly to urogomphal lip; urogomphal lip (figure 12 A) with posterior margin strongly arcuate; urogomphal tubercles arranged in semicircle; distribution: trans - Nearctic.

Description

Head with frontal arms of epicranial suture V-shaped basally, slightly sinuate in some specimens; antennomere 1 elongate, distinctly sinuate laterally; antennomere 2 feebly enlarged apically; antennomere 3 cylindrical; ratio of antennomere lengths approximately 2 : 2 : 1. **Parabasal ridge processes** (figure 11 A) short, extending only slightly anterad of parabasal ridge; inner margins arcuate, convergent anteriorly; distance from anterior tip of processes to posterior margin of tergites 2-7 approximately ten times length of process. **Parabasal setae** (figure 11 A) variable in size, at least six per side, majority posterior of parabasal ridge processes; on some specimens and tergites, pattern of four, linearly arranged setae present with extra, smaller setae. **Urogomphus** (figure 12 A) with basal, inner tooth large, separated from lateral margin of urogomphal lip by less than width of basal tooth; middle, inner tooth small, separated from basal tooth by slightly greater than length of basal tooth; apical, inner tooth absent; urogomphal plate gradually sloping posteriorly to urogomphal lip. **Urogomphal lip** (figure 12 A) with posterior margin strongly arcuate, in

some specimens slightly trapezoidal; ratio of urogomphal lip width at base to length down midline approximately 1 : 0.6. **Urogomphal tubercles** (figure 12 A) variable in size and number, most specimens with 8-12 per side; tubercles arranged in semicircle, with tips directed posteriorly; apical urogomphal tubercle with or without one long seta. **Ventral asperities** 13 to 17 in number, large, with conspicuous longitudinal ridges.

Material examined: Approximately 300 larvae were examined in this study.

Association Methods: Large larvae were collected in association with pupae and teneral adults in British Columbia. Confirmation of larval identity was achieved by rearing nine larvae collected in New Hampshire and New York to adults. Also, six larvae collected in Manitoba were reared to adults. Several borrowed specimens consisted of adults with their larval exuviae.

9.1.3 Pupal Stage

Diagnostic Combination

Abdominal tergites 2-6 with more than three discal tubercles (figure 13 C); labrum with anterior margin truncate; pronotum with lateral margins parallel-sided.

Description

Head with single, ocular tubercle; antennal denticles large, conspicuous; anterior margin of labrum truncate. **Pronotum** with shape as in adult, lateral margins straight and subparallel; 12-13 large marginal

tubercles per side with variable number of smaller tubercles. **Abdominal tergites 2-6** (figure 13 C) with four lateral marginal tubercles, some specimens rarely with five on one or two segments; three to six small to moderately large discal tubercles; two posterior, marginal tubercles, the outer larger; two pleural tubercles, the anterior smaller; overall shape of dorsal abdominal tubercles evenly tapered to apex. **Abdominal sternites 2-6** (figure 13 D) with two posterior, marginal tubercles, the inner tubercle larger.

Material examined: Sixteen pupae were examined during this study.

Association Methods: One pupa was collected with large larvae and teneral adults in British Columbia. A larva collected in Manitoba was reared to pupa. Ten larvae from New Hampshire and New York were reared to and preserved at the pupal stage. Two pupae from New Hampshire with associated larval exuviae were borrowed.

9.1.4 Natural History

Nothing is published regarding the life cycle, host preferences or any other aspect of the biology of this species. Therefore, personal observations and label data are the only sources of this information. Adults have been collected in every month except January, February and November. Adults have been collected "under bark" on 24.viii.1984 (British Columbia) (in pupal cells), 26.x.1986 (Manitoba) and on 20.v.1984 (New Hampshire). Larvae collected by the author on 23.x.1986 (Manitoba) did not pupate in the laboratory until after being placed in a snow pile outside for approximately four months. Once brought back

into the lab (on 1.ii.1987), development continued and by 20.v.1987, all larvae had successfully pupated. At room temperature, P. seidlitzii has an average pre-pupal duration of about 4 days and a pupal stage of about 10 days (based on all reared pupae).

Pytho seidlitzii has a wide host acceptability throughout its range as is evident from the numerous host records for this species: Pinus monticola Dougl. (British Columbia), P. banksiana Lamb. (Manitoba), P. contorta Dougl. (Alberta), Larix occidentalis Nutt. (British Columbia), Picea glauca (Moench) Voss (British Columbia), P. mariana (Mill.) BSP. (British Columbia, Manitoba), Tsuga heterophylla (Raf.) Sarg. (British Columbia), Abies balsamea (L.) Mill. (Nova Scotia), A. grandis (Dougl.) Lindl. (Idaho).

9.1.5 Distribution

Pytho seidlitzii occurs across North America from British Columbia and the Northwest Territories to Nova Scotia (figure 15). The northern extent of its range probably closely coincides with tree line; the southern range extent is not well delimited. The southeast corner of Idaho is the most southerly record. I interpret the absence of P. seidlitzii from Saskatchewan as merely an artifact of its relative rareness; similar habitat and other conditions occur in the northern region of all the prairie provinces. Therefore, I expect that P. seidlitzii should occur in Saskatchewan. This gap does not have biogeographic significance.

9.1.6 Chorological Relationships

Pytho seidlitzii is broadly sympatric with P. niger and P. planus across North America, and with P. strictus in the latter's restricted eastern North American distribution.

9.1.7 Phylogenetic Relationships

Pytho seidlitzii is regarded as the most plesiomorphic species of Pytho, and forms the sister taxon of the remainder of the genus. Pytho seidlitzii is the sole member of the P. seidlitzii species-group.

9.2 PYTHO STRICTUS LeConte 1866

(figures 2 B; 11 B; 16)

Pytho strictus LeConte 1866: 167 [**Type locality**- Canada. **Type repository**- MCZ]; Blair 1928: 7; Austin and LeConte 1874: 268 (distribution); Bowditch 1896: 10 (distribution); Tanner 1927: plate VII, figs. 68-69 (female genitalia).

9.2.1 Adult Stage

Derivation of specific epithet

The name "strictus" is derived from the Latin word meaning "drawn together", which probably refers to the base of the pronotum (figure 2 B), which is somewhat constricted in this species.

Type information and taxonomic notes

LeConte (1866) mentions in the description that he saw only one specimen from Canada. This specimen is necessarily the HOLOTYPE. The female holotype has the following label information: [round label] white above and pale pink beneath / [square red-orange label] "Type 4751" / [handwritten det. label] "P. strictus Lec." / [red holotype label] "HOLOTYPE *Pytho strictus* LeConte 1866 examined by D.A. Pollock 1837". The specimen has the following identifying features: right antenna with only two basal antennomeres; large pin hole through right elytron extending through to venter; left middle leg broken off near apex of femur; left metatarsus with two basal segments only, right metatarsus with three only; colour of body uniformly rufous.

Diagnostic combination

adult P. strictus may be recognized by the following characters: pronotum (figure 2 B) with short, basal, parallel-sided portion; lateral margins of pronotum angulate and widest near midlength; elytra non-metallic rufous or piceous, strongly convex dorsally; distribution: eastern Nearctic.

Description

TL 13.4-16.2 mm; GEW 4.9-5.8 mm, other measurements given in Table 2. **Head** with lateral, frontal areas abruptly elevated above level of disc of frons; clypeus significantly elevated above level of frons; area on frons between eyes with two, subcircular shallow depressions; apical maxillomere weakly securiform; mandibles with lateral margins evenly arcuate to apices; pit on mentum of male with moderately elevated margin; antennae with sensilla on apices of antennomeres 7-10; punctation irregular, fine, very sparse on disc of frons and on elevated, lateral, frontal areas. **Pronotum** (figure 2 B) with basolateral margins subparallel for a short distance; lateral margins arcuate anteriorly, margin somewhat angulate near middle; pronotum widest at angulate point on lateral margin, near midlength; areas laterad of depressions at same level as disc; anterior bead present, in some specimens feebly delimited medially; posterior bead present; pronotal depressions deep and linear, with inner margins divergent anteriorly; depressions with one or two smaller depressions posteriorly and laterally; lateral depressions bifurcate in some specimens; median line variably well impressed, in some specimens deepened anteriorly and

posteriorly into subcircular depressions; punctation not uniform; coarse on median area and basal area posterad of depressions; fine in depressions and on area laterad of depressions. **Prosternum** with intercoxal process short, extending to about half length of procoxae; process with distinct bead; bead complete apically and laterally on process. **Mesoscutellum** with greater than ten setigerous punctures, in most specimens. **Mesepisternum** uniformly, coarsely punctate; punctures separated by their own diameter or less. **Mesepimeron** evenly, coarsely punctate; punctures separated by their own diameter or less. **Mesosternum** with long, acute intercoxal process, extending nearly to metasternal, intercoxal process; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation coarse medially, and absent laterally. **Elytron** strongly convex dorsally, with nine markedly convex intervals; tenth interval visible posterad of midlength of elytron; striae with confused double row of punctures; posterolateral elytral flange with moderately long pubescence. **Metasternum** with short, rounded to slightly acute, intercoxal process, not extending to half length of mesocoxae. **Male aedeagus** (as in figure 3 D) with apicale and basale subequal in length; apicale not expanded, evenly tapered to apex; apicale narrowest apically with straight lateral margins; accessory lobes attaining apex of fused paramere. **Colour** consisting of two forms among specimens examined; most specimens (including holotype) uniformly dark rufous dorsally and ventrally with elytra lighter in colour than head and pronotum in some of these rufous-coloured specimens; femora darker than tibiae and tarsi; several specimens examined piceous dorsally and ventrally, with sutural interval and epipleuron of elytra lighter in colour; mouthparts, antennae, trochanters, tibiae and tarsi dark rufous (lighter than dorsal colouration).

TABLE 2

Measurements of selected features of samples of P. strictus from various localities in eastern North America. The samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter for females is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	M (1)	F (9)
EL	8.7	9.5-11.2 10.0 \pm .49
GEW	4.9	5.1-5.9 5.5 \pm .29
PL	2.2	2.2-2.6 2.4 \pm .16
GPW	3.4	3.2-3.8 3.6 \pm .22
HL	2.4	2.1-2.6 2.4 \pm .19
GHW	2.2	2.0-2.3 2.2 \pm .12
TL	13.4	13.8-16.2 14.8 \pm .70
GPW/PL	1.5	1.4-1.6 1.5 \pm .05

Material examined: Eleven adults, including only one male, were examined in this study.

9.2.2 Larval Stage

Diagnostic combination

Parabasal ridge processes (figure 11 B) short, convergent anteriorly; basal, inner urogomphal tooth larger than middle tooth (as in figure 12 B); apical urogomphal tooth very small, or absent; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (as in figure 12 B); with posterior margin trapezoidal; urogomphal tubercles five to seven per side with medial gap; distribution: eastern Nearctic.

Description

Head with frontal arms of epicranial suture V-shaped basally, slightly arcuate in some specimens; antennomere 1 elongate, feebly sinuate laterally; antennomere 2 gradually enlarged apically; antennomere 3 swollen basally; ratio of antennomere lengths approximately 3.0 : 2.0 : 1.1. **Parabasal ridge processes** (figure 11 B) short, extending anterad of parabasal ridge by half their lengths; inner margins arcuate, convergent anteriorly; distance from anterior tip of processes to posterior margin of tergites 2-7 approximately seven times length of process. **Parabasal setae** (figure 11 B) large, in most specimens two per side, arranged sublinearly, immediately posterior of parabasal ridge processes; some segments with one on a side; no smaller extra setae present. **Urogomphus** (as in figure 12 B) with basal, inner tooth large, separated from lateral margin of urogomphal lip by greater

than length of basal tooth; middle, inner tooth small, separated from basal tooth by slightly more than length of basal tooth; apical, inner tooth minute or absent in some specimens; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (as in figure 12 B) with posterior margin trapezoidal, in some specimens nearly arcuate; ratio of urogomphal lip width at base to length down midline approximately 2.9 : 1. **Urogomphal tubercles** (as in figure 12 B) large, in some specimens medial tubercles smaller, five to seven per side; tubercles arranged in slightly elliptical semicircle with tips directed posteriorly; apical urogomphal tubercle with at least two to four long setae. **Ventral asperities** 16 to 18 in number, small, with inconspicuous longitudinal ridges.

Material examined: four larvae and two exuviae were examined in this study.

Association methods: One larva collected in June, 1986 at Mt. Marcy, Essex Co., New York was reared to adult. The exuvium was then compared to other preserved larvae from the same site; three additional larvae were discovered in the material collected at Mt. Marcy.

9.2.3 Pupal Stage

The pupa of P. strictus is heretofore undescribed.

Diagnostic combination

The pupa of P. strictus is most similar to that of P. kolwensis, but may be separated by the following characters: four lateral marginal

tubercles on most tergites; pronotum with 7-8 tubercles per side; single posterior marginal tubercle on sternites 2-6.

Description

Head with single, ocular tubercle; antennal denticles large, conspicuous; anterior margin of labrum deeply emarginate. **Pronotum** with shape as in adult, lateral margins anterior of short, basal parallel-sided portion, variably arcuate, somewhat angulate near middle; widest at midlength or slightly posterad; seven or eight large, marginal tubercles per side. **Abdominal tergites 2-6** with four lateral, marginal tubercles; two large, discal tubercles; two posterior marginal tubercles, the outer larger; one pleural tubercle; overall shape of dorsal abdominal tubercles spade-shaped, broadly dilated at base. **Abdominal sternites 2-6** with one posterior, marginal tubercle.

Material examined: A single pupa of this species was examined.

Association methods: A number of larvae were collected by the author and R.E. Roughley on Mt. Marcy, Essex Co., New York. After rearing an adult P. strictus and associating the larval stage, an exuvium from a pupa which died before emerging was examined and was found to be P. strictus.

9.2.4 Natural History

Almost nothing is known regarding the natural history of this species. The only known host tree is Pinus strobus (near Lincoln Pond, Maine). The host under the bark of which specimens were collected by the author and R.E. Roughley on Mt. Marcy, Essex Co., New York was

unfortunately not determined. Two larvae collected on Mt. Marcy on 3.vi.1986 pupated in the laboratory on 25 and 27.vii.1986. One adult emerged after 10 days under laboratory conditions (based on one reared pupa).

9.2.5 Distribution

Pytho strictus is apparently restricted to eastern North America (figure 16) with the westernmost record being Clingman's Dome in the Great Smoky Mountains, Tennessee. Additional records of specimens not seen by me include Mt. McIntire, New York; Camp Caribou, and near Lincoln Pond, Maine (T. Spilman, pers. comm.) Because these localities were not verified, they are not included in the locality list or the distribution map. Austin and LeConte (1874) and Bowditch (1896) list P. strictus from Mt. Washington, New Hampshire; this record is not on the distribution map or in my locality records.

9.2.6 Chorological relationships

In eastern North America, where Pytho strictus is found, all other North American species are present. P. strictus is sympatric with P. seidlitzii, P. niger, and P. planus.

9.2.7 Phylogenetic relationships

Pytho strictus forms the sister species of P. kolwensis + P. nivalis. Pytho strictus is the Nearctic representative of the P. kolwensis species-group.

9.3 PYTHO KOLWENSIS C. Sahlberg 1833

(figures 2 C; 12 B; 17)

Pytho kolwensis C. Sahlberg 1833: 445 [**Type locality** - Finland (see below) **Type repository** - type not examined; see below]; Blair 1928: 7; Burakowski 1962: 173-203; 1976: 12, 14, 17 (key to Polish species in all stages); Pettersson 1983: 23-29, fig. 5.

var. sahlbergi Pic 1912: 49 [**Type locality** Finland. **Type repository** - type not examined]; Blair 1928: 7.

Incorrect subsequent spellings: kolvensis Sahlberg 1875: 224; Horn 1888: 46; Grill 1896: 245; Lindroth 1960: 326, 328; Iablokoff-Khnzorian 1985: 205.

9.3.1 Adult Stage

Derivation of specific epithet

J. Sahlberg (1875) states that C.R. Sahlberg collected this species near "Kolva" which was apparently changed to "Huvitus" (Sahlberg 1875). C. Sahlberg (1833) collected this species in "sylva Kolwensi." Therefore the name "kolwensis" refers to the original type locality of P. kolwensis. The numerous incorrect subsequent spellings of this epithet in the literature, are due to the fact that Sahlberg (1833) changed the stem to "kolw" rather than "kolv", as is the spelling in the original place name [according to J. Sahlberg (1875)].

Type information and taxonomic notes

Requests for type specimens of P. kolwensis were sent to ZMH and DBTU. H. Silfverberg (pers. comm.) stated that the Sahlberg collection is kept in DBTU. Two specimens of P. kolwensis were received from DBTU, both of which are from the type locality, but collected by J. Sahlberg. S. Koponen (pers. comm.) states that no specimens of P. kolwensis collected by C. Sahlberg exist in DBTU. It is therefore probable that the original types were destroyed or were never designated as such by C. Sahlberg. According to ICZN (1985), Article 75 (b), a neotype is to be designated only in exceptional circumstances when a neotype is necessary in the interests of nomenclatural stability. Because P. kolwensis is a well-known species taxonomically, and with a minimum of nomenclatural confusion, the above condition of exceptional circumstance does not apply. Also, there is a chance that material collected by C. Sahlberg may be located, in which case the appropriate type designations may be made.

Pytho kolwensis var. sahlbergi Pic (1912) was based on a specimen(s) from Finland with reddish elytra, tarsi, and antennae. It is possible that the specimen examined was teneral. See Type information and taxonomic notes for P. nivalis for additional information.

Diagnostic combination

adult P. kolwensis can be distinguished on the following combination of characters: Pronotum (figure 2 C) with lateral margins angulate and widest near midlength; lateral areas of pronotum elevated above disc, and interrupted by transverse furrow in most specimens; mandible

abruptly bent near apex; scutellum with several setigerous punctures; elytra strongly convex dorsally, non-metallic piceous to black; distribution: known from Fennoscandia, Poland and Siberia.

Description

TL 10.9-15.9 mm; GEW 4.0-5.9 mm; other measurements given in Table 3. **Head** with lateral, frontal areas abruptly elevated above level of disc of frons; clypeus not significantly elevated above level of frons; area on frons between eyes longitudinally elevated on some specimens; apical maxillomere securiform; mandibles with lateral margins arcuate laterally, abruptly bent near apex; pit on male mentum with strongly elevated margin; posterior limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 7-10; punctation relatively fine and sparse, especially on elevated, lateral, frontal areas. **Pronotum** (figure 2 C) with basolateral margins subparallel for a very short distance; lateral margins only feebly arcuate to widest point, in some specimens straight or sinuate; pronotum widest at angulate point on lateral margin, near midlength; lateral margin evenly arcuate anteriorly; areas laterad of depressions elevated above level of disc; anterior bead present, in some specimens feebly delimited medially; posterior bead present; pronotal depressions deep and linear, extending laterally as a sharply engraved groove interrupting lateral margins, in most specimens; median line absent to weakly impressed, deepened anteriorly and posteriorly into subcircular depressions in some specimens; punctation not uniform, densest in and near depressions, punctures separated by 1-2 times their own diameters; sparser along midline and on areas laterad of depressions

TABLE 3

Measurements of selected features of samples of P. kolwensis from various localities in Finland. The samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	M (6)	F (13)
EL	7.1-9.5 8.2 \pm .86	7.8-10.7 9.2 \pm .96
GEW	4.0-5.6 4.8 \pm .57	4.3-5.9 5.2 \pm .59
PL	1.8-2.3 2.1 \pm .19	1.8-2.6 2.2 \pm .27
GPW	2.6-3.1 2.9 \pm .21	2.6-3.8 3.0 \pm .41
HL	1.9-2.5 2.2 \pm .22	1.9-2.6 2.3 \pm .23
GHW	1.7-2.1 1.9 \pm .16	1.6-2.2 1.9 \pm .23
TL	10.9-14.2 12.6 \pm 1.22	11.6-15.9 13.6 \pm 1.44
GPW/PL	1.3-1.4 1.4 \pm .04	1.2-1.5 1.4 \pm .06

Prosternum with intercoxal process long, extending past half length of procoxae; process with strong bead; bead complete apically and laterally on process. **Mesoscutellum** in most specimens with less than ten setigerous punctures; in some specimens, impunctate. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** with long, acute intercoxal process, extending nearly to metasternal, intercoxal process; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation reduced laterally and down midline. **Elytron** strongly convex dorsally, with nine markedly convex intervals; tenth interval visible posterad of midlength of elytron; striae with confused double row of punctures; posterolateral elytral flange without extra pubescence. **Metasternum** with short, blunt intercoxal process, extending to near half length of mesocoxae. **Male aedeagus** (as in figure 3 D) with apicale and basale subequal in length; apicale not expanded, evenly tapered to apex; apicale narrowest apically with straight lateral margins; accessory lobes variable in length, attaining or exceeding apex of fused paramere. **Colour** with no significant variation among specimens examined; uniformly non-metallic piceous to black dorsally and ventrally; in some specimens, elytra lighter in colour than head and pronotum; mouthparts, antennae, coxae, trochanters, apices of tibiae, and tarsi dark rufous (lighter than dorsal colouration).

Material examined: 26 adults of this species were examined.

9.3.2 Larval Stage

The larva of P. kolwensis was described originally by J. Sahlberg (1875), and illustrated and/or redescribed subsequently by Burakowski (1962, 1976) and Pettersson (1983).

Diagnostic combination

Parabasal ridge processes (as in figure 11 B) short, convergent anteriorly; basal, inner urogomphal tooth larger than middle tooth (figure 12 B); apical urogomphal tooth very small or absent; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (figure 12 B) with posterior margin trapezoidal; urogomphal tubercles five to seven per side with medial gap; distribution: known from Fennoscandia, Poland and Siberia.

Description

Head with frontal arms of epicranial suture V-shaped basally, slightly arcuate in some specimens; antennomere 1 slender, feebly sinuate laterally; antennomere 2 distinctly enlarged apically; antennomere 3 cylindrical or slightly swollen basally in some specimens; ratio of antennomere lengths approximately 1.5 : 1.1 : 0.7. **Parabasal ridge processes** (as in figure 11 B) short, extending anterad of parabasal ridge by half their lengths; inner margins arcuate, convergent anteriorly; distance from anterior tip of processes to posterior margin of tergites 2-7 approximately nine times length of process. **Parabasal setae** (as in figure 11 B) large, in most specimens two per side, arranged sublinearly, immediately posterior of parabasal ridge

processes; some specimens with one or two smaller setae per side.

Urogomphus (figure 12 B) with basal, inner tooth large, separated from lateral margin of urogomphal lip by length of basal tooth; middle, inner tooth very small, separated from basal tooth by length of basal tooth; apical, inner tooth minute, or absent in some individuals; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (figure 12 B) with posterior margin trapezoidal; ratio of urogomphal lip width at base to length down midline approximately 1.6 : 1. **Urogomphal tubercles** (figure 12 B) large, uniform in size, five or six per side; tubercles arranged in slightly elliptical semicircle, with tips directed posteriorly; apical urogomphal tubercle with four or five long setae. **Ventral asperities** 17 to 20 in number, small, with inconspicuous longitudinal ridges.

Material examined: A total of 19 larvae of this species were examined.

Association methods: The larvae used in this diagnosis were already identified when they were received. Their identity was verified by consulting the literature e.g. Burakowski (1962, 1976) and Pettersson (1983).

9.3.3 Pupal Stage

The pupa of P. kolwensis was illustrated and described by Burakowski (1962).

Diagnostic combination

The pupa of P. kolwensis most resembles that of P. strictus but has the following diagnostic features: 5 lateral marginal tubercles on tergites 2-6; pronotum with at least 20 variably-sized tubercles per side; 3 posterior marginal tubercles on sternites 2-6.

Description

Head with single, ocular tubercle; antennal denticles small, inconspicuous; anterior margin of labrum deeply emarginate. **Pronotum** with shape as in adult, lateral margins variably arcuate, somewhat angulate near middle; widest at midlength or slightly posterad; 12 large, marginal tubercles and about eight smaller tubercles per side. **Abdominal tergites 2-6** with five lateral marginal tubercles, one or two sides with four or six; one to three large, discal tubercles; two posterior marginal tubercles, subequal in size, three on one side on some segments; one pleural tubercle, with minute process anterad; overall shape of dorsal abdominal tubercles spade-shaped, broadly dilated at base. **Abdominal sternites 2-6** with three posterior marginal tubercles: inner tubercle minute, middle large, outer small.

Material examined: A single pupa was examined in this treatment. Two pupae from UZIL were not used because they had been affixed to cardboard plates, and had shrivelled badly.

Association method: The one pupa used in this study was reared from known larvae of P. kolwensis by R. Pettersson (Sweden).

9.3.4 Natural History

Pytho kolwensis according to Pettersson (pers. comm.; 1983) is one of the few "fire refugium organisms" in the northern European forests. This beetle is apparently being threatened by large-scale forest clear cutting. This species inhabits only primeval spruce forests throughout its range and is found exclusively on or in Picea (Saalas 1917; Pettersson 1983, pers. comm.). Pytho kolwensis demands sun-exposed habitat, but the inner bark of the host tree must be very moist and without fungal growth for 5-10 years. Larvae are often found in logs lying horizontally near brooks or cold springs (Pettersson, pers. comm.).

Saalas (1917) provides details as to the preferred habitat of P. kolwensis. This species prefers lying dead Picea excelsa Link. trunks over 35 cm in diameter and decayed but still fairly "fresh". Pytho kolwensis is found most often in swampy areas. Additional details of the life cycle and other natural history are given in Burakowski (1962). A summary of the life cycle of P. kolwensis from Burakowski (1962) is given in Chapter III.

9.3.5 Distribution

Pytho kolwensis is known from Finland, Sweden, and the U.S.S.R. according to label data of specimens examined in this study (figure 17). More detailed information on the Fennoscandian distribution of this species may be found in Grill (1896), Saalas (1917), Lindroth (1960) and Silfverberg (1979). According to Pettersson (pers. comm.) today there

are six localities for P. kolwensis in Sweden and four or five in Finland. Many of the older collection localities no longer support populations of P. kolwensis. Iablokoff-Khnzorian (1985) describes the distribution of this species as being found in Poland, Baltic countries, Scandinavia, and Siberia. Information on the Polish distribution of P. kolwensis is given in Burakowski (1962). As can be seen from the distribution map, there is a large gap between the localities in Finland and the locality near Lake Baikal. I believe that increased collecting in central to eastern U.S.S.R. would produce more records of P. kolwensis, although according to Pettersson (1983), this beetle is considered threatened, at least in Sweden.

9.3.6 Chorological relationships

Pytho kolwensis is sympatric with P. abieticola and P. depressus in the more restricted range of P. kolwensis.

9.3.7 Phylogenetic relationships

Pytho kolwensis is the sister species of P. nivalis; these two taxa may in fact be conspecific. More material of the latter is needed for examination. These two species form the sister group to P. strictus; all three are members of the P. kolwensis species-group.

9.4 PYTHO NIVALIS Lewis 1888

(figures 2 D; 18)

Pytho nivalis Lewis 1888: 109 [Type locality- Nikko, Niohosan (Japan).

Type repository- BMNH]; Blair 1928: 7; Schoenfeldt 1891: 262; Lewis 1895: 294; Hayashi et al. 1959: 484, figs. A-E; Hayashi 1969: 6, plate VI, A-N; Iablokoff-Khnzorian 1985: 205 (revision of Palearctic species).

9.4.1 Adult Stage

Derivation of specific epithet

The name "nivalis" is derived from the Latin word for "snow" (Jaeger 1966). This name was used by Lewis (1888) because the mountain on which this species was collected was still snow-covered among the pines.

Type information and taxonomic notes

There are seven specimens of the type series of P. nivalis in BMNH. One of these is hereby designated as lectotype. This male specimen bears the following labels: [round BMNH label with light blue border] "Syntype" / [rectangular label] "Nikko 3.VI. - 21.VI.80" / [rectangular label with yellow horizontal line near middle] "Japan. G. Lewis 1910-320" / [rectangular label] "LECTOTYPE Pytho nivalis Lewis 1888 Design. D.A. Pollock 1987". The specimen has all appendages intact and is glued to a cardboard plate with "Nik" handwritten beneath. The remaining six specimens (five males, one female) are designated as

paralectotypes. The five males differ from the lectotype in what is written on the reverse of the cardboard plate. Four specimens have the following: "Nikk" , "Nik" , "snow 6/80" , "snow on Niohosan 6/80". One male paralectotype, which is mounted on a narrow plate has a label "Niohosan" with nothing written beneath the plate. The single female paralectotype has the following labels: [round BMNH label with light blue border] "Syntype" / [round BMNH label with orange border] "Type" / [rectangular label, 14 x 9 mm] "PYTHO nivalis Lewis Type" / [rectangular label] "Nikko 3.VI. - 21.VI.80" / [rectangular label with yellow horizontal line near middle] "Japan. G. Lewis. 1910-320" / [large red label] "PARALECTOTYPE Pytho nivalis Lewis 1888 Design. D.A. Pollock 1987". The specimen is mounted on a cardboard plate, with "Niohosan" handwritten beneath.

Seidlitz (1916) did not treat P. nivalis in his key to world species. As a note however, he correctly suggests that P. nivalis could be similar to P. kolwensis on the basis of Lewis's description of the pronotum of the former. Very few specimens of P. nivalis were examined by me and therefore limits of variation of this species are not known. The seven specimens of the type series exhibit little variation in structure and colour. Since this species is apparently very rare in Japan, the probability of studying large numbers of specimens is not great. As discussed below, under Distribution, Iablokoff-Khnzorian (1985) states that P. nivalis is known from the far eastern U.S.S.R. as well as from Japan. I have seen no specimens from the U.S.S.R. resembling the typical form of P. nivalis. One specimen, which was already determined as P. nivalis from near Ussurijsk, U.S.S.R. (ZMMU)

is included in the locality list under P. kolwensis. In all seven typical specimens of P. nivalis, the scutellum is impunctate and the elytra have a brassy, metallic lustre. In the above specimen from the U.S.S.R., the scutellum is punctate and the elytra are a non-metallic piceous colour. According to my concept of P. nivalis, which is admittedly narrow due to the scarcity of material, any records of this species from the U.S.S.R., such as in Iablokoff-Khnzorian (1985) refer to P. kolwensis.

Diagnostic combination

Adult P. nivalis may be separated from its congeners by the following characters: lateral margins of pronotum (figure 2 D) angulate and widest near middle; lateral areas of pronotum elevated above disc, and interrupted by transverse furrow; mandible abruptly bent near apex; scutellum impunctate; elytra strongly convex dorsally, piceous with brassy metallic lustre; distribution: known from Japan.

Description

TL 11.8-15.0 mm; GEW 4.3-5.5 mm; other measurements given in Table 4. **Head** with lateral, frontal areas abruptly elevated above level of disc of frons; clypeus not significantly elevated above level of frons; area of frons between eyes smooth; apical maxillomere securiform; mandibles with lateral margins evenly arcuate, abruptly bent near apex; pit on male mentum with strongly elevated margin; posterior limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 7-10; punctation uniform and fine, slightly sparser on elevated, lateral, frontal areas. **Pronotum** (figure

2 D) with posterolateral margins divergent anteriorly and almost straight to near midlength, then arcuate to anterior pronotal margin; areas laterad of depressions elevated above level of disc; anterior bead present, in some specimens weakly impressed medially; posterior bead present; pronotal depressions deep and linear, extending laterally as a sharply engraved groove interrupting lateral margins; inner margins of depressions divergent anteriorly; median line present but weakly impressed, without anterior or posterior deepenings; punctation very reduced on disc and on areas laterad of depressions; moderate within depressions. **Prosternum** with intercoxal process long, extending almost entire length of procoxae; process with strong bead; bead complete apically and laterally on process. **Mesoscutellum** impunctate in all specimens examined. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** with long, acute intercoxal process, extending almost entire length of mesocoxae; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation coarse anteromedially, reduced laterally. **Elytron** strongly convex dorsally, with nine convex intervals; tenth interval visible posterad of midlength of elytron; striae with single row of fine punctures; intervals uniformly but sparsely punctate; posterolateral margins without extra, longer pubescence. **Metasternum** with long, rounded intercoxal process, not extending to half length of mesocoxae. **Male aedeagus** (as in figure 3 D) with apicale and basale subequal in length; apicale not expanded, evenly tapered to apex; apicale narrowest apically with straight lateral margins; accessory lobes attaining apex of fused paramere. **Colour** exhibiting no variation among specimens examined; head piceous to black, dorsally; pronotum lighter, especially

TABLE 4

Measurements of selected features of samples of P. nivalis from Nikko-Niohosan, Japan. The samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter for males is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	M (6)	F (1)
EL	7.6-9.8 8.7 \pm .74	9.0
GEW	4.3-5.5 4.8 \pm .44	5.2
PL	1.9-2.6 2.2 \pm .22	2.2
GPW	2.6-3.2 3.0 \pm .23	2.9
HL	2.2-2.7 2.5 \pm .19	2.2
GHW	1.8-2.3 2.1 \pm .18	2.0
TL	11.8-15.0 13.4 \pm 1.13	13.36
GPW/PL	1.3-1.4N 1.3 \pm .04	1.3

along lateral margins; elytra rufopiceous with distinct brassy or violaceous metallic lustre; mesepisternum, mesepimeron, mesosternum and metepisternum piceous, metasternum lighter; coxae and femora piceous; mouthparts, antennae, tibiae and tarsi light rufous (lighter than dorsal colouration).

Material examined: Only seven specimens of this species were examined, and all of them are in the type series.

9.4.2 Larval Stage

The larva of P. nivalis is apparently described by Hayashi et al. (1959: 484). However, the figures for P. nivalis (Figs. A-E) are very unlike any known larva of Pytho. Because the description is in Japanese, and was not translated, I do not know whether or not it pertains to P. nivalis, or like the figures, pertains to something quite different. Subsequently, Hayashi (1969) mentions that he is describing the larva of P. nivalis for the first time, and this description is that of a typical larva of Pytho. He provides descriptions and figures, as well as a key to the larvae of the two known Japanese Pytho. Iablokoff-Khnzorian (1985), in his treatment of the larval stage of Pytho, states that he obtained the characters of the larva of P. nivalis from Hayashi et al. (1959). Therefore, the Japanese description in Hayashi et al. (1959) probably is accurate.

Diagnostic combination

Parabasal ridge processes (as in figure 11 B) short, convergent anteriorly; basal, inner urogomphal tooth larger than middle tooth (as

in figure 12 B); apical urogomphal tooth very small or absent;
 urogomphal plate sharply sloping posteriorly to urogomphal lip;
 urogomphal lip (as in figure 12 B) with posterior margin trapezoidal;
 urogomphal tubercles five to seven per side with medial gap;
 distribution: known from Japan.

Description

Head with frontal arms of epicranial suture V-shaped basally;
 antennomere 1 slender, slightly sinuate laterally; antennomere 2 not
 markedly enlarged apically; antennomere 3 noticeably narrower apically;
 ratio of antennomere lengths approximately 3.0 : 2.0 : 1.5. **Parabasal
 ridge processes** (as in figure 11 B) short, extending anterad of
 parabasal ridges by half their lengths; inner margins arcuate,
 convergent anteriorly; distance from anterior tip of process to
 posterior margin of tergites 2-7 approximately nine times length of
 process. **Parabasal setae** (as in figure 11 B) large, two per side,
 arranged sublinearly immediately posterad of parabasal ridge processes.
Urogomphus (as in figure 12 B) with basal, inner tooth large, separated
 from lateral margin of urogomphal lip by length of basal tooth; middle,
 inner tooth very small, separated from basal tooth by length of basal
 tooth; apical tooth minute; urogomphal plate sharply sloping posteriorly
 to urogomphal lip. **Urogomphal lip** (as in figure 12 B) with posterior
 margin trapezoidal, ratio of urogomphal lip width at base to length down
 midline approximately 1.6 : 1. **Urogomphal tubercles** (as in figure 12 B)
 large, uniform in size, six per side; tubercles arranged in slightly
 elliptical semicircle, with tips posteriorly directed; apical urogomphal
 tubercle with two long setae. **Ventral asperities** 18 in number, small,
 with inconspicuous longitudinal ridges.

Material examined: Unfortunately only one larva was available for examination in this study.

Association methods: The one larva used in the diagnosis and description was previously identified by Dr. N. Hayashi. However, it was verified using the description in Hayashi (1969).

9.4.3 Pupal Stage

The pupa of P. nivalis is unknown.

9.4.4 Natural History

Exceedingly little is known of the habits of this species. There have been few literature accounts of its natural history, and these provide the sole basis for the knowledge on this subject. Lewis (1888) mentions that he collected the first specimens of P. nivalis in a dense forest of "pines" (Abies) at about 7,000 feet elevation. The only other reference to a host of P. nivalis is Picea jezoensis (Kôno, 1936). Iablokoff-Khnzorian (1985) gives Pinus koreanus as a host of P. nivalis in the U.S.S.R.

9.4.5 Distribution

The exact distribution of this species is difficult to define because of the very few specimens examined (figure 18). Pytho nivalis is apparently found on the islands of Hokkaido and Honshu (Kôno 1936). Other localities are given in Hayashi (1969). Iablokoff-Khnzorian (1985) states that P. nivalis is also known from the U.S.S.R., but this

was not substantiated by me (see also Type information and taxonomic notes).

9.4.6 Chorological relationships

Pytho nivalis is presumably sympatric with P. jezoensis in Japan, but may also be sympatric with P. depressus and P. kolwensis in far eastern U.S.S.R. according to Iablokoff- Khnzorian (1985).

9.4.7 Phylogenetic relationships

See "phylogenetic relationships" for P. kolwensis.

9.5 PYTHO NIGER Kirby 1837

(figures 2 E; 4 A,B; 6 A; 7 B; 8 A; 10 A,B,C; 12 C; 19)

Pytho niger Kirby 1837: 164, plate 7, fig. 2 [**Type locality**- New York to Cumberland House. **Type repository**- BMNH]; Blair 1928: 7; Bethune 1872: 52; Böving and Craighead 1931: 194-195, plate 54 I-O (larval description); Arnett 1968: 713, fig. 1.78; 1985: 351, fig. 24.158. Pytho fallax Seidlitz 1916: 409 [**Type locality**- Pennsylvania. **Type repository**- ZMHB] **NEW SYNONYMY**. Blair 1928: 7.

9.5.1 Adult Stage

Derivation of specific epithet

The species name "niger" means "black, or darkly coloured" in Latin (Jaeger 1966), and obviously refers to the dark colour of this species. Kirby (1837) actually calls this species "black Pytho".

Type information and taxonomic notes

In the original description, Kirby (1837: 164) states that "several [P. niger were] taken in Lat. 54 and in the Journey from New York to Cumberland house." He also states that "many individuals of the present species were taken in the Expedition" (Kirby 1837: 165). Only three syntypes were located in BMNH, one of which is hereby designated as lectotype. The male specimen has the following label information: [round BMNH label with yellow border] "Co-type" / [round label] above "N. Amer. var. B"; below "5873 d" / [large, red, rectangular label]

"LECTOTYPE *Pytho niger* Kirby 1837 design. D.A. Pollock 1987." The lectotype is missing the following structures: apical nine right antennomeres, right palpi, right mesotibia and mesotarsus, left apical mesotarsomere, and left metatarsus. The specimen is pinned through a cardboard plate with a cut-off, short pin. A male and female paralectotype are also designated. The male specimen has the following label data: [round BMNH label with yellow border] "Co-type" / [round label] above: "N. Amer."; below: "5873 c" / [large red label] "PARALECTOTYPE *Pytho niger* Kirby 1837 design. D.A. Pollock 1987". The specimen is pinned through a card with an entire, small pin. The female paralectotype bears the following labels: [round label with orange border] "Type" / [round label] above: "N amer"; below: "5873 b" / [large rectangular label, 27 x 11 mm, folded in 4, with red line on reverse] "*Pytho niger* Kirby. n. amer 5873. Rev. W. Kirby" / [large red label] "PARALECTOTYPE *Pytho niger* Kirby 1837 design. D.A. Pollock 1987". The specimen is pinned onto a cardboard plate with a short, cut off pin.

A lectotype and paralectotype are also designated for *P. fallax* Seidlitz. The specimens examined by Seidlitz (1916: 408) are a female (no locality given), a male from Pennsylvania, and a male from Tewsk. [sic], Massachusetts. The specimen from Pennsylvania [ZMHB] is hereby designated as lectotype, and bears the following label data: [small green label, handwritten] "Penns." / [orange rectangular label] "Type" / [rectangular label] "16007" / [rectangular label] "v. Seidlitz det." / [long, rectangular label] "3" / [large green label, 26 x 12 mm] "fallax Seidl." (label with asterisk in upper right corner) / [large red label]

"LECTOTYPE *Pytho fallax* Seidlitz design. D.A. Pollock 1987". The male from Massachusetts (ZSM) is hereby designated as paralectotype and has the following label information: [white rectangular label] "Tewks Mass." / [small rectangular label] (handwritten word not recognizable) / [small rectangular label] "Sammlung Cl. Müller" / [large label, 18 x 9 mm with blue margin on bottom] "niger Ki" / [large red label] "PARALECTOTYPE *Pytho fallax* Seidlitz design. D.A. Pollock 1987". A female specimen from ZMHB was sent to me as a "type" and has the following labels: [large green label with light coloured reverse, 20 x 12 mm, folded in half, lengthwise] "Niger Pensylv. Knoch" / [rectangular label] "16007". This specimen could be the female that Seidlitz had seen from the Sahlberg collection. However, the label clearly shows "Pensylv." which Seidlitz would have indicated in his diagnosis. Therefore, this latter specimen is not designated as a paralectotype at this time.

In Seidlitz's (1916) key to world species of *Pytho*, his *P. niger* was in fact an undescribed species, *P. seidlitzii* Blair (see Type information and taxonomic notes for *P. seidlitzii*). As Blair (1925: 211) suggests, specimens of the true *P. niger* Kirby key out to *P. fallax* in Seidlitz's key. However, Blair (1925) states that *P. niger* Kirby and *P. fallax* Seidlitz do not agree with respect to colour of the underside and legs, "impression" of elytra (probably meaning depth of elytral striae or interneurs) body length, and deepness of thoracic impressions. Each of these characters was variable in specimens examined. Blair (1925) suggests the retention of the name *P. fallax* Seidlitz for a "well-marked variety" of *P. niger* Kirby. The type specimens of *P. fallax* occur well within the limits of variation of the true *P. niger* Kirby. Had Seidlitz

(1916) realized that the specimens of P. fallax were in fact P. niger Kirby and that his P. niger was an undescribed species, the species P. fallax would have probably not been proposed and described.

Diagnostic combination

Adults of P. niger may be recognized on the combination of the following characters: lateral margins of pronotum (figure 2 E) strongly arcuate, widest near midlength; apex of prosternal, intercoxal process (figure 6 A) incorporated into posterior bead of prosternum; posterior bead of mesosternum (figure 7 B) visible laterad of mesotrochantin; distribution: trans - Nearctic.

Description

TL 7.2-13.7 mm; GEW 2.6-5.5 mm; other measurements given in Table 5. **Head** with lateral, frontal areas variably elevated above level of disc of frons; clypeus slightly elevated above level of frons; apical maxillomere moderately securiform; mandibles with lateral margins evenly arcuate to apices; pit on male mentum with slightly elevated margin; posterior limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 8-10; punctation uniform and coarse, especially dense on elevated, lateral, frontal areas. **Pronotum** (figure 2 E) with posterolateral margins straight to arcuate to near midlength; anterolateral margins strongly arcuate to anterior margin; pronotum widest near middle; areas laterad of depressions at same level as disc; anterior bead absent; posterior bead present; pronotal depressions variable, in some specimens quite shallow and poorly defined, in others deep and well defined; inner

margins of depressions divergent anteriorly, in some specimens with additional circular depressions laterally; median line only weakly impressed; punctation coarse within depressions and slightly finer on disc and areas laterad of depressions. **Prosternum** with intercoxal process (figure 6 A) long, extending to half length of procoxae; process with bead thickened near apex, bead at same level as entire apex of procoxal process. **Mesoscutellum** with variable number of setigerous punctures. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** (figure 7 B) with long, acute intercoxal process, extending to half length of mesocoxae; posterior bead impressed laterally to margin of mesosternum; punctation coarse, with midline and lateral areas less punctate in most specimens. **Elytron** flat to slightly convex dorsally, with nine feebly convex intervals; tenth interval barely suggested; striae with single or confused double row of punctures; intervals with only scattered punctures; posterolateral elytral flange with extra pubescence. **Metasternum** with short, triangular intercoxal process, extending to about half length of mesocoxae. **Male aedeagus** (as in figure 3 D) with apicale and basale subequal in length; apicale not expanded, evenly tapered to near apex; apicale narrowest at apex, with straight lateral margins; accessory lobes variable in length, at most attaining apex of fused paramere. **Colour** with little variation among specimens examined, uniformly non-metallic piceous to black dorsally and ventrally; elytra in some specimens lighter in colour than head and pronotum; mouthparts, antennae, apex of tibiae, and tarsi dark rufous (lighter than dorsal colouration).

Material examined: In this study, 400 adults were examined.

TABLE 5

Measurements of selected features of samples of P. niger from Sandilands Provincial Forest, Manitoba, and from Lenox, Massachusetts. Samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	MANITOBA		MASSACHUSETTS	
	M (5)	F (7)	M (12)	F (12)
EL	5.4-6.2 5.8 \pm .34	5.2-8.2 6.3 \pm 1.12	6.4-7.4 6.9 \pm .29	6.2-8.4 7.6 \pm .58
GEW	3.1-3.5 3.4 \pm .20	3.2-5.5 4.0 \pm .89	3.2-4.2 3.6 \pm .33	3.2-4.5 4.0 \pm .35
PL	1.4-1.6 1.5 \pm .10	1.3-2.0 1.6 \pm .28	1.5-1.8 1.6 \pm .08	1.4-1.9 1.7 \pm .13
GPW	1.8-2.3 2.1 \pm .17	1.8-3.0 2.1 \pm .17	2.2-2.6 2.4 \pm .18	2.2-2.9 2.6 \pm .21
HL	1.3-1.6 1.5 \pm .12	1.2-1.9 1.5 \pm .28	1.6-2.1 1.9 \pm .16	1.6-2.0 1.8 \pm .14
GHW	1.2-1.5 1.4 \pm .12	1.3-1.8 1.5 \pm .23	1.5-1.8 1.6 \pm .09	1.4-1.8 1.7 \pm .12
TL	8.1-9.4 8.7 \pm .54	7.8-12.1 9.4 \pm 1.67	9.7-11.2 10.4 \pm .47	9.2-12.3 11.1 \pm .82
GPW/PL	1.4-1.5 1.4 \pm .07	1.3-1.6 1.4 \pm .09	1.4-1.6 1.5 \pm .07	1.5-1.6 1.5 \pm .04

9.5.2 Larval Stage

The larva of this species was "described" by Böving and Craighead (1931), in the form of several figures only. There is a figure of the urogomphal plate of the larva of P. niger, the caption of which erroneously reads "P. depressus", found in Smith and Sears (1982).

Diagnostic Combination

Parabasal ridge processes (as in figure 11 C) long, subparallel; basal, inner urogomphal tooth larger than middle tooth (figure 12 C); apical urogomphal tooth present; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (figure 12 C) with posterior margin slightly arcuate to truncate; urogomphal tubercles four per side with medial gap; distribution: trans - Nearctic.

Description

Head with frontal arms of epicranial suture V-shaped basally, in some specimens slightly arcuate; antennomere 1 slender, markedly sinuate laterally; antennomere 2 cylindrical, in most specimens not markedly enlarged apically; antennomere 3 cylindrical; ratio of antennal lengths approximately 1.9 : 1.5 : 1.0. **Parabasal ridge processes** (as in figure 11 C) long, extending anterad of parabasal ridge by a third their lengths; inner margins subparallel; distance from anterior tip of processes to posterior margin of tergites 2-7 approximately five times length of process. **Parabasal setae** (as in figure 11 C) variable in size, two large setae per side, posterior of parabasal ridge processes; four or five smaller setae laterad of processes. **Urogomphus** (figure 12

C) with basal, inner tooth large, separated from lateral margin of urogomphal lip by less than width of basal tooth; middle, inner tooth smaller, separated from basal tooth by slightly greater than width of basal tooth; apical tooth variable, smaller but well developed in most specimens; barely present and oriented ventrally in other individuals; urogomphal plate sharply sloping posteriorly to urogomphal lip.

Urogomphal lip (figure 12 C) with posterior margin weakly arcuate; ratio of urogomphal lip width at base to length down midline approximately 3 :

1. **Urogomphal tubercles** (figure 12 C) small, uniform in size, three to five per side; tubercles arranged in semi-ellipse, with tips directed posteriorly; apical urogomphal tubercle with one long seta. **Ventral asperities** 20 to 30 in number, small, with inconspicuous longitudinal ridges.

Material examined: Approximately 450 larvae of P. niger were examined in the course of this study.

Association methods: Association of the larva of P. niger was accomplished through rearing field-collected larvae to adults (Manitoba).

9.5.3 Pupal Stage

Diagnostic combination

At present, pupae of P. niger and P. abieticola are inseparable, except on the basis of geography. The diagnosis for pupae of these two species is as follows: pronotum widest near middle; four or five lateral marginal tubercles on tergites 2-6; usually two discal tubercles on tergites 2-6; abdominal tubercles not spade-shaped.

Description

Head with two ocular tubercles, one large and one smaller antennal denticles small, inconspicuous; anterior margin of labrum slightly emarginate. **Pronotum** with shape as in adult, lateral margins strongly arcuate, constricted anteriorly; widest near midlength; seven large, marginal tubercles per side. **Abdominal tergites 2-6** with four lateral, marginal tubercles, in some specimens with a very small tubercle between the two pairs; in most specimens two, but as many as four small, discal tubercles; two posterior marginal tubercles, the outer larger; one pleural tubercle; overall shape of dorsal abdominal tubercles evenly tapered to apex. **Abdominal sternites 2-6** with two posterior, marginal tubercles, the outer small.

Material examined: A total of 15 pupae were examined.

Association methods: Identity of pupae of this species was ascertained by rearing known larvae of P. niger to pupal and adult stages (Manitoba).

9.5.4 Natural History

Very little is published on the natural history of Pytho niger. Label data has furnished some information, as has personal observation. Records of dispersal, from label data, is as follows: window trap, 25-30.vi.1981 (Manitoba); lake shore, 6.vi.1936 (Quebec); "in flight" 8, 14.vi.1974 (Alaska); sticky trap, 1-23.v.1977 (Maine); window trap, 8-14.vi.1985 (New Hampshire); malaise trap, 23.v / 4.vi.1985 (New Hampshire). Adults were collected under bark in pupal cells on the

following dates: 26.ix.1985, 5.x.1986, 15.iv.1987 (Manitoba); 16.v.1987 (Saskatchewan). Teneral adults were collected in pupal cells on 12.viii.1986 (Manitoba). Teneral adults were seen from Pennsylvania, 15.ix. Pupae and large larvae were collected in Ontario on 28.vii.1986. From the above information, it is possible to hypothesize that P. niger has a dispersal period beginning in early to mid May and extending to late June. Adults that do not emerge by this time stay beneath the bark within their pupal cells and overwinter there. Generally, P. niger adults are not found within the pupal cells during the early summer months. This type of life cycle is probably not unique to P. niger, but rather a strategy for all Pytho species (at least those in North America).

According to label data and my own observations, P. niger has a moderate range of host acceptability: Pinus strobus L. (Massachusetts, Maine, New York), P. banksiana Lamb. (Manitoba, Saskatchewan), P. contorta Dougl. (Alberta), Picea mariana (Mill.) B.S.P. (Manitoba), Picea sp. (Alberta, Manitoba, Northwest Territories), Abies balsamea (L.) Mill. (Manitoba), Abies sp. (Quebec).

9.5.5 Distribution

Pytho niger occurs across North America without significant gaps longitudinally (figure 19). The northern limit of the range probably follows the tree line quite closely. To the south, the limit is fairly-well defined, from southern New York to mid-Wisconsin. No specimens were seen from the conterminous United States west of Isanti Co., Minnesota. Surprisingly, there is only one record of P. niger from

British Columbia. The numerous records of this species from eastern North America may be a consequence of collecting bias rather than relative abundance.

9.5.6 Chorological relationships

Pytho niger is widespread across North America and is therefore broadly sympatric throughout its range with P. seidlitzi and P. planus. Pytho niger also co-occurs with P. strictus in eastern North America.

9.5.7 Phylogenetic relationships

Pytho niger belongs to the P. niger-group, along with P. abieticola and P. jezoensis. The exact relationships among these three species is yet undetermined, but may be deduced from the zoogeographic analysis.

9.6 PYTHO ABIETICOLA J. Sahlberg 1875

(figures 2 F; 7 A,C,D; 11 C; 13 B; 20)

Pytho abieticola J. Sahlberg 1875:222 [**Type locality**- Ruovesi, Finland.

Type repository- ZMH] Blair 1928: 4; Burakowski 1962: 193,195 (key to all stages of Polish species); Kaszab 1969: 95 [key to European species (adults)]; Burakowski 1976: 14, 15, 16 (key to species in all stages); Pettersson 1983: 28, fig. 5 (natural history and larval diagnosis); Iablokoff-Khnzorian 1985: 205 (revision of Palearctic species).

Pytho niger : J. Sahlberg 1892: 236, et auct. (nec Kirby 1837).

9.6.1 Adult Stage

Derivation of specific epithet

The species name abieticola is derived from the genitive of the Latin words "abietis" meaning "name of the fir-tree", and "colo" meaning "to inhabit" (Jaeger 1966). This refers to the original collection of this species by J. Sahlberg, from a dead fir tree (Picea abies).

Type information and taxonomic notes

In the original description, Sahlberg states that four adults were collected from a fir tree on the margin of a fen called Sūkaneva, in the "district" of Ruovesi. He also collected numerous mature larvae, two of which pupated and later eclosed. Therefore, the adult type material of this species consists of the original four adults plus the two subsequently obtained through rearing.

"Type" specimens of *P. abieticola* were borrowed from TMB, ZMH, and DBTU. The single specimens from ZMH and DBTU have the label "Spec. typ.", while the specimen from TMB is labelled as "ind. typ." I have been unable to find the meaning of these labels, and their differences (if any) in importance with respect to type designation. S. Koponen, DBTU (pers. comm.) states that normally, the types in the Sahlberg collection are labelled "Spec. typ". He also speculates that the specimen in TMB labelled "ind. typ" has been identified by comparing it with the Sahlberg type. Since all three specimens examined were collected at the type locality, and no clear designation of a type specimen exists in the original description, I feel that all three are equivalent in value for designation of a lectotype. I chose the specimen from ZMH as the lectotype for the following reasons: all appendages are intact, it is a male, and is housed in ZMH, with which J. Sahlberg was apparently associated.

The male lectotype bears the following labels: [small rect. label] "Ruovesi" / [small rect. label] "J. Sahlbg." / [small rect. label] "Spec. typ." / [large rect. label] "Mus. Zool. H:fors Spec. typ. No (558 Pytho abieticola J. Sbg.) [parts in parentheses handwritten] / [large, red, rectangular label] "LECTOTYPE Pytho abieticola J. Sahlberg 1875 design. D.A. Pollock 1988". The specimen is straight-pinned and is missing no external structures. One of the paralectotypes (DBTU) is labelled as follows: "Ruovesi" / "J. Sahlb." / "Spec. typ." / "387 ." / "Coll Sahlb." / [PARALECTOTYPE Pytho abieticola J. Sahlberg 1875 design. D.A. Pollock 1988]. This specimen is a female; the left antenna missing distad of the scape. It is also straight-pinned. The second

paralectotype is labelled as follows: "Ruovesi" / "Fennia" [this label not original] / "J. Sahlb. ind. typ." / "Paratypus 1875 Pytho abieticola J. Sahlberg" / "Pytho abieticola J. Sahlb." / "P. niger Kirby Coll. Reitter" / [PARALECTOTYPE Pytho abieticola J. Sahlberg 1875 design. D.A. Pollock 1988]. This specimen is a male, and is glued to a cardboard plate. It was evidently pinned originally because of a hole in the right elytron. It is missing the following structures: entire left antenna, left front leg at trochanter, right hind leg at trochanter, left hind tarsus, and the entire left half of the abdomen (could be insect pest damage).

Diagnostic combination

Adult P. abieticola possess the following diagnostic features: lateral margins of pronotum (figure 2 F) strongly arcuate, widest near midlength; mesosternum (figure 7 C) in most specimens impunctate, or with only several large punctures; legs rufous, contrasting and lighter in colour than elytra; distribution: known from Europe and possibly the U.S.S.R. (Iablokoff-Khnzorian 1985).

Description

TL 5.6-10.6 mm; GEW 1.9-4.2 mm; other measurements given in Table 6. **Head** with lateral, frontal areas slightly elevated above level of disc of frons; clypeus not significantly elevated above frons; area of frons between eyes not, or only slightly elevated longitudinally; apical maxillomere variable; in some specimens, only feebly expanded apically; in others, securiform; mandibles with lateral margin evenly arcuate to apices; pit on male mentum with very slightly elevated margin; posterior

limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 8-10; punctation variable in density; reduced on elevated, lateral, frontal areas, and on disc of frons. **Pronotum** (figure 2 F) with lateral margins arcuate from base to anterior margin; in some specimens, posterolateral margins straight, almost cordiform; areas laterad of depressions at same level as disc in most specimens; pronotum widest near middle; anterior bead absent; posterior bead present; pronotal depressions variable; in most species, depressions shallow and oval, with inner margins anteriorly divergent; some specimens with each depression divided into two distinct impressions; some specimens with depressions reduced to slight concavities only; median line absent to weakly impressed; punctation dense and coarse in and around depressions, reduced along midline and on areas laterad of depressions. **Prosternum** with intercoxal process short, extending to less than half length of procoxae; process with weakly developed bead; bead complete laterally and nearly complete apically, on process. **Mesoscutellum** with variable number of setigerous punctures. **Mesepisternum** with inner margin impunctate in some specimens, other areas uniformly, coarsely punctate. **Mesepimeron** (figure 7 D) in most specimens uniformly, coarsely punctate; in some individuals, punctures restricted to lateral margin only. **Mesosternum** (figure 7 C) with intercoxal process long, slender, extending posterior of half length of mesocoxae; posterior bead not impressed laterad of anterior margin of mesocoxal cavity; punctation reduced to six or less medial, punctures; on some specimens impunctate. **Elytron** depressed to slightly convex dorsally, with nine moderately convex intervals; striae with single or confused double row of punctures; intervals with only scattered

TABLE 6

Measurements of selected features of samples of P. abieticola from various localities in Finland and from Kulbäcksliden, Sweden. Samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	FINLAND		SWEDEN	
	M (7)	F (3)	M (10)	F (10)
EL	4.8-5.8 5.3 ± .39	5.4-6.8 6.2 ± .76	3.8-6.2 5.0 ± .75	4.7-7.3 5.7 ± .91
GEW	2.7-3.3 3.1 ± .21	3.0-3.8 3.4 ± .41	1.9-3.7 2.8 ± .50	2.5-4.2 3.2 ± .58
PL	1.1-1.4 1.2 ± .09	1.2-1.4 1.4 ± .14	0.88-1.35 1.11 ± .15	0.96-1.60 1.26 ± .19
GPW	1.6-1.9 1.8 ± .11	1.8-2.2 2.1 ± .21	1.3-2.1 1.7 ± .26	1.6-2.5 2.0 ± .31
HL	1.0-1.4 1.3 ± .13	1.1-1.6 1.4 ± .26	0.88-1.52 1.3 ± .19	1.04-1.76 1.4 ± .27
GHW	1.1-1.4 1.2 ± .09	1.2-1.5 1.4 ± .17	0.88-1.44 1.2 ± .17	1.04-1.60 1.3 ± .19
TL	7.0-8.6 7.8 ± .56	7.7-9.8 9.0 ± 1.14	5.6-9.0 7.4 ± 1.06	6.7-10.6 8.4 ± 1.36
GPW/PL	1.4-1.5 1.5 ± .06	1.5-1.6 1.5 ± .03	1.5-1.6 1.5 ± .07	1.5-1.7 1.6 ± .07

punctures; posterolateral elytral flange without extra pubescence.

Metasternum with short, triangular intercoxal process; apex of process blunt, extending less than half length of mesocoxae. **Male aedeagus** (as in figure 3 D) with apicale subequal in length to basale; apicale not expanded, evenly tapered to near apex; apicale narrowest subapically, with straight lateral margins; accessory lobes attaining apex of fused paramere, or slightly beyond. **Colour** with little variation among specimens examined; uniformly, non-metallic brown to piceous, dorsally and ventrally; elytra in most specimens lighter in colour than head and pronotum; mouthparts and antennae dark rufous (lighter than dorsal colouration); legs light rufous; in some specimens, legs and mouthparts similar in colouration.

Material examined: 46 adults of this species were examined in the course of this revision.

9.6.2 Larval Stage

The larva of P. abieticola was described by J. Sahlberg (1875). It has been illustrated or redescribed by Burakowski (1962, 1976) and Pettersson (1983).

Diagnostic combination

Parabasal ridge processes (figure 11 C) long, subparallel; basal, inner urogomphal tooth larger than middle tooth (as in figure 12 C); apical urogomphal tooth present; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (as in figure 12 C) with posterior margin slightly arcuate to truncate; urogomphal tubercles four

per side with medial gap; distribution: known from Europe and possibly the U.S.S.R. (Iablokoff- Khnzorian 1985).

Description

Head with frontal arms of epicranial suture V-shaped basally, variably arcuate in some specimens; antennomere 1 slender, slightly sinuate laterally; antennomere 2 feebly enlarged apically; antennomere 3 cylindrical; ratio of antennomere lengths approximately 2 : 2 : 1. **Parabasal ridge processes** (figure 11 C) long, extending anterad of parabasal ridge by a third their lengths; inner margins subparallel; distance from anterior tip of process to posterior margin of tergites 2-7 approximately five times length of process. **Parabasal setae** (figure 11 C) variable in size, two large setae per side, posterior of parabasal ridge processes; from one to three smaller setae laterad of processes. **Urogomphus** (as in figure 12 C) with basal, inner tooth large, separated from lateral margin of urogomphal lip by width of basal tooth; middle, inner tooth smaller, separated from basal tooth by slightly greater than width of basal tooth; apical tooth variable, in most specimens small, but sharp; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (as in figure 12 C) with posterior margin truncate to weakly arcuate; ratio of urogomphal lip width at base to length down midline approximately 3.7 : 1. **Urogomphal tubercles** (as in figure 12 C) small, four or five per side; tubercles arranged in semi-ellipse, with tips directed posteriorly; apical tubercle with one long seta. **Ventral asperities** 17 to 30 in number, small, with inconspicuous longitudinal ridges.

Material examined: Fourteen larvae of this species were examined.

Association methods: Borrowed larvae were previously identified. The identity of these specimens was verified by consulting the literature (Burakowski 1962; Pettersson 1983).

9.6.3 Pupal Stage

The pupa of *P. abieticola* was described and illustrated by Burakowski (1976).

Diagnostic combination

See diagnostic combination for pupae of *P. niger* Kirby.

Description

Head with single, ocular tubercle; antennal denticles small but conspicuous; anterior margin of labrum slightly emarginate. **Pronotum** (figure 13 B) with shape as in adult, lateral margins strongly arcuate, constricted anteriorly; widest near midlength; seven to 10 large, marginal tubercles. **Abdominal tergites 2-6** (figure 13 B) with four lateral, marginal tubercles; two small, discal tubercles; two posterior, marginal tubercles, the outer tubercle much larger; one pleural tubercle present; overall shape of dorsal abdominal tubercles evenly tapered to apex. **Abdominal sternites 2-6** with two posterior, marginal tubercles, the outer tubercle indistinct.

Material examined: Two pupae were examined in this study.

Association methods: The two pupae examined were reared from larvae by R. Pettersson, and were compared to figures and descriptions in Burakowski (1976).

9.6.4 Natural History

Pytho abieticola is exclusively a spruce beetle (Saalas 1917; Pettersson pers. comm.) and demands fairly dry and sun-exposed habitats. An example of a typical habitat for P. abieticola (Pettersson pers. comm.) is a Picea abies tree which has been dead for about three or four years and which is leaning against another tree. It is found most often in primeval forests. Saalas (1917) lists the following preferences for P. abieticola: swampy habitats, trees lying horizontally, with trunks 6 to 25 cm in diameter. The tree is usually rotting, but still reasonably "fresh". This species probably does not differ significantly from the general life cycle given in Chapter III. Pytho abieticola is considered as very rare, at least in Finland (Pettersson pers. comm.).

9.6.5 Distribution

According to label data, P. abieticola is known from Austria, Finland, Poland, and Sweden (figure 20). There is a recent new collection of this species from Czechoslovakia (Maca et al. 1984) and the first record of P. abieticola from Sweden has been obtained by Pettersson (pers. comm.). Detailed regional records of the Fennoscandian distribution of this species are given in Grill (1896), Saalas (1917), Lindroth (1960), and Silfverberg (1979). Iablokoff-Khnzorian (1985: 205) states that P. abieticola is found in the mountains of central Europe, Scandinavia and the Russian taiga. However, no specimens from the U.S.S.R. were examined in this study.

9.6.6 Chorological relationships

Pytho abieticola is broadly sympatric with P. depressus over the entire range of the former, which is also sympatric with P. kolwensis in Fennoscandia and Siberia.

9.6.7 Phylogenetic relationships

Pytho abieticola is allied with P. niger and P. jezoensis, but as of yet, this relationship remains unresolved.

9.7 PYTHO JEZOENSIS Kôno 1936

(figures 2 G; 21)

Pytho jezoensis Kôno 1936: 36 [**Type locality** -Japan, Hokkaido, Jozankei.

Type repository -HUS] Hayashi 1969: 7, plate VI, O-P (description of larva); Iablokoff-Khnzorian 1985: 205 (key to world species, natural history).

9.7.1 Adult Stage

Derivation of specific epithet

Kôno collected the type specimens of this species in association with Picea jezoensis.

Type information and taxonomic notes

Kôno (1936: 37) examined six individuals of the type series and designated a male holotype, four male paratypes, and one female "allotopotype". Two male specimens were received from HUS, with the holotype bearing the following label data: [rectangular label] above: "Hokkaido H. Kôno" /below: Jozankei 1935 VI/2" / [large pink/orange label] "Pytho jezoensis Kôno Type" (the biological symbol for "male" appears in the upper right corner) / [large yellow label] "Picea jezoensis d. 25C711 (Japanese handwriting)" / [large, red, label] "HOLOTYPE Pytho jezoensis Kôno 1936 examined by D.A. Pollock 1987". The holotype is in good condition with no missing structures. The right flight wing is exposed and folded across the left elytron, and the

genitalia are extruded and pointing anteriorly. The male paratype has the same data as holotype. Another male paratype from the Kôno collection was not loaned by HUS and consequently it was not examined.

Iablokoff-Khnzorian (1985) obviously examined the holotype because he includes the oddly-extruding genitalia of this specimen as a taxonomic character separating *P. jezoensis*. This condition is undoubtedly abnormal, and therefore, cannot be used as a taxonomic character.

Diagnostic combination

Adult *P. jezoensis* may be separated from the rest of the genus by the following combination of characters: lateral margins of pronotum (figure 2 G) strongly arcuate, widest near middle; antennomeres 7-10 with sensilla at their apices; metasternal, intercoxal process blunt, truncate apically; distribution: known from Japan.

Description

TL 7.8-13.4 mm; GEW 3.0-5.0 mm; other measurements given in Table 7. **Head** with lateral, frontal areas slightly elevated above level of disc of frons; clypeus slightly elevated above level of frons; area on frons between eyes with two poorly defined impressions separated by raised area; apical maxillomere securiform; mandibles with lateral margins evenly arcuate to apices; pit on male mentum with slightly elevated margin; posterior limit of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 7-10; punctation fine, scattered; sparser on elevated, lateral, frontal areas. **Pronotum** (figure 2 G) with lateral margins arcuate through entire length

in most specimens; in some specimens, lateral margins at maximum width almost truncated; areas laterad of depressions at same level as disc; pronotum widest near middle; pronotal depressions variable in depth, oval; in most specimens only moderately deep; inner margins of depressions divergent anteriorly; some specimens with lateral subcircular impressions also; anterior bead absent in most specimens; feebly defined anterior bead present medially in some individuals; posterior bead present; median line deeply impressed; punctation heavy on median area, lighter in depressions and near the anterior and posterior margins. **Prosternum** with long intercoxal process, extending at least half length of procoxae; process with strong bead; bead complete apically and laterally on process. **Mesoscutellum** with variable number of setigerous punctures, in most specimens less than five. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** with long, acute intercoxal process, extending about half length of mesocoxae; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation very coarse anteromedially, reduced on extreme lateral regions. **Elytron** depressed to slightly convex dorsally with nine moderately convex intervals; striae with single or confused double row of punctures; intervals with only scattered punctures; posterolateral elytral flange without extra, longer pubescence. **Metasternum** with short intercoxal process, extending to less than half length of mesocoxae; apex of process truncate, in some specimens rounded and blunt. **Male aedeagus** (as in figure 3 D) with apicale subequal in length to basale; apicale not expanded, evenly tapered to near apex; apicale narrowest subapically, with straight to slightly sinuate lateral margins; accessory lobes attaining apex of

TABLE 7

Measurements of selected features of samples of P. jezoensis from various localities in Japan. The samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	M (5)	F (5)
EL	5.0-7.9 6.5 \pm 1.02	8.2-9.0 8.8 \pm .34
GEW	3.0-4.7 3.8 \pm .62	4.6-5.0 4.8 \pm .22
PL	1.4-2.0 1.7 \pm .23	1.9-2.2 2.1 \pm .13
GPW	1.8-2.9 2.3 \pm .37	2.8-3.2 3.0 \pm .17
HL	1.4-2.2 1.8 \pm .26	1.9-2.2 2.0 \pm .09
GHW	1.4-2.0 1.6 \pm .23	1.8-2.0 1.9 \pm .09
TL	7.8-12.1 9.9 \pm 1.51	12.0-13.4 12.9 \pm .53
GPW/PL	1.3-1.4 1.4 \pm .05	1.4-1.5 1.4 \pm .05

fused paramere, or slightly beyond. **Colour** exhibiting little variation among the few specimens examined; uniformly non-metallic piceous dorsally and ventrally; elytra lighter in colour than head and pronotum in some individuals; mouthparts, antennae, tibiae and tarsi rufous; abdomen lighter than venter of thorax in some specimens.

Material examined: I examined 10 adults of this species.

9.7.2 Larval Stage

Diagnostic combination

Parabasal ridge processes (as in figure 11 C) long, subparallel; basal, inner urogomphal tooth larger than middle tooth (as in figure 12 C); apical urogomphal tooth present; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (as in figure 12 C) with posterior margin slightly arcuate to truncate; four urogomphal tubercles per side, with medial gap; distribution: known from Japan.

Description

Head with frontal arms of epicranial suture V-shaped basally, slightly arcuate; antennomere 1 slender, markedly sinuate laterally; antennomere 2 enlarged apically; antennomere 3 cylindrical; ratio of antennomere lengths approximately 1.3 : 1.2 : 0.8. **Parabasal ridge processes** (as in figure 11 C) long, extending anterad of parabasal ridge by a third their lengths; inner margins subparallel; distance from anterior tip of process to posterior margin of tergites 2-7 approximately four times length of process. **Parabasal setae** (as in

figure 11 C) variable in size, two large setae per side, posterad of parabasal ridge processes; one to three smaller setae. **Urogomphus** (as in figure 12 C) with basal, inner tooth large, separated from lateral margin of urogomphal lip by less than width of basal tooth; middle, inner tooth smaller, separated from basal tooth by width of basal tooth; apical tooth smallest, but well-developed; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (as in figure 12 C) with posterior margin weakly arcuate; ratio of urogomphal lip width at base to length down midline approximately 3 : 1. **Urogomphal tubercles** (figure 12 C) small, uniform in size, four per side; tubercles arranged in semi-ellipse, with tips directed posteriorly; apical urogomphal tubercle with one long seta. **Ventral asperities** 28 in number, small, with inconspicuous longitudinal ridges.

Material examined: Only one larva was available for study.

Association methods: The single larva was previously identified by Dr. N. Hayashi. Its identity was verified using the description in Hayashi (1969).

9.7.3 Pupal Stage

The pupa of P. jezoensis is unknown.

9.7.4 Natural History

Very little is published, or is known, about the natural history of this species. Presumably, the basic life cycle differs little from the hypothesized general life cycle, given in Chapter III. Host trees for

P. jezoensis include Picea jezoensis (Kôno 1936), and Tsuga sieboldi Carrière (label data).

9.7.5 Distribution

Pytho jezoensis is apparently restricted to the Japanese islands (figure 21). Determination of the exact distribution in Japan is difficult because I was unable to locate many of the localities from both label data and the literature, in atlases. Therefore, this species is undoubtedly more widespread in Japan, than indicated in figure 21. Kôno (1936) collected the original specimens on Hokkaido, and additional localities are given in Hayashi (1969). I have also examined specimens from Honshu.

9.7.6 Chorological relationships

Pytho jezoensis is sympatric with P. nivalis, but the extent of this sympatry is not known completely, due to problems in interpretation of the locality data from both specimens examined and from the literature. The two species are known from several identical localities.

9.7.7 Phylogenetic relationships

Pytho jezoensis is part of an unresolved trichotomy with P. niger and P. abieticola. These three species are part of the P. niger species-group.

9.8 PYTHO PLANUS (Olivier 1795)

(figures 2 H; 3 D,E; 5 B,C,D; 8 C,D; 9; 12 D; 13 A; 22)

Tenebrio planus Olivier 1795 (No. 57): 14, plate II, fig. 17 [**Type**

locality- "Caroline méridionale." **Type repository**- unknown, type not seen]; Horn 1886: 138; Blair 1928: 5; Smith 1910: 367.

Pytho americanus Kirby 1837:165 [**Type locality**- New York to Cumberland House. **Type repository**-BMNH]; Blair 1928: 5; Mannerheim 1843: 268; LeConte 1866: 168; Bethune 1872: 52-53; Provancher 1877; Horn 1886: 138; Fauvel 1889: 155; Hamilton 1889: 152, 1890: 44; Brimley 1938: 162 (distribution); Hatch 1965: 85, plate XII, fig. 1; Ring and Tesar 1980: 763-774 (natural history); Ring 1982: 605-612 (natural history). **NEW SYNONYMY.**

Pytho deplanatus Mannerheim 1843: 268 [**Type locality**- Kwych-pach (Yukon River, Alaska). **Type repository**- Leningrad]; Blair 1928: 5; Lewis 1888: 108; Hamilton 1889: 55; Fauvel 1889: 55; Hamilton 1894b: 401; Ring 1982: 605-612 (natural history); Iablokoff-Khnzorian 1985: 205 (revision of Palearctic species). **NEW SYNONYMY.**

Pytho depressus : Hamilton 1894a: 33, 1894b: 401 (nec Linnaeus 1767).

Pytho depressus : Blatchley 1910 (nec Linnaeus 1767)

9.8.1 Adult Stage

Derivation of specific epithet

The name "planus" is derived from the Latin word for "flat, level, or even" (Jaeger 1966). This undoubtedly refers to the dorsally flattened body in this species.

Type information and taxonomic notes

Tenebrio planus Olivier, 1795 is given as a synonym of P. americanus Kirby by Blair (1928: 5). However, Blair (1928) may have been uncertain of the proposed status because he placed a question mark before the former species name. From the original description and figure of T. planus, it is indeed a Pytho. The translated description is as follows: "This insect has a close relationship with the Tenebrio depressus of Linné, and might be one variety of it. It is elongated and depressed. The antennae are moniliform, reddish. The head is black with a ferruginous mouth; the pronotum is rounded, flat, ferruginous, with two sunk-in markings. The outer wings are streaked [striate], ferruginous at the base, of dark dark blue colour in their posterior half. The legs are reddish. We find it in southern Carolina. From the cabinet of Mr. d'Orcy." Although the type of T. planus Olivier was not examined, it is my opinion that this name should have priority over P. americanus Kirby according to the provisions of Article 23 of the ICZN (1985).

Two syntypes of P. americanus from BMNH were examined, one of which is hereby designated as LECTOTYPE. The female lectotype bears the following label information: [round BMNH type label with yellow margin]

"Co-type" / [round label] above "N. Amer", below "5874 b" / [red Lectotype label] "LECTOTYPE *P. americanus* Kirby 1837 design. D.A. Pollock 1987". The specimen has the following identifying features: last 3 left antennomeres missing, last 5 right antennomeres missing; right metatarsus missing; elytra blue with purplish metallic tinge; head and pronotum piceous; legs and venter testaceous; mouthparts and antennae rufous [specimen conforms to variety "A" of Kirby (1837: 165)].

Historically, there has been much taxonomic confusion among *P. deplanatus* Mannerheim, *P. americanus* Kirby, and *P. depressus* (Linnaeus). The latter two species are quite variable in colouration, which has led to a number of named varieties of each. The varieties of *P. depressus* were given separate names, while those of *P. americanus* were merely given letters, by Kirby (1837). Kirby (1837) realized that *P. americanus* resembled *P. depressus*, but says that the former is wider in proportion to length and has the abdomen and meso- and metathorax invariably rufous. Horn (1888: 46) synonymized *P. americanus* with *P. deplanatus* and mentioned that the specimen seen by Mannerheim (1843) is merely an immature individual of *P. americanus*. He also states that *P. americanus* represents, and may be identical to, *P. depressus*. Hamilton's (1889: 152) comments regarding these three species are similar to those of Horn (1888). While *P. americanus* and *P. depressus* are very similar, they are not synonymized. Hamilton (1890:44) proposes *P. americanus* Kirby as a variety of *P. depressus* (L.) and in essence synonymizes these two species. Hamilton (1894a: 33) restated that *P. deplanatus* was considered a synonym of *P. americanus* Kirby, but he mentions that "a comparison of examples is necessary to establish this".

Further, it is again written by Hamilton (1894a) that P. americanus is identical to P. depressus. In his catalogue of the Coleoptera common to North America, northern Asia and Europe, Hamilton (1894b: 401) synonymizes P. depressus, P. americanus, and P. deplanatus. Seidlitz (1916) examined specimens of P. deplanatus from Quichpack (type), Canada, Lake Superior, and the northern shore of Lake Baikal. In his key, Seidlitz (1916) separates all three species of this complex on the bases of elytral punctation, colour, and relative length and width of the body. Each of these characters, however, is quite variable. Iablokoff-Khnzorian (1985) who also saw the type specimen of P. deplanatus synonymized it with P. depressus, and stated that the type of deplanatus is a typical member of P. depressus.

In the present treatment, the only useful character (apart from geography) to separate adults of P. planus and P. depressus is the relative lengths of the basale and apicale of the male genitalia (figure 3 D, F). I have not had the opportunity to examine the type specimen of P. deplanatus, apparently a female (Iablokoff-Khnzorian 1985) but I have a specimen from Lake Superior that was seen by Seidlitz (1916). This specimen may be teneral, and has all the characters attributed to P. planus and P. depressus. It is however, a female and cannot be checked for the male genitalic character. The concept of P. deplanatus sensu Seidlitz (1916) is far too broad, and is weakly based on very variable characters. Mannerheim (1843) described P. deplanatus from Alaska, and this falls in the geographic range of P. planus rather than P. depressus (as these species are currently defined). I believe that P. deplanatus Mannerheim should be a junior synonym of P. planus.

(Olivier) and not of P. depressus (L.) as given by Iablokoff-Khnzorian (1985).

Diagnostic combination

Adult P. planus are diagnosed on the basis of the following combination of characters: lateral margins of pronotum (figure 2 H) weakly arcuate, widest anterad of midlength; elytra with slight to strongly metallic lustre; aedeagus (figure 3 D) with apicale and basale subequal in length; distribution: trans - Nearctic.

Description

TL 7.1-14.8 mm; GEW 2.3-6.1 mm; other measurements given in Table 8. **Head** with lateral, frontal areas slightly elevated above level of disc of frons; clypeus not significantly elevated above level of frons; area on frons between eyes with poorly defined, shallow depressions in some specimens; apical maxillomere securiform (figure 5 B); mandibles with lateral margins evenly arcuate to apices; pit on male mentum (figure 5 C, D) not, or slightly elevated; posterior limit of pit anterior of suture between mentum and submentum; in some specimens anterior pit with margin coalesced with suture between mentum and submentum; antennae with sensilla on apices of antennomeres 7-10; punctation uniform and coarse, especially behind eyes; lighter on elevated, lateral, frontal areas. **Pronotum** (figure 2 H) with posterolateral margins weakly arcuate, sides not markedly constricted anteriorly; in some specimens, sides subparallel; areas laterad of depressions at same level as, or slightly lower than disc; pronotum widest anterad of middle; anterior bead absent; posterior bead present; pronotal depressions variable in depth,

oval, with inner margins subparallel or slightly divergent anteriorly; in some specimens, depressions divided into two separate impressions; median line weakly to strongly impressed; punctation reduced along median line, very coarse in depressions, coarse on areas laterad of depressions. **Prosternum** with short intercoxal process, extending less than half length of procoxae; process with strong bead; bead complete apically and laterally on process. **Mesoscutellum** impunctate or with variable number of setigerous punctures. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** with short, very acute intercoxal process, extending less than half length of mesocoxae; posterior bead not impressed laterad of inner margin of mesotrochantin; punctation light, absent down midline and on lateral areas. **Elytron** depressed dorsally, with nine weakly convex intervals; striae with confused double row of punctures; intervals with few random punctures only; posterolateral elytral margin (figure 8 C) with extra, longer pubescence. **Metasternum** with short intercoxal process, barely extending between mesocoxae; apex of process blunt. **Male aedeagus** (figure 3 D, E) with apicale subequal in length to basale; apicale not expanded, evenly tapered to near apex; apicale narrowest subapically, with straight lateral margins; accessory lobes attaining apex of fused paramere in most specimens. **Colour** quite variable among specimens examined; dorsally, head ranging from light rufous to black with palpi and antennae always rufous; pronotum non-metallic light rufous to dark piceous/black, in majority of specimens unicolourous; in some lighter-coloured individuals, lateral margins may be darker than disc; elytra ranging from rufous to piceous or black; when rufous, elytra with slight but distinct violaceous

TABLE 8

Measurements of selected features of samples of P. planus from Wakefield, Quebec and Aklavik, Northwest Territories. Samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	QUEBEC		NORTHWEST TERRITORIES	
	M (7)	F (7)	M (10)	F (10)
EL	6.4-7.9 7.1 \pm .50	7.6-9.4 8.5 \pm .60	4.6-6.6 5.8 \pm .68	6.6-8.6 7.7 \pm .63
GEW	4.0-4.6 4.2 \pm .26	4.5-5.4 4.9 \pm .29	2.3-3.5 3.1 \pm .36	2.9-4.6 3.6 \pm .48
PL	1.8-2.2 1.9 \pm .12	2.0-2.32 2.2 \pm .10	1.2-1.7 1.5 \pm .13	1.4-2.0 1.8 \pm .16
GPW	2.6-3.0 2.8 \pm .15	2.9-3.5 3.2 \pm .20	1.7-2.3 2.1 \pm .19	2.3-3.0 2.6 \pm .19
HL	1.9-2.2 2.0 \pm .08	2.0-2.4 2.2 \pm .14	1.4-1.8 1.7 \pm .16	1.7-2.3 2.0 \pm .20
GHW	1.9-2.2 2.0 \pm .11	2.0-2.3 2.1 \pm .12	1.3-1.7 1.5 \pm .12	1.6-2.0 1.8 \pm .15
TL	10.3-12.2 11.1 \pm .66	11.6-14.2 12.8 \pm .81	7.1-10.0 9.0 \pm .93	9.8-12.9 11.4 \pm .97
GPW/PL	1.4-1.6 1.4 \pm .07	1.4-1.5 1.5 \pm .03	1.3-1.5 1.4 \pm .05	1.5-1.6 1.5 \pm .05

metallic sheen; if darker piceous or black, elytra often with vivid metallic blue, green, or violet lustre; epipleuron rufous; ventral surface entirely rufous to piceous; in some specimens, metasternum and abdomen lighter in colour than remainder of ventral surface; legs invariably rufous, tibiae and tarsi of most individuals darker than femora.

Material examined: I examined 1013 adults of this species.

9.8.2 Larval Stage

Diagnostic combination

Parabasal ridge processes (figure 9A; as in figure 11 D) very long, subparallel; basal, inner urogomphal tooth subequal in size to, or smaller than, middle tooth (figure 12 D); apical urogomphal tooth present; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (figure 12 D) with posterior margin weakly arcuate to truncate; urogomphal tubercles with tips directed anteriorly, arranged in uninterrupted, anteriorly truncated semi-ellipse; distribution: trans - Nearctic.

Description

Head with frontal arms of epicranial suture U-shaped basally, in some specimens V-shaped; antennomere 1 slender, sinuate laterally; antennomere 2 slightly enlarged apically; antennomere 3 cylindrical; ratio of antennomere lengths approximately 2.0 : 1.7 : 1.0. **Parabasal ridge processes** (figure 9 A) very long, extending anterad of parabasal

ridge by a sixth their lengths; inner margins subparallel; distance from anterior tip of process to posterior margin of tergites 2-7 approximately three times length of process. **Parabasal setae** (as in figure 11 D) variable in size, four to seven per side, arranged posterad and laterad of parabasal ridge processes; posterior setae longer than lateral setae. **Urogomphus** (figure 12 D) with basal, inner tooth small, separated from lateral margin of urogomphal lip by slightly greater than width of basal tooth; middle, inner tooth slightly larger than, or subequal in size to basal tooth; middle tooth separated from basal tooth by four times length of basal tooth; apical tooth present, ventral; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (figure 12 D) with posterior margin weakly arcuate, straight in some specimens; ratio of urogomphal lip width at base to length down midline approximately 2.9 : 1. **Urogomphal tubercles** (figure 12 D) small, uniform in size, six to nine per side; tubercles arranged in anteriorly truncate semi-ellipse without medial gap; tips of tubercles directed anteriorly; apical urogomphal tubercle with one long seta; some specimens, row truncated anteriorly; tubercles 12-18 in number. **Ventral asperities** 18 to 25 in number, small, with inconspicuous longitudinal ridges.

Material examined: Approximately 550 larvae of this species were examined.

Association methods: Positively associated larvae were obtained by rearing several field-collected larvae to adult. Subsequently collected larvae were compared with these exuviae.

9.8.3 Pupal Stage

Diagnostic combination

Pupae of P. planus are separable from P. depressus on the basis of the former having one large lateral marginal tubercle on sternites 2-6; a second tubercle, if present, much smaller. Since the number of pupae of P. depressus was small (three), this diagnostic character should be examined further.

Description

Head with single, ocular tubercle; antennal denticles small, inconspicuous; anterior margin of labrum slightly emarginate. **Pronotum** (figure 13 A) with shape as in adult, lateral margins weakly arcuate, not constricted anteriorly; widest anterad of midlength; 10 marginal tubercles. **Abdominal tergites 2-6** (figure 13 A) with five lateral, marginal tubercles, rarely four in some specimens; two small, discal tubercles; two or three posterior, marginal tubercles; two pleural tubercles; anterior pleural tubercle very small, posterior tubercle large; overall shape of dorsal abdominal tubercles evenly tapered to apex. **Abdominal sternites 2-6** with two posterior marginal tubercles, the outer tubercle smaller.

Material examined: A total of 63 pupae were examined for this diagnosis.

Association methods: The pupae used in this description were reared from field-collected larvae, associated with collected larvae, or identified without associated larvae once the characters of the pupae were known to me.

9.8.4 Natural History

From label data and personal observations, P. planus is mainly a pine beetle. Host records are as follows: Pinus strobus L. (Ontario, Quebec, Maine, Massachusetts, New York, Pennsylvania), P. monticola Dougl. (British Columbia), P. ponderosa Laws. (British Columbia), P. resinosa (Maine, Minnesota), P. banksiana (Manitoba, Saskatchewan, Minnesota), P. latifolia (Alberta, British Columbia, Oregon, Utah), P. echinata (North Carolina), Pinus sp. (New Hampshire), Picea mariana (Mill.) B.S.P. (Manitoba, Northwest Territories), Picea sp. (Alberta, Manitoba, Northwest Territories, Idaho). Prepupae and pupae were collected on 11.viii.1986 (Ontario); adults were collected in a Lindgren funnel trap on 22.vii.1983 (British Columbia); two specimens were found on a street on 14.v.1984 (Manitoba). Adults have been found under bark in every month except June, July and August. Pytho planus disperses during the summer season, as do probably all other species of Pytho. Cold-hardiness and physiological studies have been done on this species by Ring (1981, 1982) and Ring and Tesar (1980, 1981).

9.8.5 Distribution

Pytho planus has a very wide distribution and occurs across Canada without significant gaps longitudinally (figure 22). To the north, the tree line presumably subtends the extent of this species. To the south, P. planus does not have a specific range limit, and occurs in areas of suitable host trees.

9.8.6 Chorological relationships

Pytho planus is broadly sympatric with P. seidlitzi and P. niger in the northern parts of the ranges of all three of these species, and with P. strictus in eastern North America.

9.8.7 Phylogenetic relationships

Pytho planus is the Nearctic member of the P. depressus group, both species of which occupy a relatively derived position in the relationship of members of Pytho.

9.9 PYTHO DEPRESSUS (Linnaeus 1767)

(figures 2 I; 3 F; 11 D; 23)

Tenebrio depressus Linnaeus 1767: 675 [**Type area** - Sweden. **Type**

repository - types not examined] Blair 1928: 5; Kôno 1934: 30 (distribution), 1936: 36 (review of Japanese species); Hansen 1945: 20, fig.8; 174, figs. 8-9; Burakowski 1962: 192, 193, 194 (key to all stages of Polish species); Kaszab 1969: 95 [key to European species (adults)]; Burakowski 1976: 5, figs. 1-8; 6, figs. 9-15; 7, figs. 16-22; 13, fig. 23; 14, 15, fig. 28; 16, figs 32-35; 17 (key to species in all stages); Pettersson 1983: 28, fig. 5 (larval diagnoses); Iablokoff-Khnzorian 1985: 204, figs. 1-6; 205 (revision of Palaearctic species).

Tenebrio lignarius Degeer 1775: 38; Blair 1928: 6.

Cucujus coeruleus Herbst in Füessly 1782: 6; Blair 1928: 6.

Cucujus coeruleus Fabricius 1792: 94; Blair 1928: 6.

Cucujus depressus var. castaneus Fabricius 1792: 95; Blair 1928: 6.

Cucujus depressus var. festivus Fabricius 1792: 95; Blair 1928: 6.

Cucujus planus Herbst 1799: 14; Blair 1928: 6.

Pytho depressus var. atriceps Pic 1912: 49; Blair 1928: 6; Pic 1929: 205.

Pytho depressus var. basipennis Pic 1912: 58.

9.9.1 Adult Stage

Derivation of specific epithet

The name depressus is similar to the word "depressed", which is derived from Latin. This may pertain to the flattened dorsum of the adult of this species.

Type information and taxonomic notes

According to Article 57c (i) (ICZN 1985), Cucujus planus Herbst 1799 and Tenebrio planus Olivier 1795 are secondary homonyms and the junior homonym is invalid. In this case Cucujus planus is the junior homonym and must have a replacement name. Tenebrio depressus Linnaeus 1767 is the oldest available synonym (Blair 1928: 6) and becomes the valid name of the taxon (as stated in Article 60b ICZN 1985). This species, along with P. planus, is unusually variable with respect to colour. All of the names listed above were based on colour varieties and were synonymized by Blair (1928) and other earlier authors. The various references to the synonyms of P. depressus are not included in this treatment; they may be found in Seidlitz (1916) and Blair (1928). Since P. depressus and its various synonyms are well known taxonomically, the fact that no types were examined is probably not of critical importance here. See the treatment of P. planus for more taxonomic information.

Diagnostic combination

Adult P. depressus possess the following diagnostic features: lateral margins of pronotum (figure 2 I) weakly arcuate, widest anterad of midlength; elytra with slight to strongly metallic lustre; aedeagus

(figure 3 F) with apicale approximately 1.5 times length of basale;
distribution: trans - Palearctic.

Description

TL 7.4-13.7 mm; GEW 2.5-5.3 mm; other measurements given in Table 9.

Head with lateral, frontal areas slightly elevated above level of disc of frons; clypeus not significantly elevated above level of frons; area on frons between eyes slightly raised in some specimens; apical maxillomere securiform; mandibles with lateral margins evenly arcuate to apices; pit on male mentum with slightly raised margin; posterior limit of margin of pit anterior of suture between mentum and submentum; antennae with sensilla on apices of antennomeres 7-10; punctation heavy behind and between eyes, light on elevated, lateral, frontal areas.

Pronotum (figure 2 I) somewhat variable in shape; posterolateral margins in most specimens slightly arcuate, in some specimens straight or sinuate; anterolateral margins rounded, not markedly constricted anteriorly; areas laterad of depressions at same level as disc; pronotum widest anterad of middle; anterior bead absent; posterior bead present; pronotal depressions variable in depth, oval, with inner margins subparallel; median line absent to weakly impressed; punctation uniform, somewhat finer on anterolateral area and down midline. **Prosternum** with short intercoxal process, extending to less than half length of procoxae; process with strong bead; bead complete apically and laterally on process. **Mesoscutellum** impunctate, or with few, setigerous punctures. **Mesepisternum** uniformly, coarsely punctate. **Mesepimeron** uniformly, coarsely punctate. **Mesosternum** with short intercoxal process, extending to a third the length of mesocoxae; posterior bead

TABLE 9

Measurements of selected features of samples of P. depressus from various localities in Finland and West Germany. Samples are segregated by sex (M = male, F = female) and the numeral in parentheses indicates the number of specimens of each sex measured. The first statistic for each parameter is the range and the second is the mean and standard deviation. Abbreviations for these measurements and their explanation are given on pages 36-37.

	FINLAND		WEST GERMANY	
	M (10)	F (10)	M (10)	F (10)
EL	5.0-8.0 6.4 \pm 1.03	6.0-8.9 7.3 \pm .93	4.9-7.0 6.0 \pm .60	5.9-8.2 7.0 \pm .81
GEW	2.6-4.4 3.5 \pm .64	3.3-5.3 4.1 \pm .65	2.6-3.9 3.4 \pm .42	3.1-4.2 3.8 \pm .45
PL	1.1-1.8 1.5 \pm .24	1.4-2.1 1.7 \pm .21	1.2-1.7 1.5 \pm .15	1.4-1.9 1.7 \pm .21
GPW	1.6-2.6 2.2 \pm .36	2.2-3.1 2.5 \pm .32	1.6-2.3 2.0 \pm .23	1.8-2.8 2.4 \pm .33
HL	1.4-2.0 1.7 \pm .25	1.5-2.2 1.9 \pm .24	1.3-1.8 1.6 \pm .17	1.4-2.2 1.8 \pm .26
GHW	1.2-1.8 1.6 \pm .22	1.5-2.2 1.7 \pm .21	1.2-1.8 1.5 \pm .16	1.3-2.0 1.7 \pm .22
TL	7.4-11.8 9.6 \pm 1.50	9.0-13.2 10.9 \pm 1.33	7.4-10.4 9.1 \pm .90	8.3-11.7 10.4 \pm 1.29
GPW/PL	1.39-1.52 1.45 \pm .05	1.33-1.50 1.45 \pm .05	1.33-1.42 1.38 \pm .03	1.35-1.52 1.43 \pm .05

not impressed laterad of inner margin of mesotrochantin; punctation weak, absent down midline and on lateral areas. **Elytron** depressed dorsally, with nine feebly convex intervals; striae with punctures; intervals with scattered punctation only; posterolateral elytral flange with extra, long pubescence. **Metasternum** with short, blunt intercoxal process, extending slightly anterad of posterior mesocoxal cavities. **Male aedeagus** (figure 3 F) with apicale approximately 1.8 times length of basale; apicale not expanded, evenly tapered to apex; apicale narrowest near apex with straight to slightly sinuate sides; accessory lobes attaining apex of fused paramere or slightly beyond. **Colour** quite variable dorsally; head usually piceous to black, dark rufous in some specimens; pronotum testaceous to black; if lighter in colour, disc infuscated in some specimens; elytra ranging from testaceous/rufous to black; specimens with rufous elytra may have violet metallic sheen pronounced on lateral margins and/or entire apical half of elytra (giving bicoloured effect); specimens with piceous to black elytra have often vivid green, blue or violaceous metallic lustre; ventrally, head and thorax dark, contrasting against lighter coloured abdomen; legs rufous to piceous, with tibiae and tarsi lighter than femora.

Material examined: I was able to examine 290 adults of this species.

9.9.2 Larval Stage

The larval stage of *P. depressus* has been previously described by many authors. The earlier references dealing with the larva of this species are listed in Seidlitz (1916: 123-124). The larva has been redescribed by more recent authors, including Burakowski (1976).

Diagnostic combination

Parabasal ridge processes (figure 11 D) very long, subparallel; basal, inner urogomphal tooth subequal in size to, or smaller than, middle tooth (as in figure 12 D); apical urogomphal tooth present; urogomphal plate sharply sloping posteriorly to urogomphal lip; urogomphal lip (as in figure 12 D) with posterior margin weakly arcuate to truncate; urogomphal tubercles with tips directed anteriorly, arranged in uninterrupted, anteriorly truncated, semi-ellipse; distribution: trans - Palearctic.

Description

Head with frontal arms of epicranial suture V-shaped basally, some specimens U-shaped, arcuate; antennomere 1 slender, feebly sinuate laterally; antennomere 2 slightly enlarged apically; antennomere 3 cylindrical; ratio of antennomere lengths approximately 2.5 : 2 : 1. **Parabasal ridge processes** (figure 11 D) very long, extending anterad of parabasal ridges by a sixth their lengths; inner margins subparallel; distance from anterior tip of process to posterior margin of tergites 2-7 approximately three times length of process. **Parabasal setae** (figure 11 D) variable in size, at least seven per side, arranged posterad and laterad of parabasal processes; posterior parabasal setae longer than lateral setae. **Urogomphus** (as in figure 12 D) with basal, inner tooth small, separated from lateral margin of urogomphal lip by slightly greater than basal width of basal tooth; middle, inner tooth slightly larger than, or subequal in size to basal tooth; middle tooth separated from basal tooth by four times length of basal tooth; apical

tooth present, ventral; urogomphal plate sharply sloping posteriorly to urogomphal lip. **Urogomphal lip** (as in figure 12 D) with posterior margin weakly arcuate, straight in some specimens; ratio of urogomphal lip width at base to length down midline approximately 3 : 1.

Urogomphal tubercles (as in figure 12 D) small, uniform in size, six to seven per side; tubercles arranged in anteriorly truncate semi-ellipse, without medial gap; tips of tubercles directed anteriorly; apical tubercle with one long seta. **Ventral asperities** 17-24 in number, small, with inconspicuous longitudinal ridges.

Material examined: 33 larvae were examined.

Association methods: All of the larval specimens of P. depressus were previously determined; I did, however, use the literature to confirm the identifications.

9.9.3 Pupal Stage

Diagnostic combination

Pupae of P. depressus can be separated from those of P. planus on the basis of the former possessing two large, subequal, lateral marginal tubercles on sternites 2-6.

Description

Head with two ocular tubercles, one large and one smaller; antennal denticles small, inconspicuous; anterior margin of labrum slightly emarginate. **Pronotum** with shape as in adult, lateral margins weakly arcuate, not constricted anteriorly; widest anterad of midlength; 10-12

marginal tubercles. **Abdominal tergites 2-6** with five lateral, marginal tubercles; two discal tubercles; two or three posterior, marginal tubercles; two pleural tubercles; anterior pleural tubercle very small, posterior tubercle large. **Abdominal sternites 2-6** with two posterior, marginal tubercles, subequal in size.

Material examined: three pupae were available for examination.

Association methods: The previous identifications of the pupae of this species were confirmed by examining the pertinent literature.

9.9.4 Natural History

Because this species is very widespread, and because it is Palearctic, *P. depressus* has had a comparatively large amount written on its natural history. Many of the older references are anecdotal, do not reveal any peculiarities in this species, and are too numerous to mention here. References pertaining to the natural history of *P. depressus* may be found in Seidlitz (1916) and Blair (1928).

According to Saalas (1917), *P. depressus* is associated with *Picea excelsa* Link., *Pinus silvestris* L. and "other" coniferous trees. Host trees are found in dry forests, swamps, and on hills ("Fjeldabhängen"), and can be standing, lying, or stumps. Size of host tree trunk can range from 6 to over 35 cm in diameter. *Pytho depressus* prefers trees which are decayed, but still "fresh" and without fungal attacks.

9.9.5 Distribution

Pytho depressus is the most widespread Palearctic species, and is known from Scotland (locality not mapped) to far eastern U.S.S.R. (figure 23). Kôno (1934) lists this species as inhabiting Sachalin. The large gap in central U.S.S.R. may be an artifact of several factors including infrequent collecting, difficulties in obtaining material from the U.S.S.R. for study, or patchy host tree abundance. The real reason is probably a combination of all of these.

9.9.6 Chorological relationships

Pytho depressus is widespread in the Palearctic (except Japan) and is therefore sympatric with P. kolwensis and P. abieticola in the ranges of the latter two species.

9.9.7 Phylogenetic relationships

See "Phylogenetic relationships" for P. planus.

9.10 SPECIES OF UNCERTAIN PLACEMENT

The name Pytho erotis Gistel, 1857, was not found in any subsequent reference concerning Pytho, and from the short description, it appears that this name is not associated with any species of Pytho in the modern sense of the genus.

Chapter X

PHYLOGENY

10.1 PYTHINAE AS A MONOPHYLETIC UNIT

The subfamily Pythinae (Watt 1987) is composed of four genera, the monobasic Australian Synercticus, the monobasic western North American Sphalma Horn, the monobasic trans-North American Priognathus LeConte, and the relatively more diverse Pytho. This subfamily is close to the Pythini of Horn and LeConte (1883), except for Boros and Lecontia, which are now the sole North American genera of Boridae (Young 1985; Watt 1987) along with the genus Osphyoplesius, which is restricted to southeastern Europe (Lawrence 1982).

The monophyly of these four genera is based on a single, larval stage synapomorphy, the presence of a transverse row of tubercles on tergite 9 (Watt 1987). This character occurs also in the genus Elacatis (Othniidae) and could have arisen twice, or more, independently within Pythinae. Because the pythine group of genera was not analyzed cladistically, Watt's (1987) contention that his Pythinae is a monophyletic sister taxon to Pilipalpinae, the latter of which is based on one larval and three adult synapomorphies, is accepted here. This assumption concerning the monophyletic nature of Pythinae will have direct impact upon the hypotheses regarding the zoogeography of Pytho and of the entire subfamily.

10.2 PYTHO AS A MONOPHYLETIC UNIT

Several unique characters of both adult and larval stages of all species of Pytho support the contention that this taxon is monophyletic. Two characters of the adult stage are as follows: 1) paired, longitudinal pronotal depressions (character 11) (figure 2); 2) raised carinae (intervals) on elytra (character 15) (figure 8 B). Pytho larvae possess well-developed parabasal ridge processes on the abdominal tergites (character 1) (figure 11). The individual states within each of these autapomorphies are difficult to polarize because they are present only in Pytho among the "salpingid group" of families (Watt 1987). However, their uniqueness to Pytho may support the phyletic independence of this genus.

10.3 METHODS

In order to determine the hypothetical relationships that existed, and exist, among species of Pytho, cladistic methods were used. These are discussed in Hennig (1966), Kavanaugh (1972, 1978), Wiley (1981) and elsewhere. There is still much argument among the proponents of the various schools of reconstructing relationships of organisms. It is not my desire to present the various arguments; one has only to peruse the last ten years of Systematic Zoology to appreciate the depth of these arguments.

The methods by which a group of organisms is analyzed using cladistics are basically similar among workers involved in phylogenetics. It is uncommon for an author to list in detail the steps

used; this has been done by Marshall (1987), who examined the systematics of Bitheca (Diptera: Sphaeroceridae). He did so to "clarify the method by which information was incorporated into this cladogram" (Marshall 1987: 380). The four steps used by Marshall (1987) are as follows: 1) establish monophyly of group; 2) search for a sister group; 3) break group into monophyletic subgroups by possession of unique characters; 4) resolve cladogram as fully as possible by incorporating information about character polarities. These four operations are generally similar to those used in this study.

Paramount in phylogenetic analysis is character analysis; relative polarities of the character states in a given morphocline or transformation series will directly affect the final hypotheses regarding the classification of the group under study. Character state polarities within Pytho were determined using out-group comparison methods as discussed in Watrous and Wheeler (1981) and Maddison et al. (1984). An obvious subjective feature of out-group comparison is the choice of out-group. According to Watrous and Wheeler (1981), an out-group should be "related" to the in-group. In many taxa of Coleoptera, and especially in the Heteromera, it is very difficult to say which groups are most closely related to the one under study, because full phylogenetic analysis has been done in relatively few groups. Because I did not undertake a cladistic analysis of Pythinae (sensu Watt 1987), I could not determine which genus was the sister taxon to Pytho. However, based on mere similarity and geographical distribution, Priognathus may be the sister taxon to Pytho. Therefore, in order to polarize characters within the genus Pytho by using

out-group comparison, I used a generalized out-group composed of the three other genera of Pythinae, Synercticus, Sphalma and Priognathus. For those characters of Pytho which are not represented in the other genera, in-group comparisons were used to determine the relative polarities of these character states. The basis for determination of character polarities is given in Table 10.

All characters of both larval and adult stages were initially given equal weight in reconstructing the phylogeny. However, larval characters, namely those of the parabasal ridge processes and the urogomphal plate, were more important in delimiting the basal stems on the cladogram. That is, the six characters included from the larval stage were effective in defining the species-groups in the relationship. The adult characters, on the other hand, had less importance in the basal portion of the cladogram, but they helped delimit the relationships within the species-groups or towards the terminal ends of the cladogram. Therefore, even though the characters selected were given equal weight at the outset, they eventually developed a different relative weight once they were interpreted and used to develop the proposed phylogeny of Pytho.

TABLE 10

Characters, character states and polarities
of features used to reconstruct the phylogeny of
of the members of Pytho Latreille

	PLESIOTYPIC	APOTYPIC	BASIS
<hr/> LARVAE <hr/>			
ABDOMINAL TERGITES			
1. parabasal processes	absent	present	OUT
2. size of p. processes	short, triang.	long, narrow	IN
UROGOMPHAL PLATE			
3. apical urog. tooth	absent	present	OUT
4. rel. sizes of middle and basal urog. tooth	basal>middle	middle>basal	IN/OUT
5. apical urog. tubercle	unisetose	pleurisetose	IN
6. no. ventra asperities	reduced	increased	IN
<hr/> ADULTS <hr/>			
HEAD			
7. mandible (sub-apex)	evenly arcuate	abruptly bent	IN
8. antennal sensilla	on # 8-10	on # 7-10	IN
PROTHORAX			
9. ant. pronotal bead	absent	present	IN
10. post. pronotal bead	present	absent	IN/OUT
11. pron. depressions	absent	present	OUT
12. pron. depressions	simple, shallow	complex, deep	IN
13. prosternal process	short, blunt	long, acute	IN/OUT
MESOTHORAX			
14. mesepimeron punct.	reduced	normal	IN/OUT
ELYTRA			
15. carinate intervals	absent	present	OUT
16. colour	non-metallic	metallic	IN/OUT
AEDEAGUS			
17. apicale shape	evenly tapered	dilated	IN/OUT
18. rel. sizes of apicale and basale	apicale=basale	apicale>basale	IN/OUT

10.4 ANALYSIS OF CHARACTERS

In developing the hypothetical relationships among the species of Pytho, a total of six larval stage, and eleven adult stage characters were used. These characters, along with the polarities assigned, are discussed below.

10.4.1 Larval characters

Parabasal ridge processes (characters # 1, 2)

The presence of well-developed parabasal ridge processes on abdominal tergites 2-8 is judged to be autapomorphic for Pytho, although the possible larva of Synercticus heteromerus has what may be very feebly developed processes. Parabasal ridge processes are absent in larvae of Sphalma and Priognathus. Among the members of Pytho, three states are present. Pytho seidlitzii has short, triangular processes (figure 11 A) as do members of the P. kolwensis-group (figure 11 B). Pytho niger-group larvae have processes more elongate and parallel-sided (figure 11 C). The P. depressus-group larvae possess the highly derived state, in which these processes are very elongate (figure 11 D).

Apical urogomphal tooth (character # 3)

An apical, or third, inner urogomphal tooth is developed in all species of Pytho except P. seidlitzii as well as in Synercticus, and in Sphalma. Young (1976: 229) considers the apical urogomphal tooth of the larva of Sphalma quadricollis to be one of two branches of the urogomphi. In the P. kolwensis- and P. niger-groups (figure 12 B, C)

the apical tooth is oriented on the inner margin of the urogomphus. In the P. depressus-group, however, the apical urogomphal tooth projects more or less ventrally (figure 12 D). In this case it does appear as a branch of the urogomphus. I consider the third tooth to be an inner urogomphal tooth and not an actual branch of the urogomphus. In Pytho, the presence of the third tooth is judged to be apomorphic, with independent derivations in Synercticus and Sphalma. The third inner, apical urogomphal tooth is absent in larvae of Priognathus monilicornis.

Relative sizes of middle and basal urogomphal teeth (character # 4)

In larvae of Synercticus, Sphalma, and Priognathus, the basal urogomphal tooth is markedly larger than the middle tooth (apical tooth in Priognathus). Among Pytho, all larvae except those of the P. depressus-group exhibit the same condition. Larvae of P. depressus and P. planus possess a middle, inner urogomphal tooth which is slightly larger than the basal (or subequal in length) (figure 12 D). This latter condition is considered apomorphic.

Setation of apical urogomphal tubercle (character # 5)

The apical, or posterior tubercle on the dorsum of the urogomphal plate, is beset with at least one long, subapically situated seta in larvae of all Pythinae. In larvae of Synercticus, Sphalma, and Priognathus, and all Pytho species except those of the P. kolwensis-group, short setae are irregularly placed on all urogomphal tubercles. In these species, the apical urogomphal tubercle is beset with only one long seta which is at least twice the length of the smaller setae. In P. strictus, P. kolwensis, and P. nivalis, there are

at least two and up to six of these longer setae arising subapically on the most posterior tubercle (as in figure 12 B). Thus, the presence of more than one of these longer setae is considered as a synapomorphy of the three species in the P. kolwensis-group.

Number of asperities on venter of urogomphal plate (character # 6)

Two character states are hypothesized to exist, with a reduced number of asperities, less than 20 being plesiomorphic and greater than 21 apomorphic. Both Synercticus and Sphalma along with all Pytho except the P. niger-group, possess the primitive state. Priognathus larvae have an average of 30 ventral asperities, while members of the P. niger-group have from 23-28. The derivation of the apomorphic state occurred independently in both lineages. This is admittedly subjective, and possibly a weak character.

10.4.2 Adult characters

Shape of adult mandible (character # 7)

The outer, lateral margin of the left mandible in Synercticus, Sphalma, and in all species of Pytho except P. kolwensis and P. nivalis is evenly arcuate throughout its length, to the apex. In P. kolwensis and P. nivalis the lateral margin is abruptly bent before the apex. A similar condition also exists in Priognathus, in which the mandibles are sexually dimorphic. Males of Priognathus have elongate mandibles, with an almost straight lateral margin. An abrupt curvature occurs much in the same fashion as in P. kolwensis and P. nivalis. Female Priognathus have shorter mandibles, with evenly arcuate lateral margins. It is not

clear if the curvature in the mandible of Priognathus is homologous to that of P. kolwensis and P. nivalis. I judge this condition to be apomorphic and derived twice independently, in two species of Pytho and again in Priognathus.

Extent of annular, antennal sensilla (character # 8)

Adults of Pytho possess annular sensilla surrounding the apex of the last four or five antennomeres (figure 5 A). The apical antennomere is covered completely with these sensilla. Two states occur among Pytho: members of the P. depressus- and P. kolwensis-groups and P. jezoensis have the sensilla on antennomeres 7-11, while the remaining two species of the P. niger-group and P. seidlitzii have these sensilla on antennomeres 8-11. Synercticus, Sphalma, and Priognathus have sensilla on antennomeres 11, 6-11, and 9-11, respectively. Since a variety of conditions exists within the out-group, it is difficult to polarize this character for members of Pytho. There is possibly a transformation series from three antennomeres with sensilla (as in Priognathus) to four and then to five, and higher. I interpret the distribution of these character states as follows: species of Pytho with sensilla on antennomeres 7-11 exhibit the apomorphic state (which has been developed independently three times) and the remainder, the plesiomorphic state.

Anterior pronotal bead (character # 9)

An anterior pronotal bead, well-developed medially, is present in all three species of the P. kolwensis-group (figure 2 B,C,D) as well as in Synercticus. The absence of such a structure in Sphalma, Priognathus, and the remaining species of Pytho has prompted the choice of presence

of an anterior bead as being the apomorphic state for this character. Therefore, its presence in the two former groups is interpreted as being independently derived.

Posterior pronotal bead (character # 10)

A well-marked, posterior pronotal bead is present in Synercticus, Sphalma, Priognathus, and in all Pytho species except P. seidlitzi. In this species, the bead is entirely absent (figure 2 A). This loss is considered autapomorphic for P. seidlitzi.

Longitudinal pronotal depressions (characters # 11, 12)

Paired pronotal depressions are present in Pytho, (figures 1, 2) but are absent in Synercticus, Sphalma, and Priognathus. Thus, the presence of these depressions is an autapomorphy for members of Pytho. Two states are thought to exist, with respect to shape and depth of these depressions. Species in the P. seidlitzi-, P. niger- and P. depressus-groups possess pronotal depressions which are elliptical or oval in shape, and quite shallow. In members of the P. kolwensis-group (figure 2 B,C,D) the depressions are quite deep and linear, often with lateral branching. On the basis of in-group comparison, the latter state is considered apomorphic in the P. kolwensis-group.

Size of prosternal, intercoxal process (character # 13)

In most species of Pytho, the prosternal, intercoxal process is short, not separating the procoxae, and only extending to half the length of the procoxae. According to Lawrence (1982) and Watt (1987), procoxal processes in Pythidae are often short or incomplete. This is

also the condition in Priognathus, Sphalma, and Synercticus. In P. kolwensis and P. nivalis, the intercoxal process is relatively well-developed and extends past half the length of the procoxae. This state is thought to represent the apomorphic state, and is present only in P. kolwensis and P. nivalis.

Punctuation of mesepimeron (character # 14)

The mesepimeron in all species of Pytho (except P. seidlitzii) is equally as punctate/pubescent as the metepisternum. In P. seidlitzii, punctuation of the mesepimeron is either entirely absent, or restricted to the lateral margin of the sclerite (figure 6 D). In either case, the mesepimeron strongly contrasts the metepisternum with respect to degree of punctuation. Restricted (or absent) mesepimeral punctuation also occurs in Priognathus. For Synercticus and Sphalma, it is difficult to assess this character because of an overall reduction in ventral punctuation, but it appears that the punctuation of the mesepimeron is not significantly different from that of the metepisternum in these two genera. Due to the restriction of mesepimeral punctuation in Priognathus, this state is deemed plesiomorphic, with uniform punctuation of the mesepimeron as the apomorphic state in Pytho.

Elytral carinae (character # 15)

Among Pytho species, there are a variable number of convex carinae, roughly corresponding to elytral intervals separating alternating rows of "strial" punctures (figure 8 B). In some species, punctures are not restricted to the "striae" but are also present on the carinate intervals. Synercticus has distinct striation of the elytral punctures,

but without convex, or carinate intervals. Likewise, no convex carinae are present in Sphalma or Priognathus, both of which have random, uniform elytral punctation, with only slight evidence of striation. Thus, the presence of these convex, carinate intervals is an autapomorphy for the genus Pytho. Within the genus, species exhibit variable convexity of the carinae, but because of difficulties in polarization, is a taxonomic character only.

Elytral colour (character # 16)

Most species of Pytho, as well as Synercticus, Sphalma, and Priognathus have elytra varying from non-metallic brown to black. In P. nivalis as well as P. planus and P. depressus, the elytra are variably metallic. In P. nivalis elytra are only slightly brassy or violaceous, while in P. planus and P. depressus, vividly metallic blues, greens or violets are known. Clearly, the metallic colouration of the elytra has been derived twice independently and this is the apomorphic state among Pytho.

Shape of male apicale (character # 17)

In all species of Pytho except P. seidlitzii, and in Synercticus, Sphalma, and Priognathus the apicale of the male genitalia (sensu Watt, 1987) is evenly tapered with straight sides to near the apex, at which point the lateral margins are abruptly angulate to the apex (as in figure 3 D). In Synercticus, the sides are very slightly sinuate only. In P. seidlitzii, the apicale is markedly narrowed towards its midlength, with the apex spatulate in shape (figure 3 C). This latter condition is judged to be apomorphic and is autapomorphic for P. seidlitzii.

Relative sizes of the basale and apicale (character # 18)

In most species of Pytho, and in Sphalma and Priognathus, the basale is subequal in length to the apicale. In P. seidlitzii (figure 3 C) and P. depressus (figure 3 F), the apicale is approximately 1.5 times the length of the basale. Similarly, in Synercticus, the apicale is slightly less than 1.5 times the length of the basale. This lengthened apicale (or shortened basale) is considered apomorphic and has been developed twice independently in Pytho.

Chapter XI

ZOOGEOGRAPHY

11.1 INTRODUCTION

Wiley (1981: 277) defines zoogeography as the "study of the distribution of animals in space through time." Once a phylogenetic analysis has been done for a group of insects, the next logical step is a study of the distributions of the taxa and an attempt to explain these distributions (Allen 1983). There is a profusion of recent literature concerning biogeography, most of which can be included in two general schools, dispersalist and vicariant. It is not my objective here to present a full argument for, or against any of the approaches. Both types of biogeographic explanation may be invoked to explain historical patterns exhibited by a single monophyletic taxon (e.g. Roughley 1982).

Adherents of the dispersal variety of biogeography (e.g. Darlington 1970) explain present distributions of organisms and their disjunctions by invoking dispersal across pre-existing barriers. Usually associated with this is the concept of centres of origin, which are areas of the world in which new species arise. These species subsequently disperse and migrate to other recipient areas of the world (Ball 1976). Wiley (1981) deals with this type of biogeography under "evolutionary biogeography" and discusses essential tenets and inherent weaknesses. In essence, Wiley (1981: 287) states that because every organism is

capable of some sort of dispersal, disjunctions may be explained solely by dispersal. It is understandable, according to Wiley (1981) that evolutionary biogeography was popular before the concept of continental drift came into acceptance. However, this school of biogeography is now somewhat obsolete and of low heuristic value. Rosen (1978) feels that both geology and biogeography may be mutually complementary provided a common language is used for both. This "language" is a hierarchical system of nested sets of more or less inclusiveness, based on synapomorphic characters.

Vicariance biogeography developed as an off-shoot of phylogenetic biogeography (Wiley 1981), and embodies the following hypotheses (from Croizat et al. 1974: 277-278): 1) allopatric species arise after barriers separate parts of a formerly continuous range; 2) sympatry between species of a monophyletic group implies dispersal of one or more species into the range of another; 3) allopatric speciation is predominant and sympatric speciation is the exception; 4) vicariance is of great importance in historical biogeography, with dispersal being a secondary phenomenon. From this, it is obvious that a distinction must be made between the original patterns produced through vicariance, and those patterns produced secondarily via dispersal (Rosen 1978).

One of the major arguments against the vicariance biogeographic paradigm is the reduced importance of dispersal (Rosen 1978). On the contrary, dispersal is an important part of this type of biogeography. Since primitive cosmopolitanism is assumed, biotic dispersal is obviously critical (Rosen 1978; Wiley 1981). Vicariance biogeography involves the conversion of a cladogram depicting the relative recency of

common ancestry of the organisms to one showing recency of common ancestral biotas (Platnick and Nelson 1978). In other words, taxon cladograms are transformed into corresponding area cladograms. The area inhabited by a certain species replaces the species name in the relationship. This area cladogram can be compared to a geographic cladogram illustrating the arrangement and relationships of the areas themselves (Wiley 1981). The relationships among the taxa which have been analyzed using phylogenetic methods should logically make sense with respect to accepted geologic and geographic history. According to Rosen (1978: 159) "any specified sequence in earth history must coincide with some discoverable biological patterns." By vicariance biogeography, according to Platnick and Nelson (1978) and Rosen (1978), one strives to discover congruent patterns (generalized tracks of Croizat (et al. 1974) and to explain them using hypothesized barriers and allopatric speciation.

There is much literature concerning continental drift and the historical configuration of the land masses of the world. Most of these authors agree on the events that occurred, but there is disagreement regarding the actual timing of them. Several recent works on this subject are those of Hallam (1981), Allen (1983) and Noonan (1986), which contain a synthesis of the important geological phenomena which have contributed to the present faunal distribution. These three sources are especially useful for the zoogeographic analysis of members of Pytho, because they deal primarily with Northern Hemisphere events.

There is little argument in the literature about the existence of the supercontinent Pangaea, but the exact time of its separation into the

northern Laurasia and southern Gondwanaland is uncertain. Dietz and Holden (1970) suggest that the break up of Pangaea commenced no more than 200 mya and Noonan (1986) gives 144 mya as the time of final separation. According to Hamilton (1983), two disjunct regions existed on Laurasia after the transgression of the North American midcontinental seaway in the Late Cretaceous. Asiamerica consisted of Asia plus western North America, which were attached by the region between Alaska and Siberia (Noonan 1986). Euramerica was composed of Europe and eastern North America. Each region is thought to have had distinctive insect faunas (Noonan 1986). These areas were disjunct for 21 to 27 my (Noonan 1986). It is probable that such events produced vicariance and allopatric speciation in primitively cosmopolitan species. The four major events which Noonan (1986: 84) suggests may have affected distributions of Northern Hemisphere insects are: 1) the opening of the North Atlantic, 2) severing of the Beringian land connections, 3) the transgression of the Mid-Continental Seaway, and 4) the separation of Europe from Asia by the Turgai Straits. Noonan (1986) suggests the use of Holarctic groups, such as the genus Pytho, to further examine the consequences of these four events.

An analysis of this type was done by Allen (1983) who recognized that many groups of northern temperate insects occur in eastern North America, Europe, and northeastern Asia. In this work, Allen (1983) examines eleven monophyletic lineages that have representatives in these three areas, and found that there were only three biogeographic patterns. The events which have contributed to these patterns are: 1) division of Pangaea into Laurasia and Gondwanaland, 2) transgression of

the Mid-Continental Seaway and Turgai Straits, 3) development of the western Cordilleran system, and 4) repeated connections and disjunctions between Alaska and Siberia (Allen 1983). Since only three biogeographic patterns are observed by Allen (1983), different independent lineages may have been affected by similar events. Using the ideas discussed above, I shall analyze the present distributions of the entire subfamily Pythinae as well as the four clades within the genus Pytho. I shall attempt to provide a plausible explanation of the historical biogeography of both the subfamily Pythinae in general terms, and the genus Pytho, in more detail.

11.2 ZOOGEOGRAPHY AND EVOLUTION OF PYTHINAE

Pythinae (sensu Watt 1987) exhibit a disjunct distribution with members in both northern and southern temperate regions. Two monobasic genera, Priognathus and Sphalma occur in North America. Priognathus monilicornis (Randall) is widespread across the continent, while Sphalma quadricollis Horn is restricted to western United States and adjacent Canada (Hatch 1965). Pytho is Holarctic with nine species worldwide. In the Nearctic region, the genus is found from Alaska, south to California and Georgia with no significant gaps longitudinally. One species, P. strictus LeConte, is restricted to eastern North America. In the Palearctic, Pytho inhabits coniferous forests from Great Britain to Japan. In Europe, P. depressus (L.) is found as far south as northern Spain. The southern member of Pythinae, Synercticus heteromerus Newman, is known only from eastern Australia. I have not done a cladistic analysis of the genera of Pythinae, but some general

statements may still be made concerning the geographic history of the group.

Assuming Watt's (1987) hypotheses regarding the phylogeny of Pythidae is correct, the origins of Pythinae are ancient, *i.e.* before separation of Pangaea near the end of the Jurassic (Noonan 1986). The split of Pangaea caused by expansion of the Tethys Sea (144 mya) also split the primitive stock of Pythinae. This same event also led to the Gondwanian isolation of most genera of Pilipalpinae in the Southern Hemisphere. One must assume that the ancestor of the Synercticus lineage was widespread on Gondwanaland and was isolated on what would become Australia. Upon Australia's separation from South America and the other Gondwanian continents, Synercticus was isolated there.

The ancestor of the three northern genera was widespread on Laurasia. The vicariant events that took place in the Northern Hemisphere, including transgression of the Midcontinental Seaway and Turgai Straits as well as openings of North Atlantic and Bering Strait (Matthews 1979; Hallam 1981; Allen 1983; Noonan 1986) directly affected the present distribution of Pythinae. Another important event which began in the Early Cretaceous is the orogeny which caused the formation of the Western Cordillera (Allen 1983). The western distribution of Sphalma quadricollis may be a consequence of this latter event. The distributions of Pytho and Priognathus are more difficult to explain because they are so broadly sympatric in the Nearctic. This sympatry is probably the result of subsequent dispersal following the vicariant event which caused the initial split (I am assuming without formal cladistic substantiation, that Pytho and Priognathus are sister taxa).

Priognathus is restricted to North America, and therefore, the event leading to the isolation of the genus most probably occurred on North America proper. This may have been the transgression of the Midcontinental Seaway (Allen 1983; Noonan 1986). One somewhat puzzling fact is the absence of Sphalma, and especially Priognathus from the Palearctic. At different times in the Tertiary, Beringia was available, and was important for, faunal exchange between Siberia and western North America (Kurentsov 1976; Lindroth 1979; Matys and Glushkova 1976; Noonan 1986). According to Matthews (1980), the flora of Beringia during the mid-Miocene consisted of coniferous forest. Therefore, assuming that the genus Priognathus is as old as mid-Miocene, there would have been opportunity for dispersal in either direction across the land bridge, since, according to Matthews (1979), the Miocene coniferous forest was Holarctic in expanse. If this is the case, then Priognathus has subsequently gone extinct in the Palearctic, or it never reached the Palearctic region.

In summary then, the distributions of the four genera of Pythinae as it is here defined, represent an overall amphipolar distribution as outlined in Crowson (1980). Pythinae is an example of a taxon with representatives in the north and south temperate regions, but which is absent in the tropics. Crowson (1980: 290) offers two hypotheses regarding the origins of such disjunct distributions: 1) the group formerly had members in the tropics which have subsequently become extinct; 2) the group has always been climatically limited in the way it is today, and that any crossing of tropical regions took place in exceptional circumstances. Rather than invoke the breakup of Pangaea to

explain how taxa could become isolated in this manner, Crowson (1980) postulates a high mountain range(s) connecting the north and south temperate regions, but then states that there is no geological proof for this. In any case, Crowson (1980) gives no later than Early Oligocene as the time of separation of northern from southern groups. In fact, according to Noonan (1986), the final break between Laurasia and Gondwanaland, occurred much earlier, in the Late Jurassic. Taking into consideration Watt's (1987) classification, and the recent concepts concerning continental drift, one must assume that the split between the northern and southern elements of Pythinae occurred with the breakup of Pangaea, which was completed in the Jurassic.

Important in the evolution of Pythinae or any group of insects is not only historical changes in geography, but also life history. This aspect may play a major role in the evolution of Pythinae. Hamilton (1978) suggests that taxa which are subcortical in life habit tend to be relict species. This may be true in Pythidae, in which three of four genera are monobasic. For the northern constituents of Pythinae, two of the genera (Sphalma, Pytho) have larval stages which live beneath the outer bark of deciduous and coniferous trees respectively. Larvae of these genera are flattened dorsoventrally and have well-developed legs. Priognathus monilicornis is unique in that its larval stage feeds on the inner components of rotting coniferous trees. As a result, the larva is subcylindrical, with more poorly-developed legs. It is not known whether the habitat divergence occurred more or less simultaneously with the vicariance event which delimited Pytho and Priognathus. It is possible that both genera were initially subcortical in habit when they

were separated. When they again came into contact through dispersal, Pytho may have proven a better competitor, forcing Priognathus into a new area of the dead tree habitat. It may also be probable that Priognathus developed its unique life habit once it became isolated from Pytho. This may also explain why Pytho is relatively more diverse in species than Priognathus. The fact that Sphalma lives beneath bark of dead deciduous trees (Young 1976) may account for the lack of diversity within that genus. Larvae of members of the family Pyrochroidae, represented in North America by 15 species (Young 1975) occur predominantly beneath the bark of dead, deciduous trees. This would involve both Sphalma and Pyrochroidae utilizing the same habitat, the latter of which may be better competitors than the former. Pytho is comparable to the pyrochroid subfamily Pyrochroinae, in that both groups are the dominant taxa of Coleoptera in coniferous and deciduous trees of approximately similar stages of decay. This subcortical habit is not uncommon in Heteromera, and several families allied to Pythidae have larval stages which feed beneath bark (Howden and Howden 1981, Watt 1987). The sister taxon to Pythidae, which according to Watt (1987) is Boridae, has two genera, the larvae of which feed on subcortical layers in decaying coniferous trees. Thus, the primitive feeding type within Pythinae is subcortical in decaying coniferous trees.

11.3 ZOOGEOGRAPHY OF CLADES OF PYTHO

11.3.1 Introduction

Four species-groups, or clades have been proposed among world species of Pytho (figure 14). Each species-group in Pytho was examined and the present distribution explained in the context of accepted geological events in the Northern Hemisphere. The establishment of a minimum age for Pytho is very difficult, given the available data. However, Crowson (1975) suggests that Pythidae may have been associated with coniferous trees since the Jurassic.

Critical to my biogeographic analysis is the poor ability of adults of Pytho to disperse, because relatively short distances exist between Alaska and adjacent U.S.S.R., and between mainland Asia and Japan. I am assuming, in spite of the lack of supporting evidence, that adults of Pytho have relatively low vagility. The facts leading me to this assumption are: 1) according to label data and personal observation, Pytho adults are usually collected from under the bark of coniferous trees, and very rarely while they are in flight; 2) the habitat in which Pytho is found, is relatively uniform, and the beetles need not disperse long distances in order to colonize new host trees. Members of Pytho are capable of dispersing, but only through continuous areas of coniferous forest. There are no references to document the ability of adults of Pytho to disperse relatively long distances. Another method by which Pytho species may be dispersed is by rafting, within coniferous trees. There is no evidence to refute this. If it is found that adults of Pytho can and do disperse over long distances, the hypotheses presented here will need to be revised, or at least have alternatives

with emphasis on dispersal. Indeed, the hypotheses presented below rely on post-vicariance dispersal to account for the present distribution of the various species. However, I believe that dispersal over relatively long distances, especially across bodies of water must be discounted as a mechanism by which the species of Pytho have differentiated and come to occupy their present distributions.

11.3.2 P. seidlitzii-group

This lineage consists of one species, P. seidlitzii, the most plesiomorphic species. This species is isolated in North America, where it occurs without significant gaps longitudinally. There is no Palearctic sister species. Thus P. seidlitzii failed to disperse across the Beringian land bridge in the Miocene when this area was covered with coniferous forest (Matthews 1979, 1980). Alternatively, P. seidlitzii may have been more widespread in the Holarctic region, with subsequent extinction in the Palearctic.

11.3.3 P. kolwensis- and P. niger-groups

The general distributions of these two clades are similar and are treated here together. Both groups have a North American species which is predominantly eastern in distribution. Pytho strictus is restricted to eastern North America, while P. niger is more widespread. Although considerably more widespread than P. strictus, there is evidence that P. niger may have originally been eastern. This latter species is known from British Columbia by a single specimen only. Pytho niger may have only relatively recently begun to disperse westward.

The second component of both species-groups is a species in Europe. Pytho kolwensis and P. abieticola are both regarded as being quite rare in Europe. The former species is known from Finland, Sweden, Poland and various localities in the U.S.S.R. as far east as Lake Baikal. Pytho abieticola is known from Fennoscandia and north, central Europe. The range of P. kolwensis is larger than that of P. abieticola. If only one vicariant event is responsible for both species' distributions, either of the species has increased and/or decreased its range subsequent to the vicariant event.

The third of the three species in each of the P. kolwensis- and P. niger-groups occurs in Japan. Pytho nivalis and P. jezoensis occur in coniferous forested regions of Japan. Pytho jezoensis is distinct from its European counterpart, P. abieticola. However, P. nivalis may be conspecific with P. kolwensis. These two species have been treated as separate in this study.

Both the P. kolwensis- and P. niger-groups exhibit a North American, European, Japanese distribution. This scenario is apparently common among north temperate groups of insects, as outlined in Allen (1983). In his examination of various monophyletic arthropod lineages, Allen (1983: 624) demonstrates that faunas of Europe and eastern North America have shared a more recent ancestor than either fauna has with Asia. This fact is in conflict with the hypothetical relationships among members of the P. kolwensis-group in which the European and Japanese species share a more recent common ancestor than either shares with the North American member. However, as noted above, the European and Japanese representatives of the P. kolwensis-group may be conspecific.

As indicated in the cladogram depicting the hypothesized phyletic relationships among species of Pytho, there is an unresolved trichotomy among species of the P. niger-group. It is possible that these three species have shared a similar geographic history to those in the P. kolwensis-group, so that P. abieticola and P. jezoensis would be sister species. Together, they would form the sister taxon of the North American species, P. niger.

Because of the similarity of the distributions of these two species-groups, the same sequence of vicariance events may have been responsible for both. There are at least two seemingly plausible explanations for a North America-Europe-Japan disjunction based on vicariance biogeography and the data collected in this study of Pytho. One may have been a trans-Beringian ancestor. Two distinct populations were then present following climatic deterioration, The Palearctic component was further vicariated into two species when Japan split from mainland Asia. The second hypothesis is similar, except that the ancestor was Euramerican. Separation into Nearctic and Palearctic vicars occurred with the opening of the North Atlantic in the Cretaceous (Noonan 1986).

When examining the patterns exhibited by only the P. kolwensis- and P. niger-groups, it is difficult to choose between the two hypotheses. However, comparison with the P. depressus-group gives more credence to the Euramerican ancestor hypothesis. The qualitative, or phenetic differences between adults of P. planus and P. depressus are the least among species pairs in the entire genus. These two species have separated more recently than either P. strictus and P. kolwensis + P.

nivalis, or P. niger and P. abieticola + P. jezoensis. The distributions of both P. planus and P. depressus are collectively circumboreal, and although this is a product of post-glacial climatic amelioration, there may have been a trans-Beringian ancestor, as discussed below. This supposition leads me to conclude that separation of the Nearctic and Palearctic components of the P. kolwensis- and P. niger-groups was relatively earlier. The concept of Euramerica, advocated in Hallam (1981), Allen (1983) and Noonan (1986) seems entirely possible in an explanation of the North America - Europe - Japan pattern of distribution among species of Pytho.

11.3.4 P. depressus-group

This clade is composed of a Nearctic-Palearctic species pair, P. planus and P. depressus, respectively. These two species are widespread, collectively circumboreal, and morphologically similar. Consequently, a relatively recent vicariant event which divided the range of their common ancestor. During the Tertiary, in the area of Beringia, this ancestral species probably extended across the land bridge in the Miocene, when this region was covered by coniferous forests (Matthews 1979, 1980). Once treeless conditions were imposed on Beringia, the two populations were effectively separated. During Pleistocene glaciation, P. planus and P. depressus followed the retreat of coniferous forest, and subsequently have attained their full present distributions once these forests moved back to higher latitudes.

11.3.5 Pleistocene events

It is now generally accepted that during the Pleistocene Epoch, much of the land mass in the Northern Hemisphere was covered by ice (Matthews 1979, 1980; Whitehead 1973; Lindroth 1953). Because of the predominantly northern distribution of species of Pytho, these recent events have had direct effect upon their present distributions. In North America, the great majority of the land presently inhabited by members of Pytho was covered by glacial ice in the Wisconsin age (Matthews 1979). The important question to be answered with respect to Pytho, as well as any other taxa of predominantly northern insects, is where did these beetles survive during glaciation.

Lindroth (1970) discusses the two types of refugia, namely "open" and "closed". An example of each, respectively, is the southern United States, and Beringia. Clearly, for a refugium to be suitable for members of Pytho, it must have also similarly been suitable for at least one species of coniferous tree. Although the Beringian refugium was important for Carabidae (e.g. Ball 1963; Lindroth 1970) it does not appear to have functioned similarly for Pytho. According to Lindroth (1970) and Matthews (1979), the Beringian refugium was not forested. The tree genera Picea and Pinus were displaced southward in front of advancing ice sheets (Matthews 1979; Ritchie and MacDonald 1986). Picea glauca survived glaciation in the United States between 40 and 35 degrees latitude (Ritchie and MacDonald 1986). Pines were displaced even further south (Whitehead 1973), and Matthews (1979) suggests that a pine refugium may have existed in the area of the southern Atlantic United States. Once the ice began to retreat northward, the boreal

forest followed closely (Matthews 1979). Ritchie and MacDonald (1986) suggest that P. glauca spread approximately 2,000 km in 1,000 years. It is natural to assume that members of Pytho followed conifers south and then north again.

A similar situation existed in Europe during the Pleistocene, in which most of the area north of the Alps was either tundra or polar desert (Matthews 1979). There is some controversy concerning the existence of an ice-free refugium in Fennoscandia (Lindroth 1970; Nordal 1987). Originally, it was assumed that all of Fennoscandia was covered with ice (Lindroth 1953), but recently, a refugium along the west coast of Norway has been postulated (Nordal 1987). It is probable that European species occupied a refugium south of the ice sheet, perhaps in the region of the Alps. The modern distributions of the three species in Europe is a reflection of the northward movement of the coniferous forest during the present interglacial interval.

Regardless of Pleistocene refugia in which members of Pytho survived, the events leading to speciation occurred much earlier, based on the reduced powers of flight and the nature of coniferous forest in the Northern Hemisphere throughout the Cenozoic and Quaternary Periods. Since there is no known fossil record for Pytho, a minimum age of origin of the genus and of the various lineages is impossible to document. It would be quite valuable to locate fossils of Pytho from both the Cenozoic and Quaternary. From the evidence available, the larval stage of Pytho has maintained some degree of morphological stasis, when compared to the adult. If fossil larvae were available, the zoogeographic and phylogenetic hypotheses discussed above could be critically tested.

Chapter XII

CONCLUDING REMARKS

In this treatment of members of the genus Pytho, I have endeavoured to provide an evolutionary portrait of a relatively little known group of beetles. Hopefully, the data presented here will change the previous obscurity of Pytho.

In my examination of the natural history and habits of the various stages of Pytho, I was surprised to discover how little was known about the Nearctic species relative to those of the Palearctic. Reasons for this are unclear, but it may be due to the relative economic insignificance of members of Pytho. The development of the rearing system used in this study has enabled the association of all life stages of the Nearctic species.

The taxonomic treatment presented here may disappoint some of the "lumpers" among Coleoptera taxonomists. I have chosen a somewhat conservative tack, and have not established any Holarctic species in Pytho. Such synonymies have been proposed in the literature, but are discounted here. For adults, characters were found which indicate species status within the species-groups. However, the corresponding larvae are indistinguishable morphologically within species-groups. This difference in divergence between adult and larval stages is intriguing; biochemical analysis, through the use of electrophoresis may prove useful for determining possible divergence of larvae within species-groups.

One of the objectives in this study was to use larvae in association with adults and to determine if the larval stage could contribute to the classification of Pytho. Clearly, this has been demonstrated. Larval stage characters were very valuable in delimiting relationships among the species-groups of Pytho. Once the pupae of the two Japanese species of Pytho, as well as all related genera, become known, characters of this life stage may be incorporated into the classification also. Hopefully, my use of larval stage characters will help relieve the over-reliance of many insect systematists on strictly adult stage characters.

For the chapter on zoogeography, I have relied heavily upon geologic and paleontologic literature in which the events which have shaped modern faunas and floras are documented. Various assumptions had to be made, including allopatric speciation and low powers of dispersal, to come to my zoogeographic conclusions. Because of the reliance of members of Pytho on coniferous trees, the two entities generally have shared similar fates and distributions through time. This relationship has important implications concerning times of separation of sister species. For example, even though the Bering land bridge existed in the Pleistocene, it was probably treeless and therefore a barrier to dispersal by adult Pytho. If Pytho adults are capable of relatively long-distance dispersal, many of the times of separation of taxa will be more recent than proposed here. As well, a strict vicariance explanation, such as advocated here, may have to be combined with a dispersal paradigm.

Even though species of Pytho do not inflict economic damage upon the forest industry, the genus is certainly worthy of detailed examination, such as I have accomplished here. I believe that my treatment of Pytho has fulfilled my objectives, and may serve as a model for subsequent similar generic revisions. This is especially true for many taxa in Heteromera, which need detailed examination with data taken from as many sources and life stages as possible. Watt's (1987) work on the higher classification within Pythidae can be considered a pioneering effort, even though the work is quite recent. Although Watt (1987) did only a preliminary study important conclusions were reached. These have shaped to a great extent, my thoughts on the classification of Pythinae and of Pytho. The conclusions reached here may be combined with those of Watt (1987) and Young (1976) to provide a fuller picture of the classification of a small, yet complex group of beetles.

Chapter XIII

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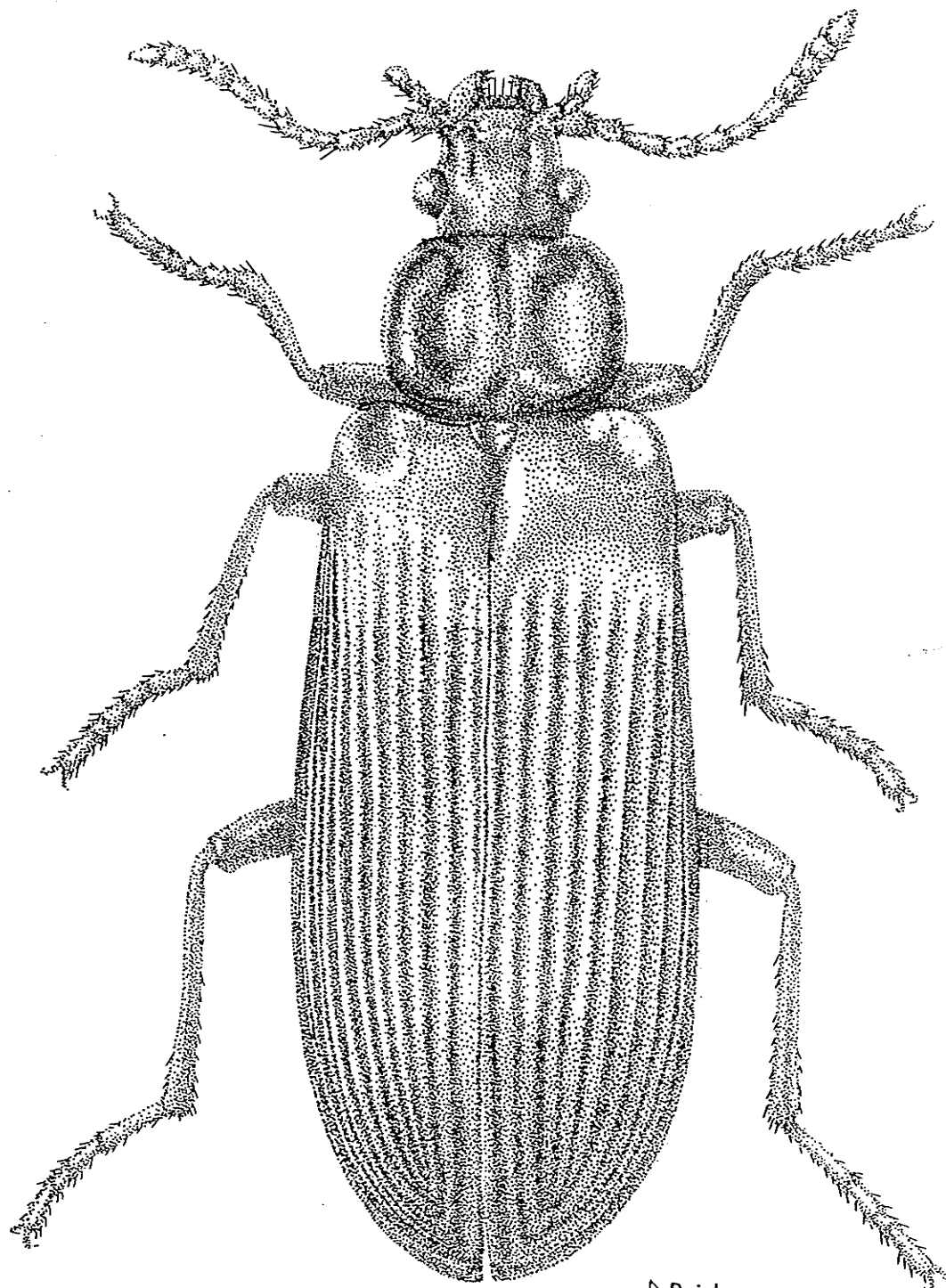
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Figure 1. Dorsal habitus of the adult stage of P. seidlitzii Blair
[total length of specimen = 14.1 mm] (drawn by Lisa A.
Reichert).



Reichert

Figure 2. Pronota of adult stages of species of Pytho Latr. A. P. seidlitzii; B. P. strictus, C. P. kolwensis; D. P. nivalis; E. P. niger, F. P. abieticola, G. P. jezoensis, H. P. planus, I. P. depressus [scale bar = 1 mm] (drawn by Lisa A. Reichert).

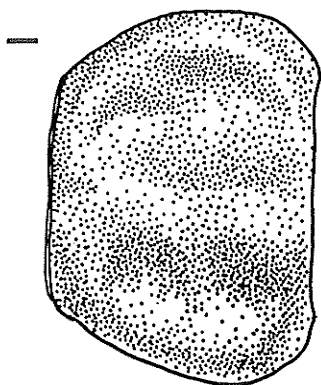
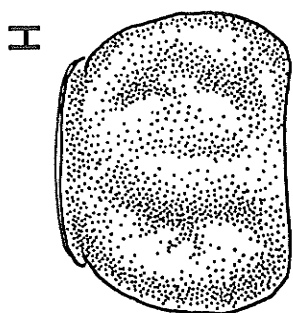
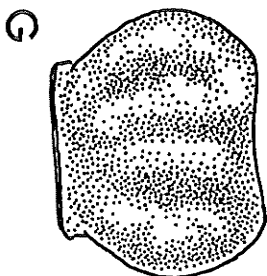
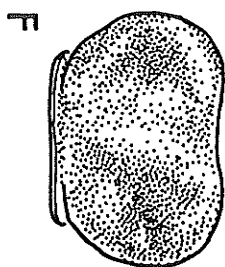
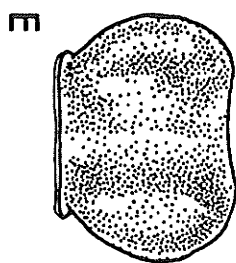
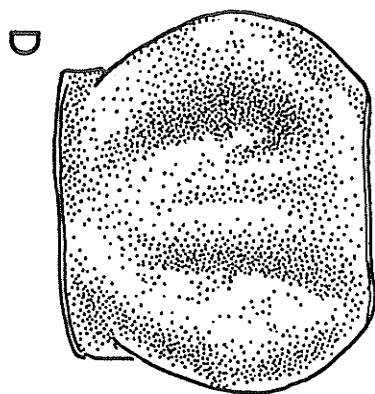
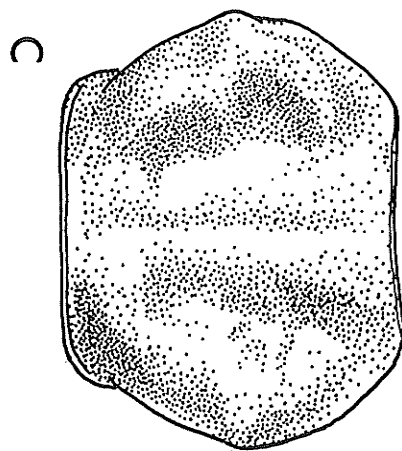
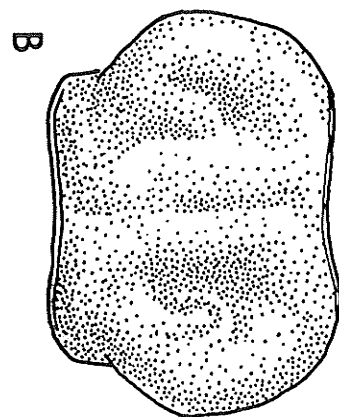
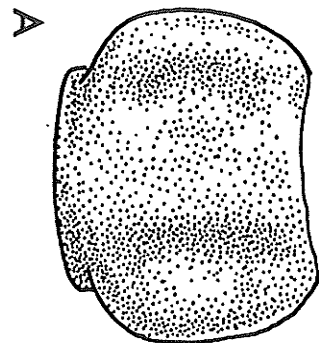


Figure 3. Male genitalia of selected species of Pytho Latr. A. P. seidlitzii, ventral view of eighth and ninth sternite, eighth tergite, and aedeagus; B. P. seidlitzii, lateral view of aedeagus, median lobe removed; C. P. seidlitzii, ventral view of aedeagus, median lobe removed; D. P. planus, ventral view of aedeagus, median lobe removed; E. P. planus, lateral view of median lobe; F. P. depressus, ventral view of aedeagus, median lobe removed [scale bar = 1 mm]. al = accessory lobe; ap = apicale; ba = basale; fp = fused paramere; ml = median lobe; sp = spiculum; s8 = eighth sternite; s9 = ninth sternite; t8 = eighth tergite.

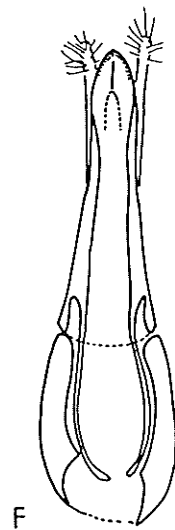
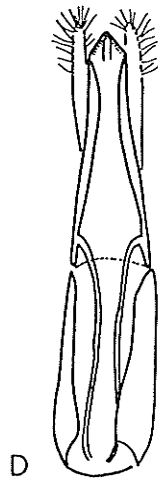
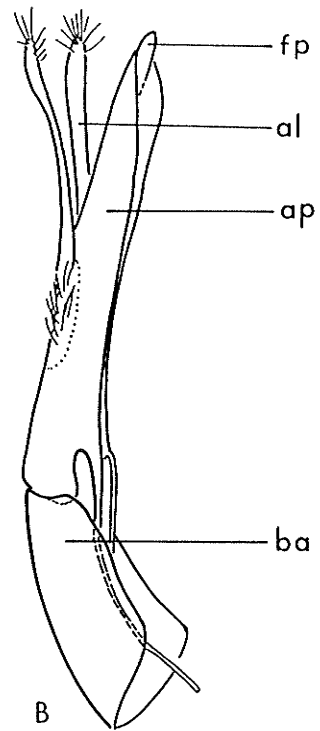
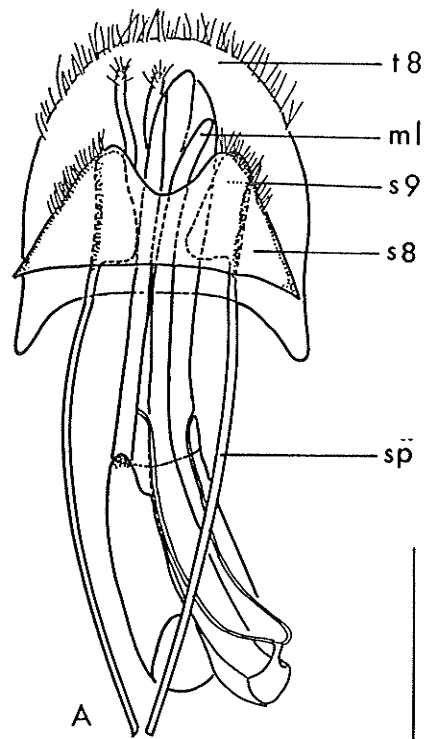


Figure 4. Female ovipositor, hindwing, and metendosternite of selected species of Pytho Latr. A. P. niger, ventral view of female ovipositor, also showing baculi from dorsal surface [terms from Wheeler (1986)] [scale bar = 0.5 mm]; B. P. niger, venation of right hindwing [scale bar = 5 mm]; C. P. seidlitzii, ventral view of metendosternite [scale bar = 1 mm]. cb = coxital baculus; cf = coxital fold; co = coxite; la = lamina; mg = median groove; pb = proctigeral baculus; st = stylus; va = valvifer; vb = valviferal baculus; 1A = first anal vein; 2A = second anal vein; Cu = cubital vein; M = medial vein; r-m = radio-medial crossvein; R = radius; RC = radial cell; W = wedge cell.

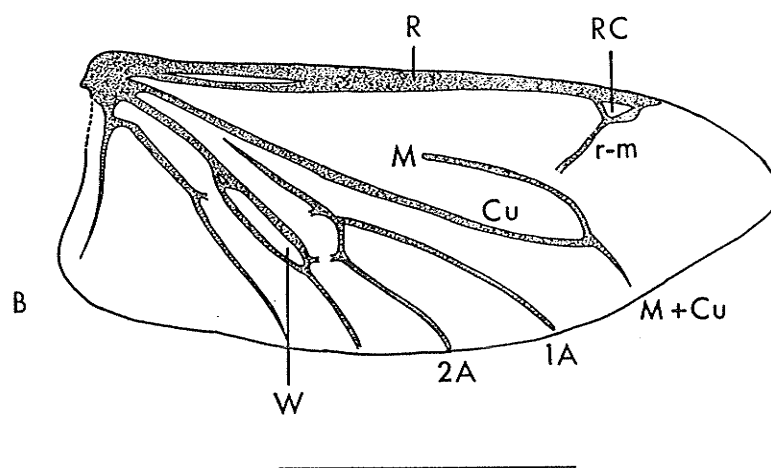
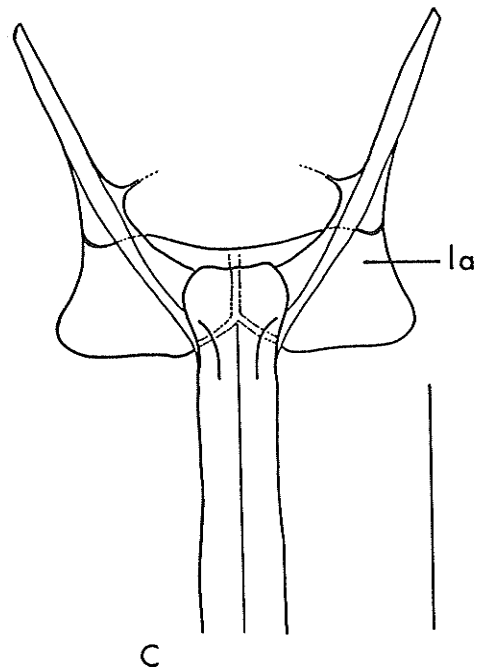
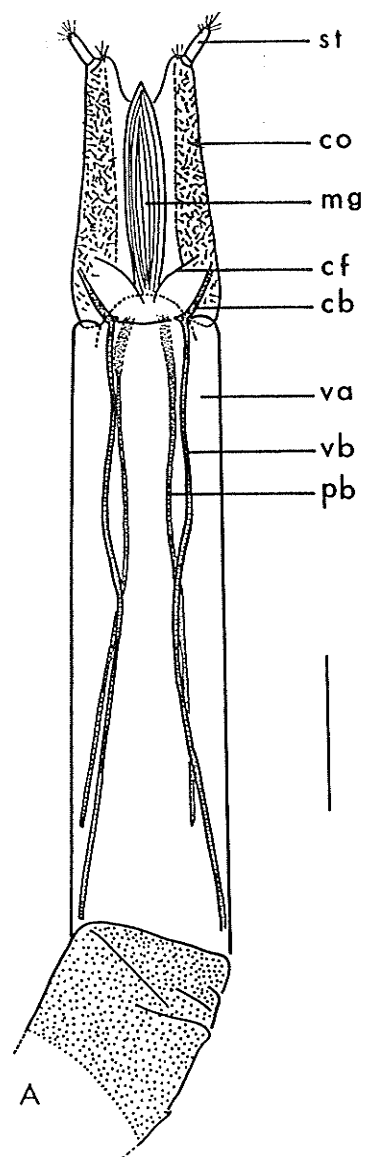


Figure 5. Scanning electron micrographs of head structures of selected adult stages of *Pytho* Latr. A. *P. seidlitzi*, detail of sensilla on apices of antennomeres 8-10 (160 x). [sensilla have been dislodged during cleaning of the specimen] [scale bar = 0.1 mm]; B. *P. planus*, apical maxillomere (200 x) [scale bar = 0.1 mm]; C. *P. planus*, male, ventral view of mouthparts (80 x) [scale bar = 0.2 mm]; D. *P. planus*, male, ventral view of mentum, showing sensilla in pit (400 x) [scale bar = 0.05 mm].

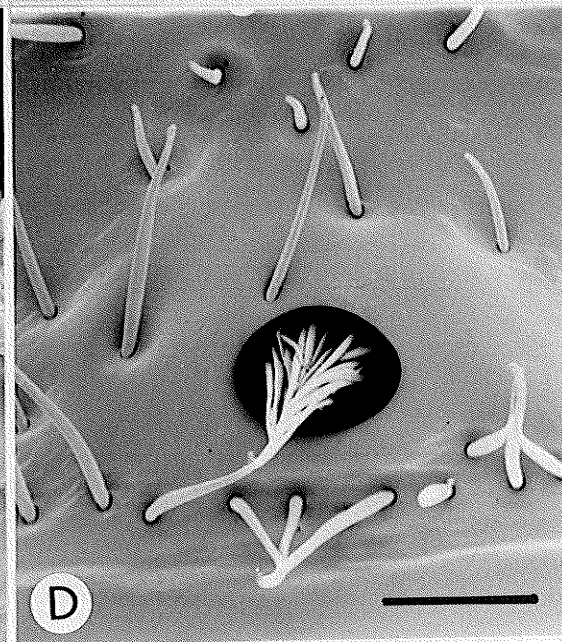
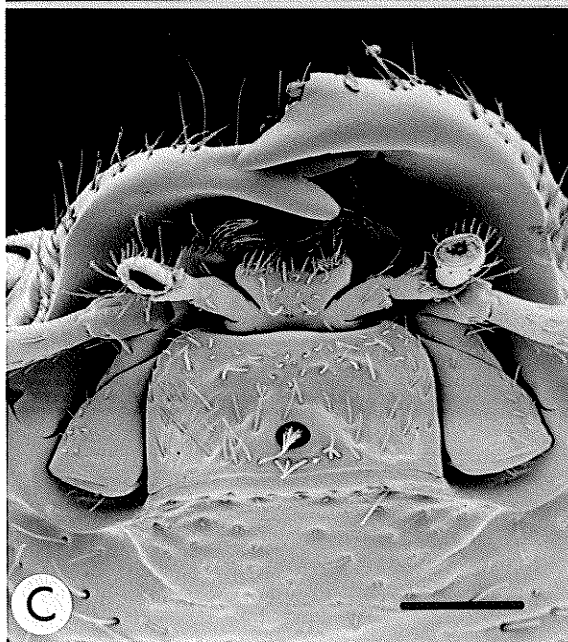
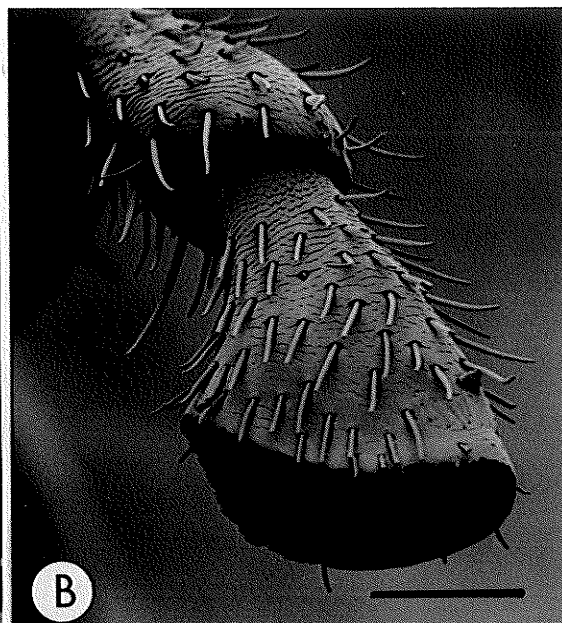
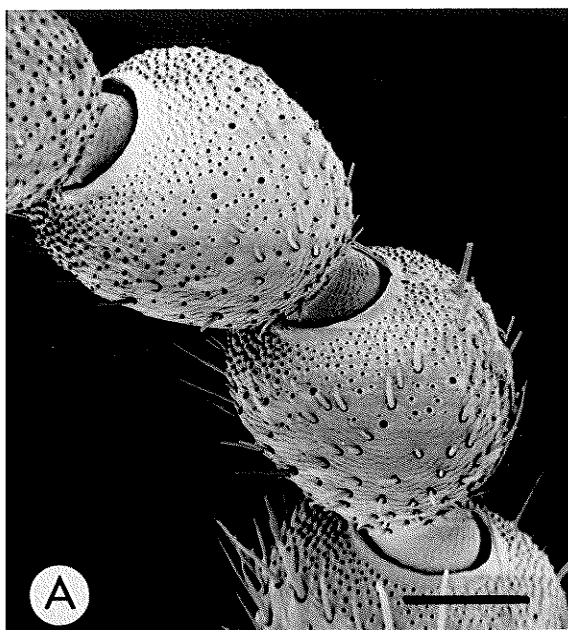


Figure 6. Scanning electron micrographs of structures on the pro- and mesothorax of selected adult stages of Pytho Latr. A. P. niger, ventral view of prosternal process (120 x) [scale bar = 0.1 mm]; B. P. seidlitzii, ventral view of prosternal process (160 x) [scale bar = 0.1 mm]; C. P. seidlitzii, mesosternum (45 x) [scale bar = 0.4 mm]; D. P. seidlitzii, detail of mesepisternum and mesepimeron (80 x) [scale bar = 0.2 mm].

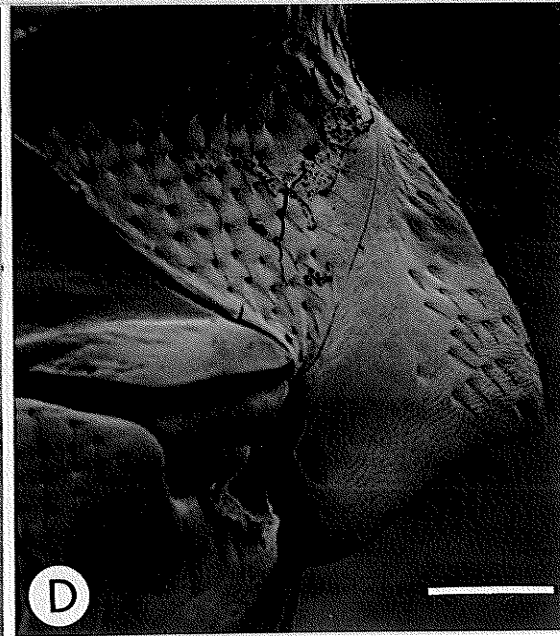
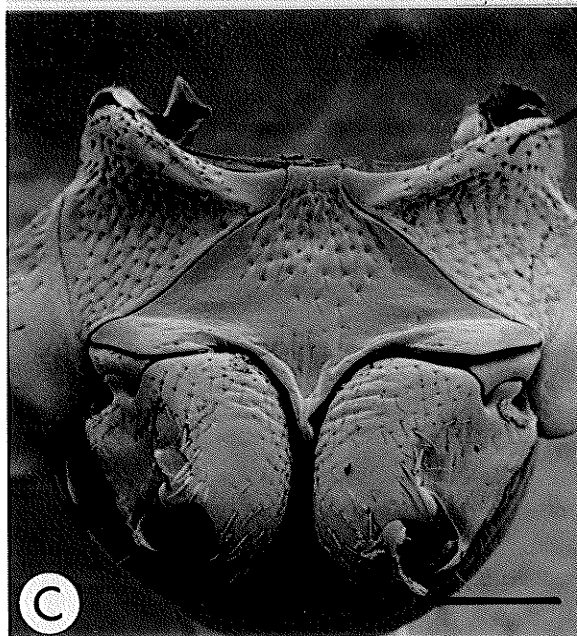
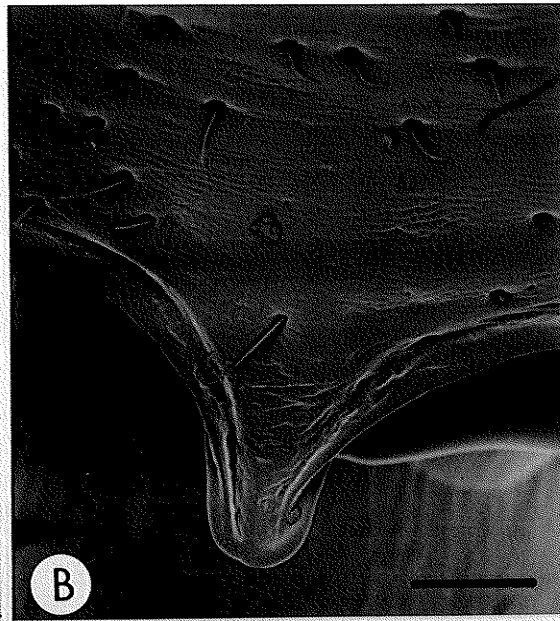
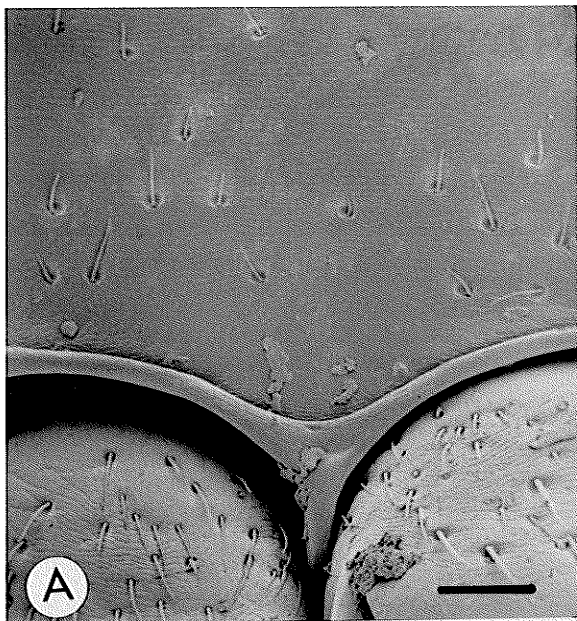


Figure 7. Scanning electron micrographs of the mesothorax of selected adult stages of Pytho Latr. A. P. abieticola, lateral region of mesosternum (180 x) [scale bar = 0.1 mm]; B. P. niger, mesosternum (45 x) [scale bar = 0.4 mm]; C. P. abieticola, mesosternum (90 x) [scale bar = 0.2 mm]; D. P. abieticola, detail of mesepisternum and mesepimeron (90 x) [scale bar = 0.2 mm].

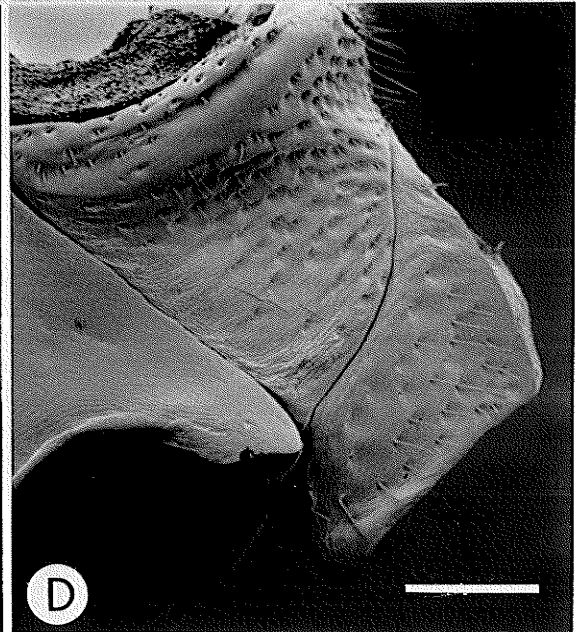
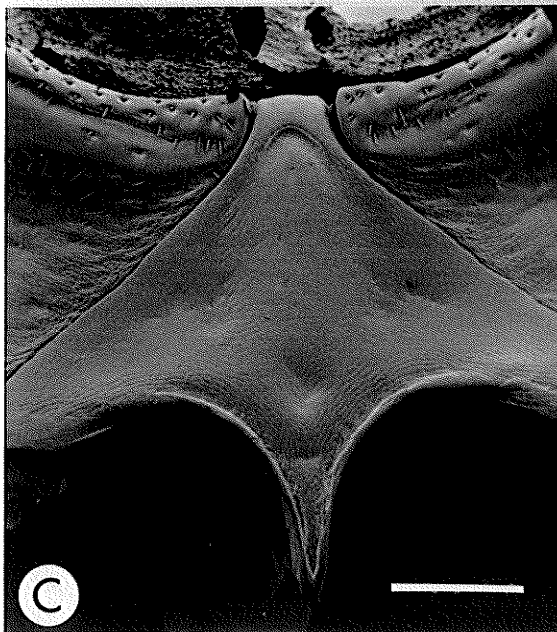
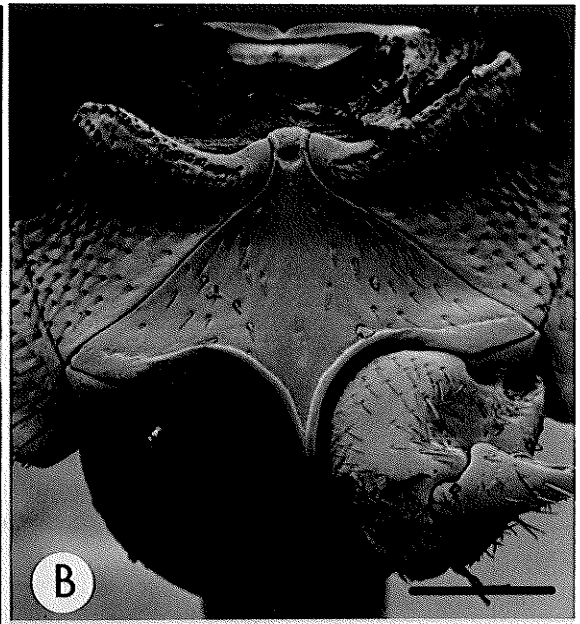
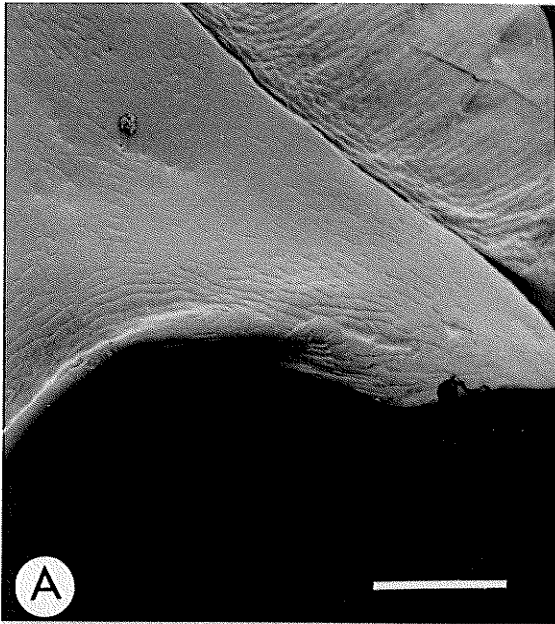


Figure 8. Scanning electron micrographs of the tarsus, elytron, and aedeagus of selected adult stages of Pytho Latr. A. P. niger, female, oblique lateral view of apical tarsomere (160 x) [scale bar = 0.1 mm]; B. P. seidlitzii, detail of elytral disc (100 x) [scale bar = 0.2 mm]; C. P. planus, posterolateral margin of left elytron (90 x) [scale bar = 0.2 mm]; D. P. planus, male, detail of apicoventral region of apicale (500 x) [scale bar = 0.05 mm].

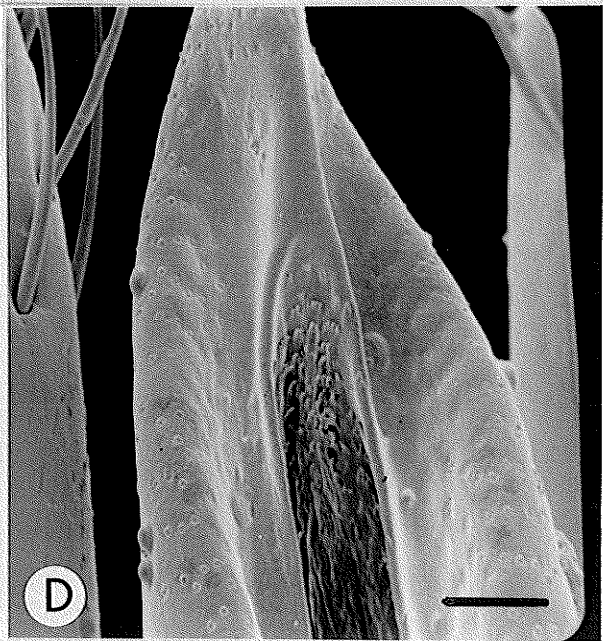
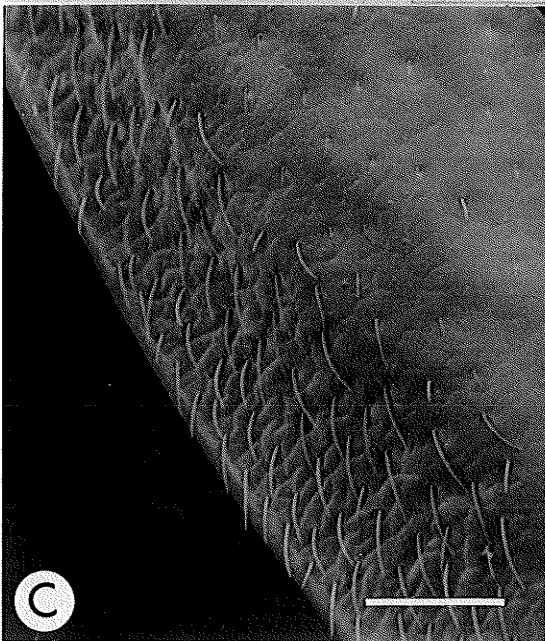
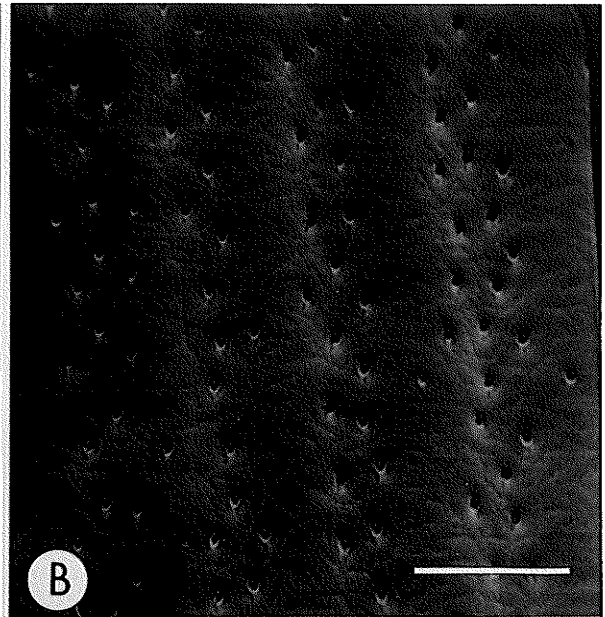
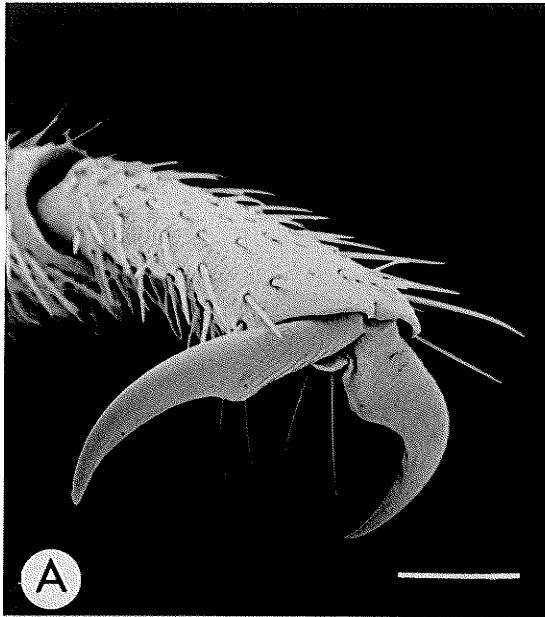


Figure 9. *P. planus*, habitus of larval stage. A. Dorsal habitus; B. Ventral habitus [scale bar = 5 mm]. as = row of asperities; cs = cervicosternum; es = epicranial suture; pp = parabasal ridge process; pr = parabasal ridge; ps = parabasal setae; tu = urogomphal tubercles; ul = urogomphal lip; up = urogomphal plate; ur = urogomphus.

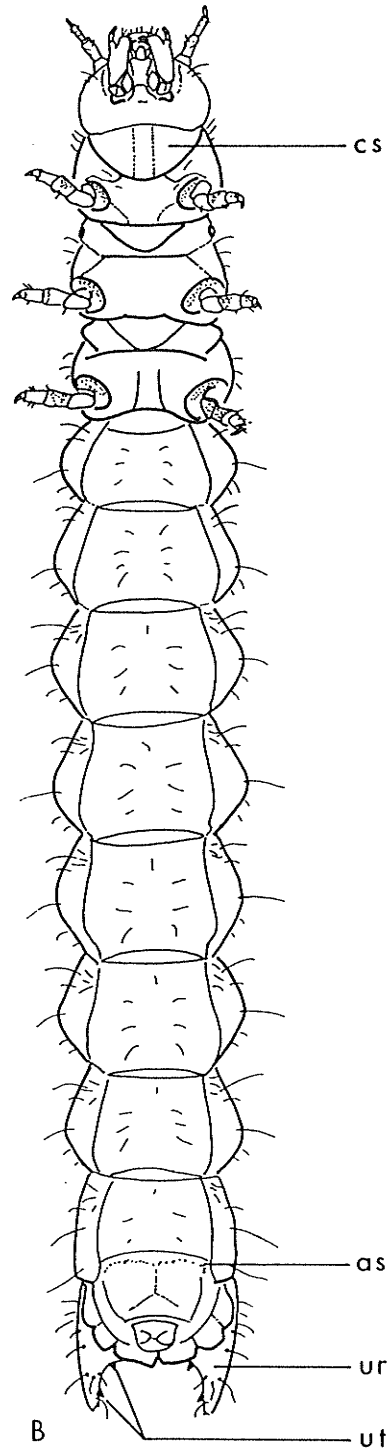
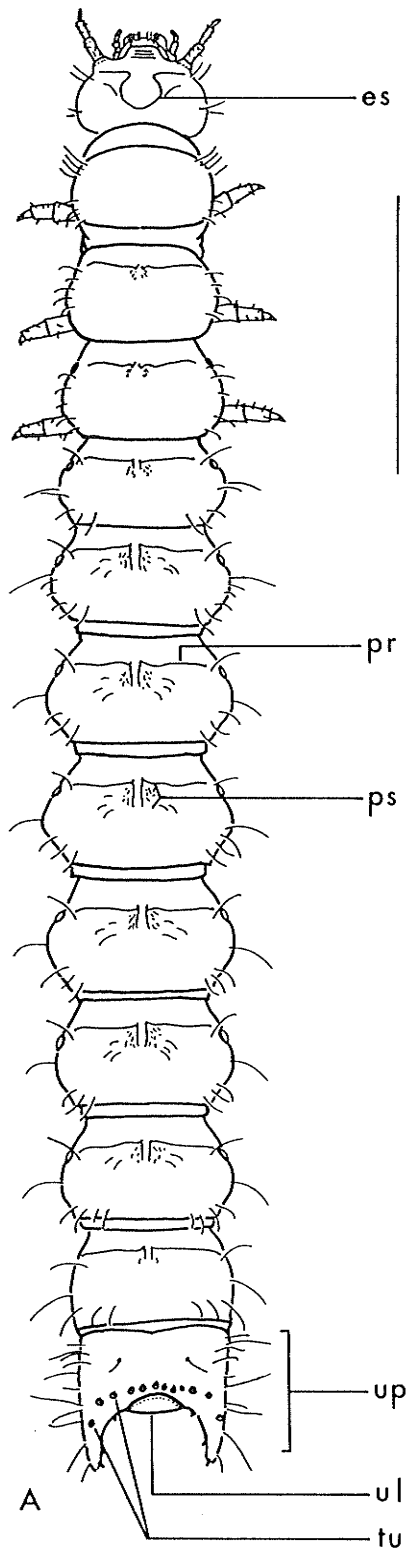


Figure 10. Legs and mouthparts of the larval stage of selected species of Pytho Latr. A. P. niger, anterolateral view of foreleg; B. P. niger, anterolateral view of middle leg; C. P. niger, anterolateral view of hind leg [scale bar = 1 mm]; D. P. seidlitzii, ventral view of left maxilla; E. P. seidlitzii, dorsal view of left mandible; F. P. seidlitzii, dorsal view of right mandible [scale bar = 0.25 mm]. ca = cardo; ma = maxillary articulating area; ca = cardo; ma = maxillary articulating area; mo = molar area; st = stipes; un = uncus.

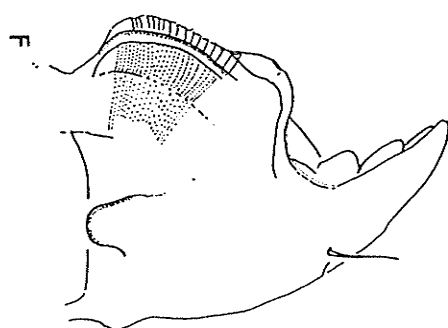
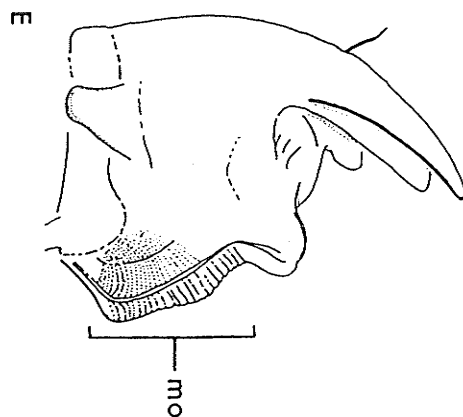
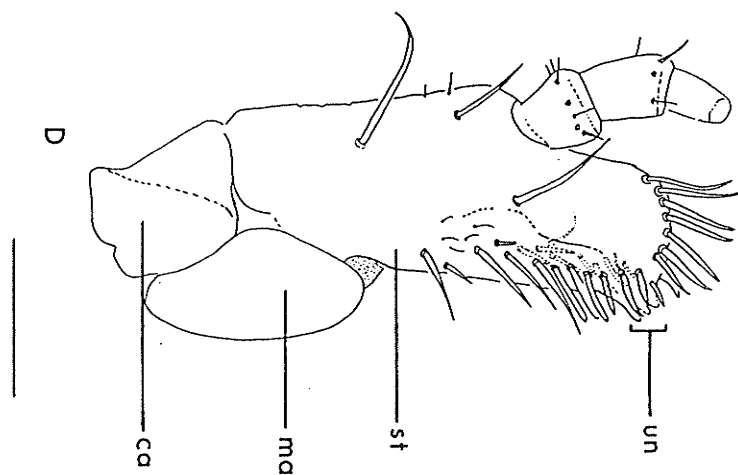
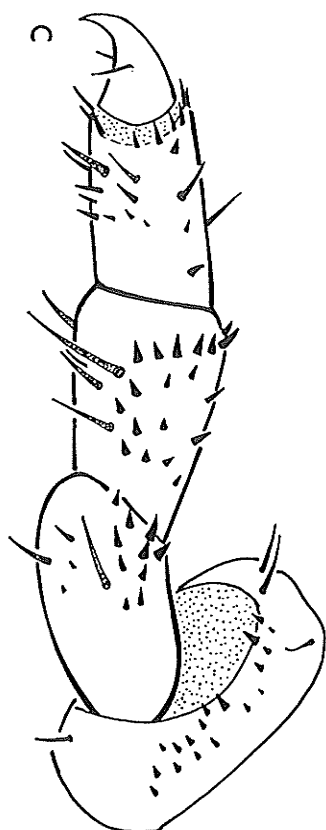


Figure 11. Third abdominal tergites of representative larval stages of the species-groups of Pytho Latr. A. P. seidlitzii-group (P. seidlitzii); B. P. kolwensis-group (P. strictus); C. P. niger-group (P. abieticola); D. P. depressus-group (P. depressus) [scale bar = 1 mm].

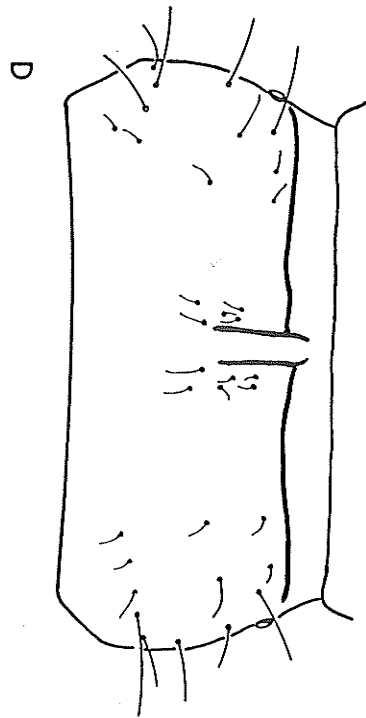
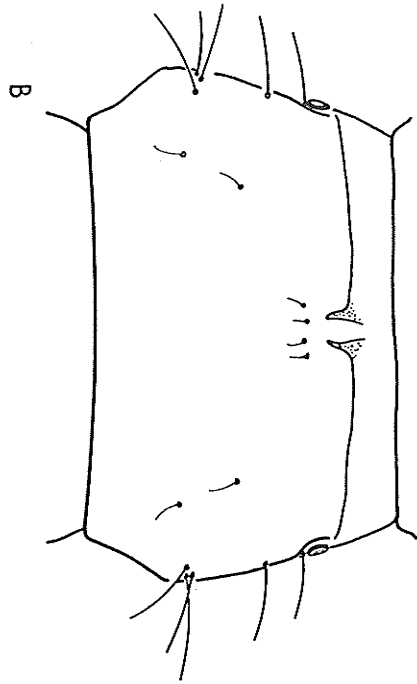
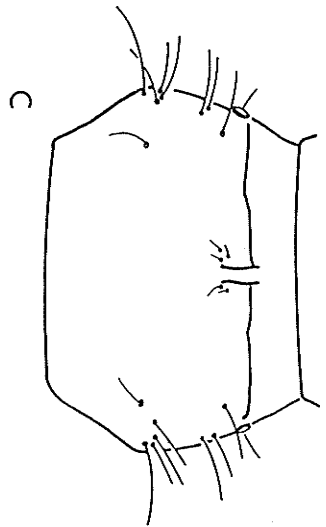
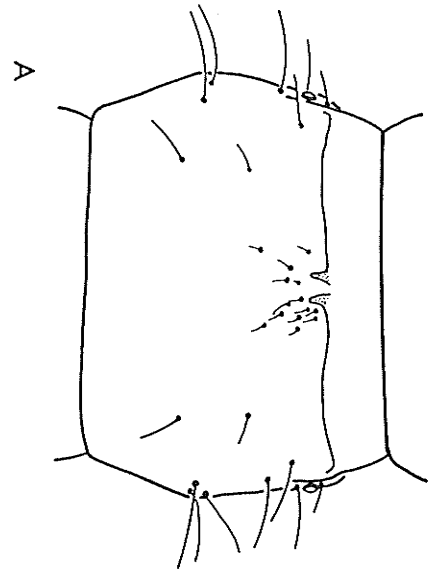
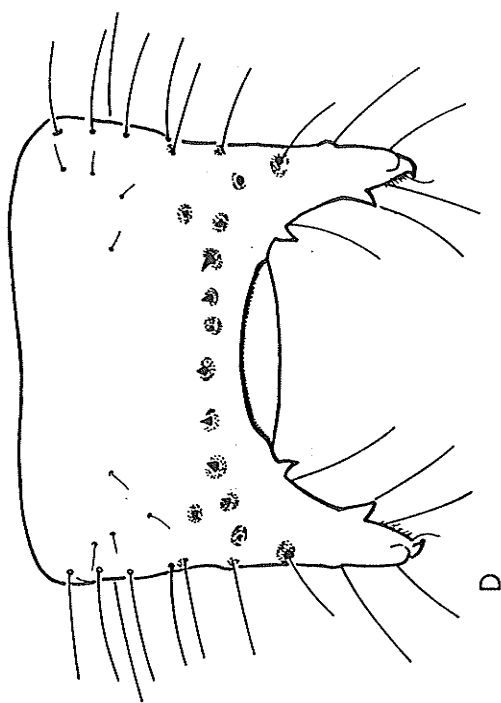
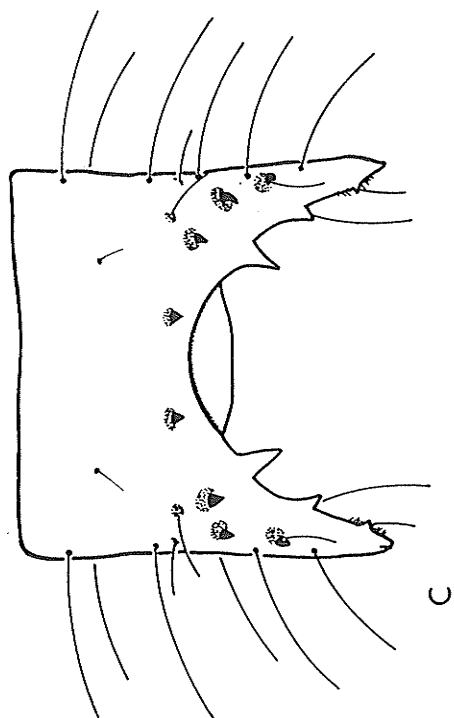
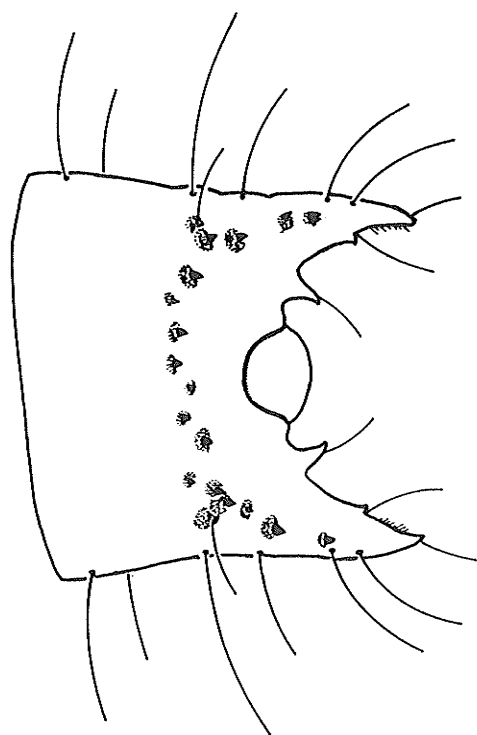


Figure 12. Urogomphal plates of representative larval stages of the species-groups of Pytho Latr. A. P. seidlitzii -group (P. seidlitzii); B. P. kolwensis-group (P. kolwensis); C. P. niger-group (P. niger); D. P. depressus-group (P. planus) [scale bar = 1 mm].

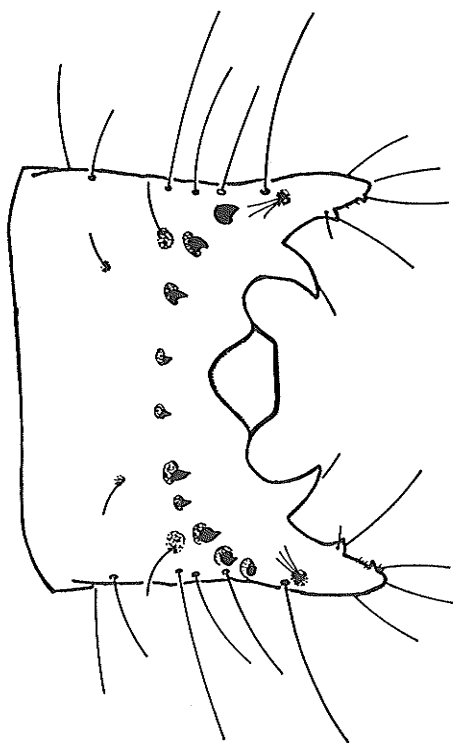


C

D



A



B

Figure 13. Dorsal and ventral habitus, and detail of third abdominal tergite and sternite of the pupa of selected species of *Pytho* Latr. A. *P. planus*, ventral habitus [scale bar = 5 mm]; B. *P. abieticola*, dorsal habitus [scale bar = 5 mm]; C. *P. seidlitzii*, detail of tubercle arrangement on third abdominal tergite (right pleural tubercle has been omitted to show arrangement of lateral marginal tubercles); *P. seidlitzii*, detail of tubercle arrangement on third abdominal sternite [scale bar = 1 mm]. dt = discal tubercles; pm = posterior marginal tubercles; pr = pronotal tubercles; pt = pleural tubercle.

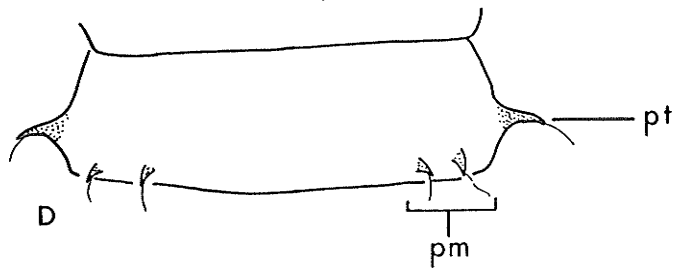
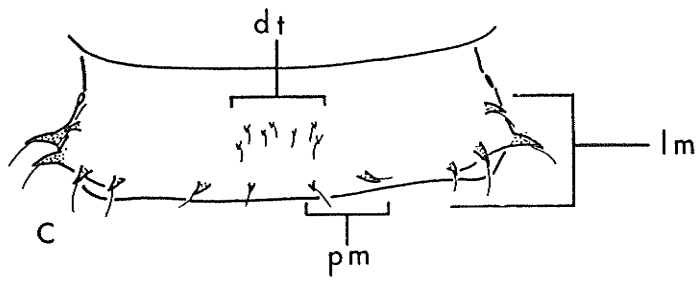
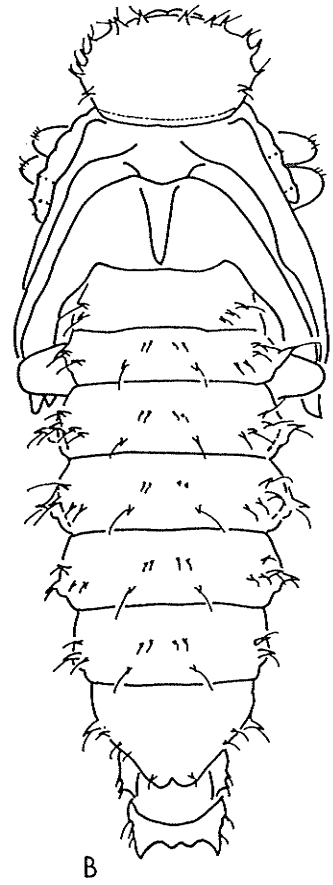
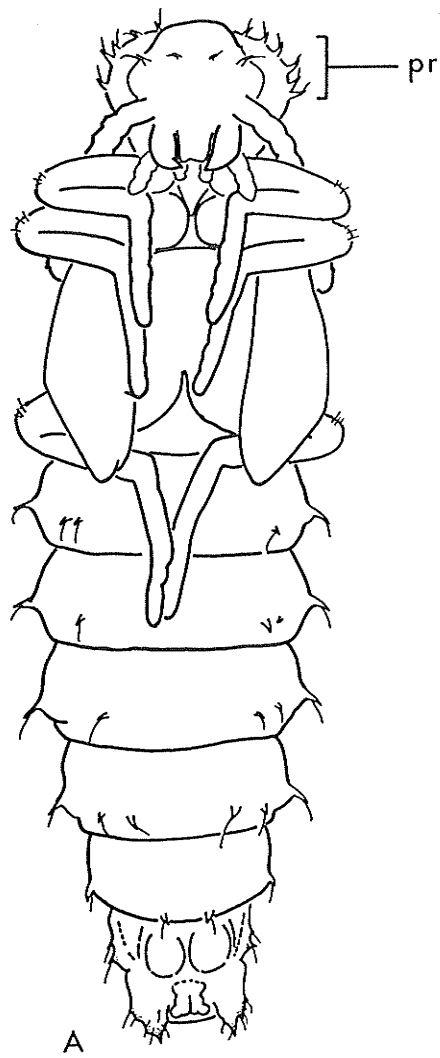


Figure 14. Cladogram of the hypothetical phylogenetic relationships among world species of Pytho Latr. Open rectangles represent plesiomorphic character states; half-filled rectangles represent larval stage synapomorphies; filled rectangles represent adult stage synapomorphies. An exclamation mark (!) denotes those derived character states thought to have arisen independently. An apostrophe (') is used to indicate the very derived state of character 2.

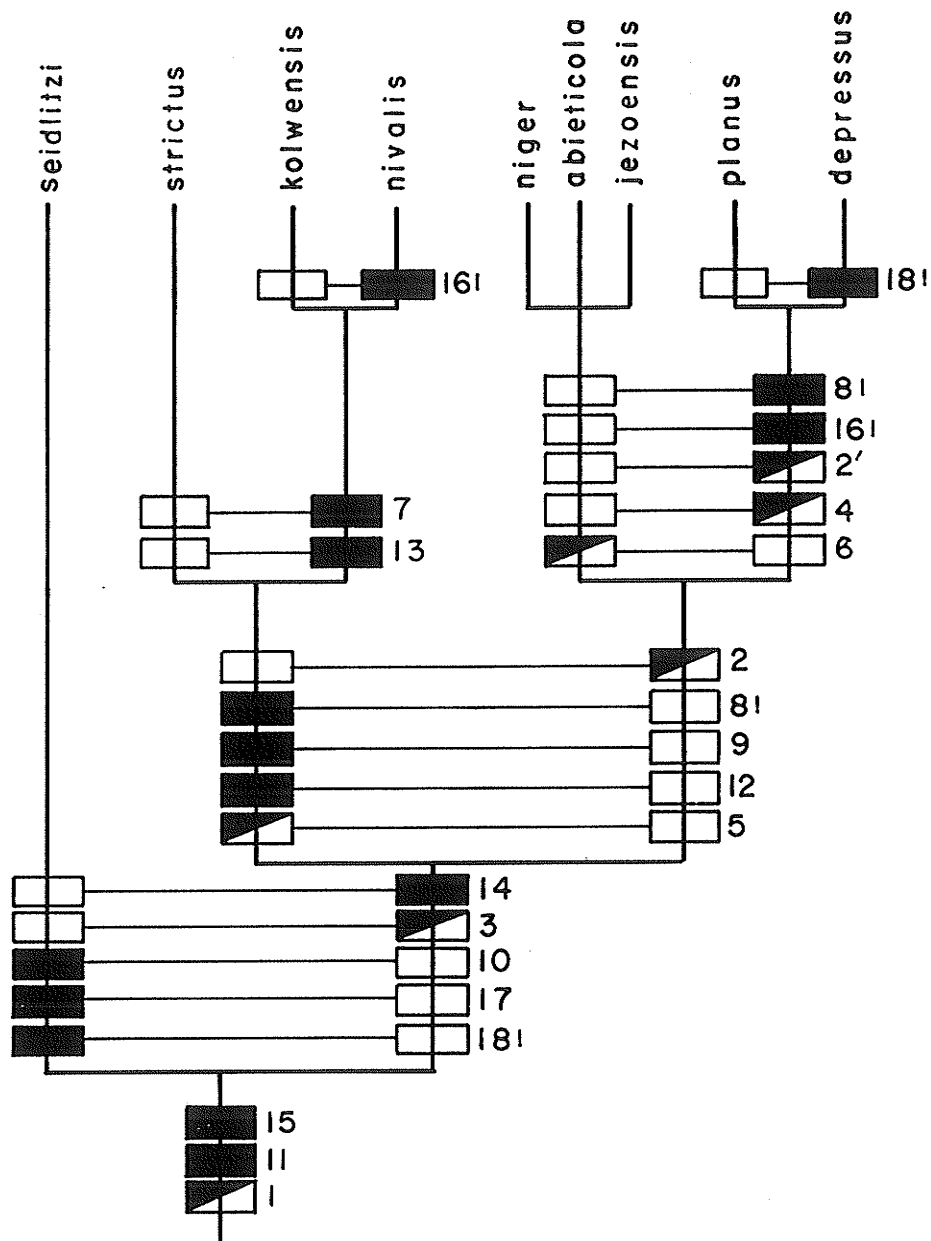


Figure 15. Distribution map derived from examined specimens of Pytho
seidlitzii Blair. Half-filled circles represent state
records only.



Figure 16. Distribution map derived from examined specimens of Pytho
strictus LeConte. Half-filled circles represent state
records only.



Figure 17. Distribution map derived from examined specimens of Pytho
kolwensis C. Sahlberg.

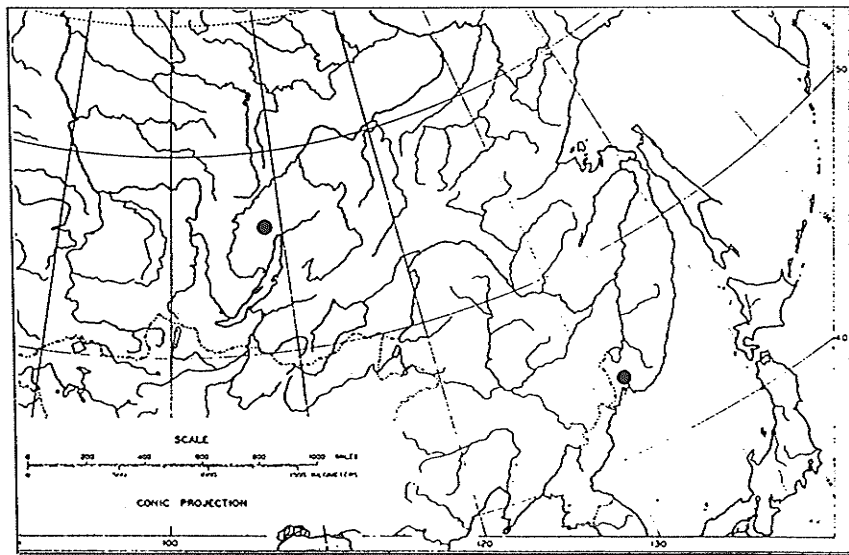
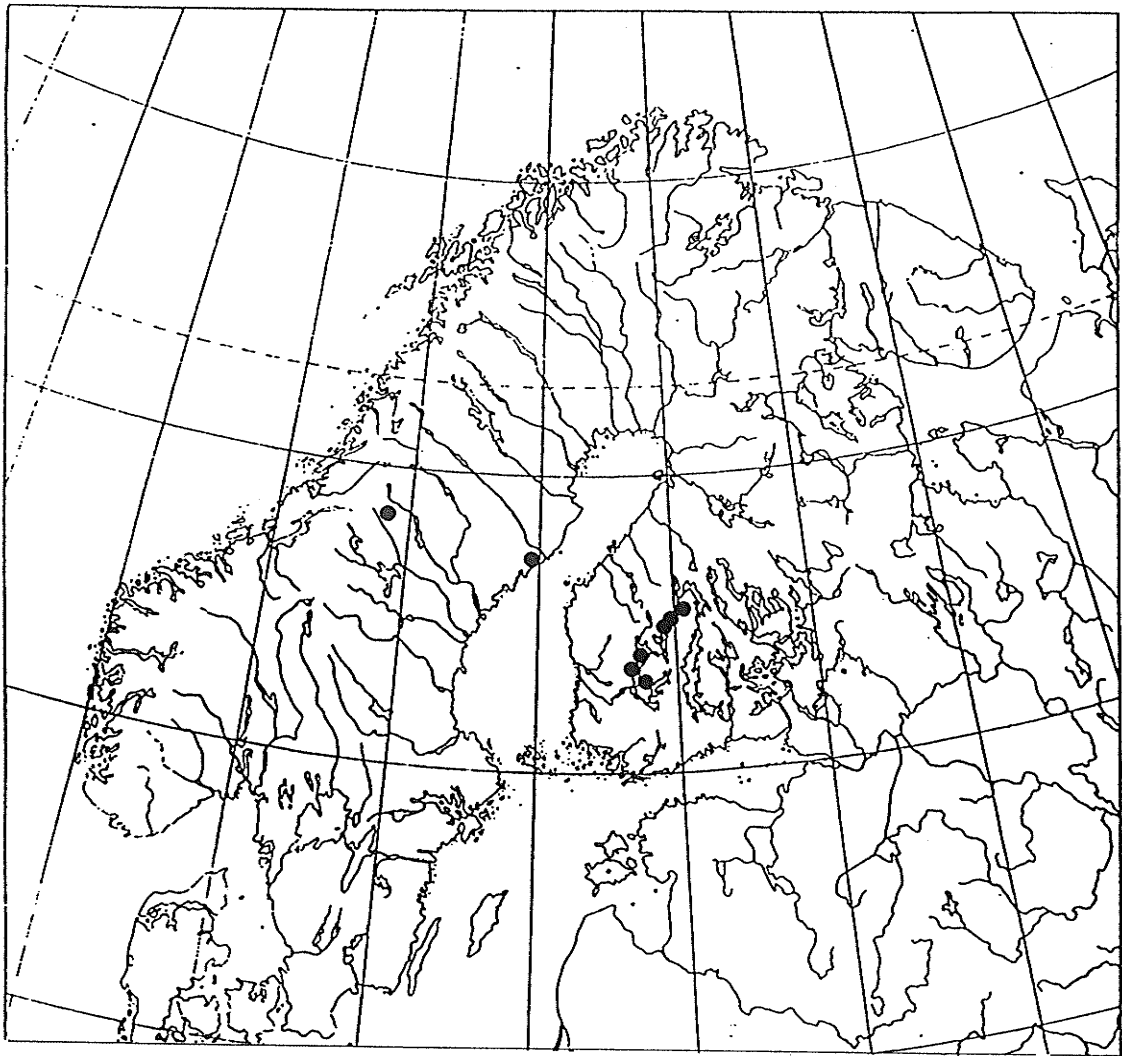


Figure 18. Distribution map derived from examined specimens and literature records of P. nivalis Lewis.



Figure 19. Distribution map derived from examined specimens of Pytho
niger Kirby. Half-filled circles represent state records
only.



Figure 20. Distribution map derived from examined specimens of Pytho
abieticola J. Sahlberg.

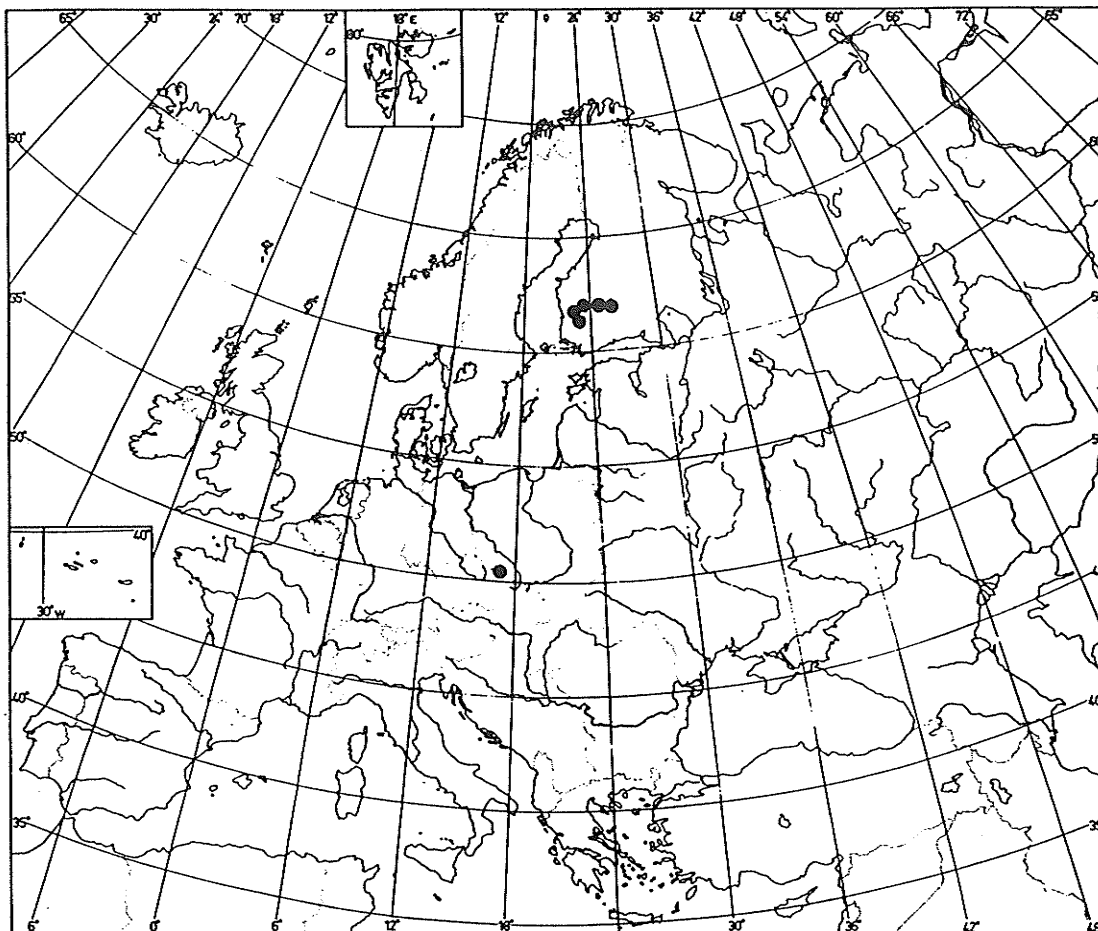


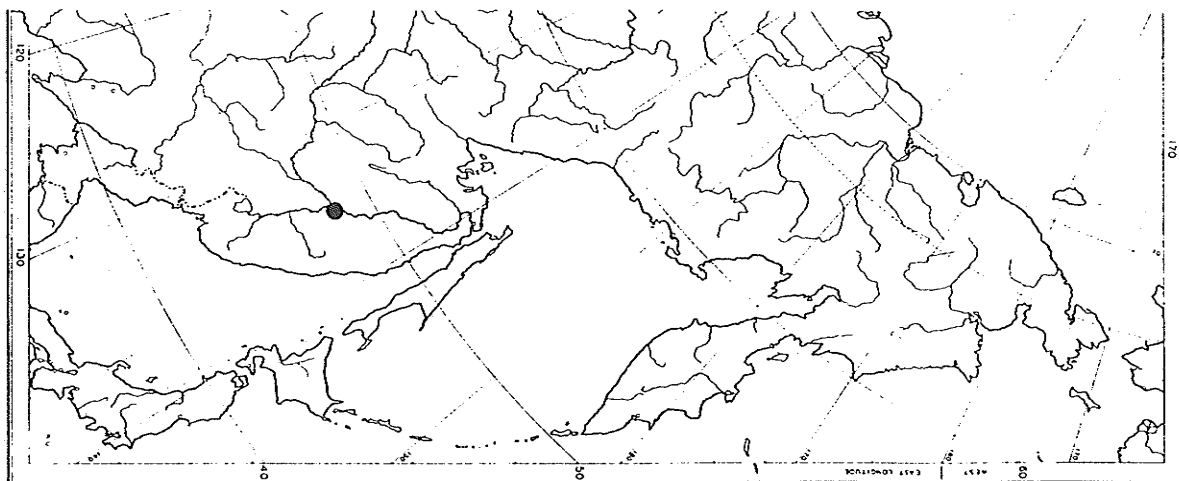
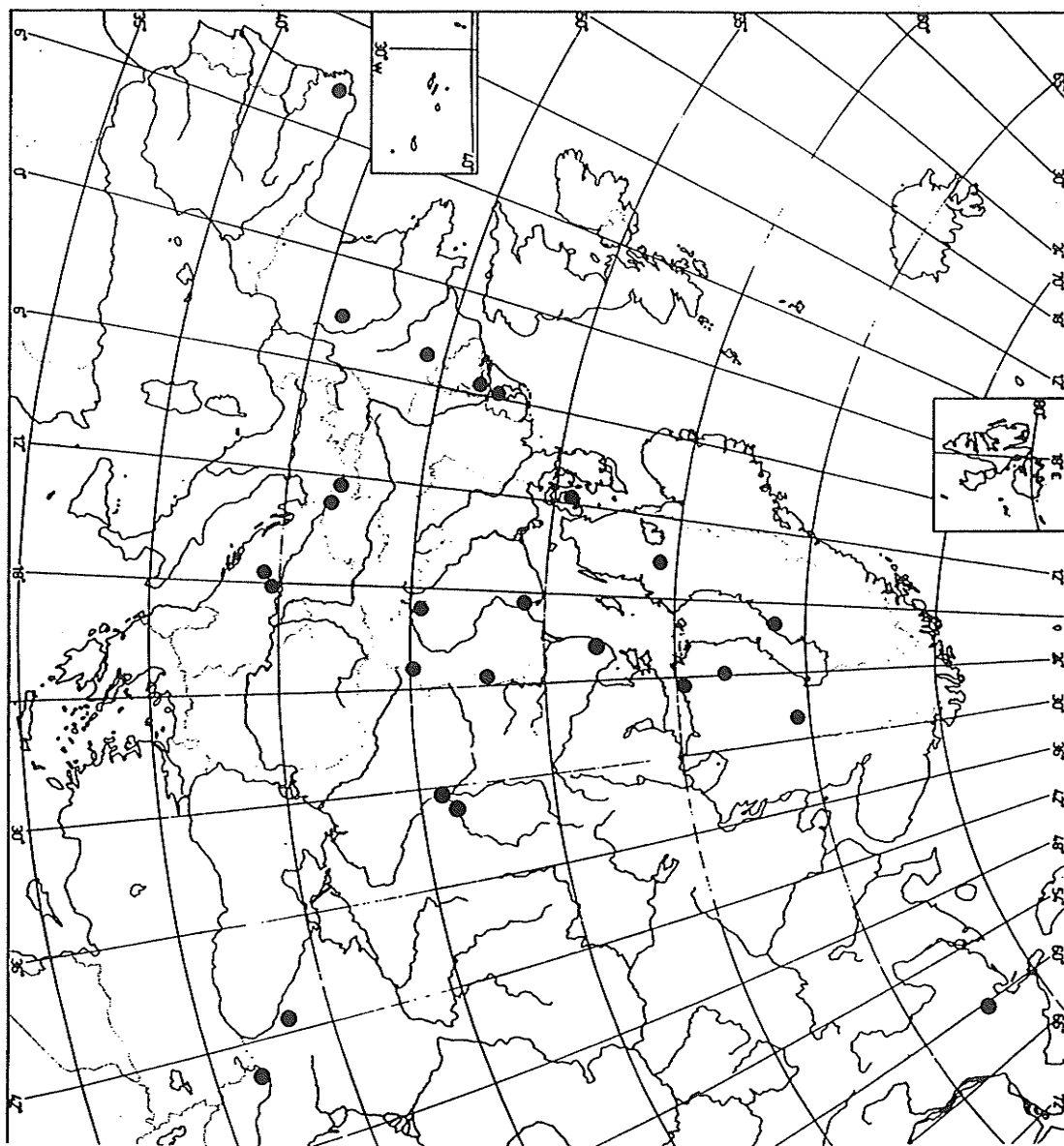
Figure 21. Distribution map derived from examined specimens and literature records of P. jezoensis Kôno.



Figure 22. Distribution map derived from examined specimens of Pytho planus (Olivier). Half-filled circles represent state records only. Half-filled circles for specimens with label data such as "S.W. Ark" have been placed in more or less corresponding areas of the state.



Figure 23. Distribution map derived from examined specimens of Pytho
depressus (Linnaeus).



Appendix A
LOCALITY RECORDS

Where there has been more than one collection from a particular locality, the second and all subsequent collections are indented one space to the right. To avoid repetition, the locality is omitted. Each new locality begins at the left margin. In several cases, (a) collector(s) made repeated collections from one locality. These entries are begun with the locality, then the collector, and then the date and museum abbreviation. Subsequent records consist of only the date and museum abbreviation; locality and collector are not repeated in each case. For P. nivalis and P. jezoensis, some locality data are taken from literature accounts. These are indicated as such in the list of localities, with the pertinent references.

A.1 PYTHO SEIDLITZI

CANADA

Alberta

adults

Ghost Dam, 1.vi.1974, lot 1, B.F. and J.L. Carr, (1, CARR)

2.vi.1979, lot 1, B.F. and J.L. Carr, (2, CARR)

2.v.1980, lot 1, B.F. and J.L. Carr, (2, CARR)

25.v.1983, lot 1, B.F. and J.L. Carr, (6, CARR)

Jumping Pound Creek, 27.v.1962, lot 1, B.F. and J.L. Carr, (1, CARR)

Laggan, 28.v.1889, (1, AMNH); 18.ix.1891, (1, AMNH)

Medicine Lake to Jasper, 4.vii.1915, (1, CU)

Nordegg, 6.ix.1957, G.E. Ball, (1, UASM)

Tp. 29, r. 5, W. 5 mer., 24.ix.1961, lot 1, B.F. and J.L. Carr, (1,
CARR)

Tp. 30, r. 6, W. 5 mer., 27.v.1978, lot 1, B.F. and J.L. Carr, (1, CARR)

larvae

Sibbald Flats (Jumping Pound Creek), 23.viii.1984, D.A. Pollock and J.L.
Carr, (2, DAPC)

British Columbia

adults

Barkerville, Quartz Cr. 4200 ft., 14.vi.1946, A.W. Ludditt, (2, UBCZ)

Spectacles Lake, 14.x.1953, G. Stace Smith, ex. Picea mariana, (3,
UBCZ)

Couldrey Creek, tributary of Flathead River, 5000 ft., 7.viii.1957, U.
Grant, (1, UBCZ)

Emerald Lake, June, A. Fenyes, (1, CAS)

Golden, 29.iv.1978, lot 10, B.F. and J.L. Carr, (2, CARR)

6 km. E. Golden on Hwy#1, 24.viii.1984, D.A. Pollock and B.F. and J.L.
Carr, teneral adults in pupal cells, collected with larvae and pupae,
(4, DAPC)

Kicking Horse Pass, 25.iv.1885, B. B., (1, ROMC)

Lorna, 16.vi.1925, H. Richmond, Abies lasiocarpa, (1, CAS)

McBride, 22.iv.1915, (1, MCZ)

McLeod Lake, 22.viii.1960, F.W. Stehr, (3, UMSP)

Mt. Revelstoke, 11.vii.1931, A.N. Gartrell, (1, CNC)

6300 ft., 18.vi.1968, Campbell and Smetana, (1, CNC)

40 mi. N. Radium Hot Springs, 28.viii.1966, A.G. Raske, Picea glauca,
(1, CNC)

Stanley, 11.vi.1932, W. Mathers, (1, CAS)

Trinity Valley, J.R. Howell, 7.ix.1927, (2, CNC); 4.v.1928, (1, CAS);
5.v.1928, (1, UBCZ); 8.v.1928, (1, CNC); 20.v.1928, (1, MCZ);
17.iv.1930, (1, MCZ); 10.v.1930, Tsuga heterophylla, (1, CAS);
10.v.1930, (1, UASM)

E.A. Rendell, 13.v.1927, (1, OSUC); 30.v.1927, (2, CNC); 8.ix.1927, (1,
CAS); 5.v.1928, (1, MCZ); 10.v.1928, (2, MCZ), (1, CAS); 11.v.1928,
(1, CAS); 19.v.1928, Pinus monticola, (1, CAS); 25.v.1928, (1, UBCZ)

H. Richmond, 7.v.1929, (1, CAS); 10.v.1929, (1, CAS), (2, UBCZ);
12.v.1929, (1, CAS); 15.v.1930, (2, UBCZ); 16.v.1930, (1, UBCZ), (1,
MCZ); 18.v.1930, (1, UBCZ), (1, MCZ)

R.T. Turner, 15.v.1928, (1, CAS); 16.v.1928, (1, MCZ);

Vermillion Pass, 31.vi.1953, lot 2, B.F. and J.L. Carr, (1, CARR)

23 mi. E. Vernon (Trinity Valley), v.1956, M.D. Atkins, (1, OSUC)

Yoho Nat. Pk., _mi. S. Takakkaw Falls, el. 4900', 5.x.1963, (1, UASM)

larvae

Glacier, 9.vi.1892, under fir bark, (5, NMNH)

6 km. E. Golden on Hwy#1, 24.viii.1984, D.A. Pollock, B.F. and J.L.
Carr, in assoc. with teneral adults and pupae, (10, DAPC)

pupae

6 km. E. Golden on Hwy#1, 24.viii.1984, D.A. Pollock, B.F. and J.L.
Carr, coll. in pupal cell in assoc. with teneral adults and large
larvae, (1, DAPC)

Manitoba**adults**

4 miles S. East Braintree on Prov. Rd. 308, 26.x.1986, W.J. Weselake,
(1, DAPC)

11 km S. East Braintree, 15.iv.1987, D.A. Pollock and W.J. Weselake, ex.
reared larvae coll. under bark of Pinus banksiana, (12, DAPC)

Goose Creek Road, 3 km S. Jct. Goose Crk. Rd. & Launch Rd, 4 km SW
Churchill, 24.vii.1988, D.A. Pollock and L.A. Reichert, coll. as pupa
under bark of Picea, (1, DAPC)

larvae

Churchill, 20.vi.1936, H.E. McClure, stump of black spruce, (1, NMNH)

9.0 km. S. East Braintree on Prov. Rd. 308, 5.iv.1987, D.A. Pollock and
L.A. Reichert, ex. Pinus banksiana, (6, DAPC)

11.0 km. S. East Braintree on Prov. Rd. 308, 5.x.1986, D.A. Pollock and
W.J. Weselake, ex. Pinus banksiana, (7, DAPC)

13.0 km. S. East Braintree on Prov. Rd. 308, 5.x.1986, D.A. Pollock and
W.J. Weselake, ex. Pinus banksiana, (3, DAPC)

Goose Creek Road, 3 km S. Jct. Goose Crk. Rd. & Launch Rd., 4 km SW
Churchill, 24.vii.1988, D.A. Pollock and L.A. Reichert, coll. under
bark of Picea, (3, DAPC)

Forest near Julius, 17.vii.1985, D.A. Pollock, (1, DAPC)

Sandilands, 13 km. SSW Hadashville at Jct. of Prov. Rd. 505 and
Whitemouth River, 12.ix.1985, D.A. Pollock and R.E. Roughley, (25,
DAPC)

26.vi.1986, D.A. Pollock, (15, DAPC)

Hwy #10, 5 mi. N. Overflowing River, 6.viii.1986, D.A. Pollock, (4,
DAPC)

Prov. Rd. 503, 4.9 mi. W. Hwy#1, 12.vii.1986, D.A. Pollock and W.J.

Weselake

pupae

11 km. S. East Braintree, 23.x.1986, D.A. Pollock, ex. reared larva

coll. under bark of P. banksiana, (1, DAPC)

5.iv.1987, D.A. Pollock and L.A. Reichert, ex. reared larva coll. under

bark of P. banksiana, (1, DAPC)

15.iv.1987, D.A. Pollock and W.J. Weselake, ex. reared larva

Ontario

adults

Frater, vi.1925, H.S. Fleming, (1, CAS), (2, CNC)

31.v.1925, E.B. Watson, (1, CAS)

vi.1925, E.B. Watson, (1, CNC)

ix.1925, (1, CNC)

Algoma Co., Lake Superior Provincial Park, 4.9.1980, R. Baranowski, (1,
UZIL)

4.9.1980, M. Sörensson, (1, UZIL)

larvae

Hwy #11, 6.9 mi. N. Beardmore, 29.v.1985, R.E. Roughley, (9, DAPC)

Quebec

adults

Duparquet, G. Stace Smith, 15.v.1934, (1, CAS); 26.viii.1934, (2, CAS);

14.x.1934, (1, CAS); 23.xi.1934, from cordwood, (1, CAS); 7.v.1936,

(1, CAS); 12.v.1936, (1, CAS); 30.iv.1937, (1, CAS); 4.v.1938, (1,

CAS); 30.v.1940, (3, CAS); 27.v.1941, (1, CAS); 20.v.1943, (2, CAS)

Forestville, 11.vii.1950, J.R. McGillis, (1, CNC)

Gaspé, 29.vi.1933, (2, LEMC)

Gaspé Co., E.B. Watson, 5.vi.1933, (2, CNC); 7.vi.1933, (1, CNC);
 16.vi.1933, (2, CNC); 27.vi.1933, (1, CNC); 4.vi.1934, (2, CNC);
 5.vi.1934, (1, CNC)

Laniel, 11.vi.1932, (FPMI, 1); 5.vi.1933, (1, CNC); 31.v.1934, (9, CNC);
 4.vi.1934, (1, CNC); 6.viii.1934 (1, CNC)

Nova Scotia

larvae

Margaree Valley, 1.viii.1980, R. Chénier, under bark of dead Abies
balsamea, (1, CNC)

Northwest Territories

adults

McPherson, 25.ix.1931, O. Bryant, (1, CAS)

UNITED STATES OF AMERICA

Idaho

adults

Bear Lake Co.

12 mi. W. Montpelier, 22.vii.1985, J.B. Johnson, ex. larva under bark
 of down spruce, (7, UIM)

Blaine Co.

3 mi. S. Galena Summit, 27.iv.1976, A. Allen, adult reared 13.vii.1976,
 (1, DKYC)

Boundary Co.

Kirk Mtns., Kanisku N. For. 5500', 11-13.vii.1967, N.M. Downie, (1,
 NMDC)

Idaho Co.

20 mi. E.S.E. Lowell, 17.v.1985, (1, UIM)
 3.v.1985, (1, UIM)

Nez Perce Co.

Central Grade, 7.8.1966, K.R. Salskov, (1, UIM)

larvae**Bear Lake Co.**

12 mi. W. Montpelier, 22.vii.1985, J.B. Johnson, under bark of wind
thrown spruce, (2, UIM)

Blaine Co.

Galena, 1.ix.1925, A.D. Allen, (5, DKYC)

Idaho Co.

Lolo Pass, 16.viii.1982, J.B. Johnson, (6, DKYC)

1.vi.1983, D.K. Young, (7, DKYC)

1 mi. S. Lola Pass, 28.v.1983, J.B. Johnson, (4, UIM)

Latah Co.

Big Meadows, 7 mi. N. Troy, 19.vi.1986, J.B. Johnson, under loose bark
on moist fir log, (6, UIM)

5 mi. N.E. Harvard, Laird Park, 15.v.1976, F.M. Tessitore, (1, WSU)

6 mi. N.E. Harvard, 1 km. up Strychnine Cr., 2.v.1972, R.F. Lagier, ex.
Abies grandis, (2, WSU)

Laird Park Wood, 20.iv.1972, J. Brunner, (10, WSU)

2.v.1972, J. Brunner, (30, WSU)

6 mi. N.E. Harvard, 1 km. up Strychnine Cr., 2.v.1972,

pupae**Bear Lake Co.**

12 mi. W. Montpelier, 22.vii.1985, J.B. Johnson, under bark of wind
thrown spruce, (1, UIM)

Idaho Co.

Lolo Pass, 16.viii.1982, J.B. Johnson, (1, DKYC)

Maine

adults

Penobscot Co.

Old Town, University Forest, 6.vi.1963, D.C. Allen & D.B. Shibles, (1,
DEUM)

Orono, 18.v.1966, (1, DKYC)

Piscataquis Co.

Mt. Katahdin, 17.vi.1934, (1, FSCA)

Washington Co.

Princeton, 9.xii.1937, (1, UNH)

Michigan

adults

Marquette Co.

Van Riper St. Pk. 12-14.vii.1972, D.K. & D.C. Young, reared larva ex
Pinus strobus, (1, DKYC)

larvae

Keweenaw Co.

Isle Royale, 10.vii.1957, R.W. Hodges, (1, MCZ)

Isle Royale Nat'l. Pk. 3 mi. Cmpgd., 16-23.viii.1974, D.K. Young, (2,
DKYC)

Isle Royale Nat'l. Pk. vic. of Todd Harbour & Minong Ridge,
16-23.viii.1974, (9, DKYC)

Minnesota

larvae

Clearwater Co.

Itasca St. Park, data and collection unknown

Montana**Mineral Co.**

6 mi. W. Saltese, ca. 4000', 25.vii.1975, A. Newton and M. Thayer,
under conif. bark, (1, MCZ)

New Hampshire**adults****Coos Co.**

0.3 mi. S. Jefferson Notch 890 m., 20.v.1984, A. Newton and M. Thayer,
(1, DAPC)

0.4 mi. S. Jefferson Notch 895 m., 23-27.vii.1980, A. Newton and M.
Thayer, Picea-Abies forest, (2, DAPC)

Hwy #2, 1.1 mi. W. Jct. Hwy #16, 9.vi.1986, D.A. Pollock, ex. reared
larvae, (4, DAPC)

larvae**Coos Co.**

Mt. Washington Auto Road 3000', 10.vi.1986, D.A. Pollock, (4, DAPC)

Hwy #2, 1.1 mi. W. Jct. Hwy #16, 9.vi.1986, D.A. Pollock, (100, DAPC)

0.4 mi. S. Jefferson Notch, 890 m., 20.v.1984, A. Newton and M. Thayer,
under bark of rotting spruce and fir logs, (1, DAPC)

2.9 mi. S. Jefferson Notch 650 m., 30.iv.1983, A. Newton and M. Thayer,
mixed conif.-hdwd. forest, (15, DAPC)

Jefferson Notch 3000', 20.ix.1974, J.F. Lawrence, under bark of
conifers, (15, MCZ)

Grafton Co.

Franconia, 15.x.1904, in spruce, (1, NMNH)

pupae**Coos Co.**

Hwy #2, 1.1 mi. W. Jct. Hwy #16, 9.vi.1986, D.A. Pollock, ex. reared larvae, (5, DAPC)

0.3 mi. S. Jefferson Notch, 895 m., 23-27.vii.1980, A. Newton and M. Thayer, ex. reared larvae, (2, DAPC)

New York**adults****Essex Co.**

Mt. Marcy nr. Indian Falls 3700', 3.vi.1986, D.A. Pollock and R.E. Roughley, ex. reared larvae, (4, DAPC)

Franklin Co.

Hwy #3, 4.7 mi. W. Saranac lake, 7.vi.1986, D.A. Pollock and R.E. Roughley, ex. reared larva, (1, DAPC)

Hamilton Co.

Raquette Lk. outlet 1762 ft., 30.iii.1980, S.A. Teale, (1, SMEK)

larvae**Essex Co.**

Mt. Marcy nr. Indian Falls 3700', 3.vi.1986, D.A. Pollock and R.E. Roughley, (100, DAPC)

pupae**Essex Co.**

Mt. Marcy nr. Indian Falls, 3700', 3.vi.1986, D.A. Pollock and R.E. Roughley, ex. reared larvae, (3, DAPC)

Franklin Co.

Hwy #3, 4.7 mi. W. Saranac lake, 7.vi.1986, D.A. Pollock and R.E. Roughley, ex. reared larva, (2, DAPC)

Oregon**adults****Benton Co.**

McDonald For., 5 mi. N. Corvallis, 29.ii.1956, N.E. Johnson, (1, OSUC)

Hood River Co.

Mt. Hood, ix.1934, E.S. Ross, (1, CAS)

Jackson Co.

Union Creek 3100-3500', 1-15.x.1950, B. Malkin, (1, OSUC)

Washington Co.

Dilley, no data, (1, CAS)

larvae**Hood River Co.**

Mt. Hood Meadows 5200', 10.vii.1975, A. Newton and M. Thayer, (35,
DAPC)

Washington**adults****Klickitat Co.**

Blockhouse, 11.vi.1941, M.C. Lane, (1, OSUC)

Skagit Co.

2 mi. N.W. Rainy Pass, 13.vii.1982, R. Baranowski, (2, UZIL)

Wisconsin

state record only, no data, (2, MPM)

larvae**Pierce Co.**

Mt. Rainier National Park, 4.4 mi. E. Sunrise, 5600', 22.vii.1975, A.
Newton and M. Thayer, under bark of conifers, (12, MCZ)

A.2 PYTHO STRICTUS**CANADA****New Brunswick**

Northumberland Co. Tabusintac, 20.vi.1939, W.J. Brown, (1, CNC)
country records only: no data, H. Ulke beetle coll'n, (1, CMP)
no data, Holotype, (1, MCZ)

UNITED STATES OF AMERICA**New Hampshire**

state record only, no data, F.C. Bowditch coll., (1, MCZ)

New York**adults****Essex Co.**

Mt. Marcy nr. Indian Falls, ca. 3700', 10.vi.1942, H. Dietrich, (1, CU)
3.vi.1986, D.A. Pollock and R.E. Roughley, adult ex. reared larva, (1,
DAPC)

larvae**Essex Co.**

Mt. Marcy nr. Indian Falls, ca. 3700', 3.vi.1986, D.A. Pollock and R.E.
Roughley, under bark of downed conifer, (3, DAPC)

pupae**Essex Co.**

Mt. Marcy nr. Indian Falls, ca. 3700', 3.vi.1986, D.A. Pollock and R.E.
Roughley, ex. reared larvae, (2, DAPC)

Pennsylvania

state records only: no data, (1, CAS); no data, W.G. Dietz Coll., (1, MCZ); no data, H.C. Fall Coll'n, (1, MCZ); no data, (1, MCZ)

Tennessee**Sevier Co.**

Gt. Smoky Mtns. N. Park, Clingman's Dome, 6000', 16.v.1946, H. Dietrich, (1, CU)

A.3 PYTHO KOLWENSIS**FINLAND****Etelä-Häme**

Kuru, no data, (1, SMF)

no data, J. Sahlberg, (1, TMB)

Ruovesi, no data, J. Sahlberg, (1, ZMH), (2, SMF), (1, TMB),

no data, U. Saalas, (1, ZMH)

Teisko, no data, (1, SMF)

no data, J. Sahlberg, (1, FMNH), (1, TMB)

"Fenn. Med", J. Sahlberg, (2, TMB)

Fennia Med., 1880, J. Sahlberg, (3, ZMHB)

Pohjois-Häme**adults**

Keuruu, no data, J. Sahlberg, (1, SMF)

Multia, no data, M. Pohjola, (2, ZMH)

country record only, no data, (1, SMF)

larvae

Saarijärvi, 22.ix.1916, U. Saalas, (8, NMNH)

Saarijärvi, Tb, Pyhähäkki 697:42, O. Biström and R. Vaisänen,
29.viii.1984, (4, ZMH); 22.ix.1984, (5, ZMH)

SWEDEN

Ångermanland

adults

RN 2015e, Gammtratten, 15.viii.1985, R. Pettersson, Picea Abies (L.),
(1, DAPC)

larvae

Locksta. Vandatberget 3.ix.1981, R. Pettersson, (1, DAPC)

RN 2015e, Gammtratten, 15.viii.1985, R. Pettersson, (1, DAPC)

Sammtratten, 15.viii.1985, R. Pettersson, (1, DAPC)

pupae

RN 2015e, Gammtratten, 15.viii.1985, R. Pettersson, (1 + exuvium, DAPC)

Jämtland

larvae

Jmtl. Frostvicken, no date, T. Palm, (1, UZIL)

Norrbotten

adults

Ö. Kalix, 21.viii.1956, T. Palm, (1, UZIL)

1/9/1957, S. Lundberg, (1, ZMHB)

larvae

N. Kalix, 6.55, (4, UZIL)

Ö. Kalix, no date, T. Palm, (2, UZIL)

pupae

Ö. Kalix, 1/9/56, (2, UZIL) [mounted on plates]

U.S.S.R.**Rossijskaja S.F.S.R.**

Ust Kut, Lena Super, no date, B. Poppius, (1, ZMH)

S. Primore, Kamenumka, bl. Ussurijsk, 29.YI.1982, Nikitskij, (1, ZMMU)

A.4 PYTHO NIVALIS**JAPAN****adults**

Nikko - Niohosan, 3.vi-21.vi.1880, G. Lewis, (7, BMNH)

larvae

Okuchichibu, Karisaka-toge to Jiumonji-toge, 28.vii.1963, H. Yamazaki,
(1, DAPC)

literature references

Oze, Ozunikko (Hayashi 1969: 7)

Yumoto, Nikko, Tochigi-ken (Hayashi 1969: 7)

Hokkaido, Berg Daisetsu, Sounkei (Kôno 1936)

A.5 PYTHO NIGER**CANADA****Alberta****adults**

Calgary, 7.v.1928, O. Bryant, (1, CAS)

Fish Cr. Calgary, 11.v.1973, lot 1, B.F. Carr, (2, CARR)

Edmonton, 6-9-1910, F.S. Carr, ex. larva under bark Picea, (1, ROMC).

21.v.1919, F.S. Carr, (1, UGA)

George Lake, H. Goulet, no date, (2, CNC)

Ghost Dam, 21.ix.1963, lot 1, B.F. and J.L. Carr, (6, CARR)

Jumping Pound Creek, 6.ix.1964, lot 4, B.F. and J.L. Carr, (4, CARR)

29.viii.1959, lot 3, B.F. and J.L. Carr, (1, CARR)

5 mi. SW Strachan, 26-28.ix.1967, A.G. Raske and B.M. Dahl, under bark

P. contorta, (1, NFRC)

Tp. 24, r.7 w.5, 14.viii.1985, lot 1, B.F. and J.L. Carr, (1, CARR)

Tp. 28, r.6 w.5, 4.x.1979, lot 1, B.F. and J.L. Carr, (3, CARR)

Tp. 29, r.5 w.5, 14.x.1961, lot 2, B.F. and J.L. Carr, (1, CARR)

13.x.1962, lot 2, B.F. and J.L. Carr, (1, CARR)

larvae

Sibbald Flats (Jumping Pound Creek), 23.viii.1984, D.A. Pollock and J.L. Carr, (2, DAPC)

British Columbia

15 mi. N.W. Beaton River, 8.vi.1950, P. Rubtsoff, (1, CAS)

Manitoba

adults

Churchill, 13.vi.1947, J.H. Freeman, (1, CNC)

5.viii.1938, W.J. Brown, (1, CNC)

7.0 km. S. East Braintree (Prov. Rd. 308), 15.iv.1987, D.A. Pollock and W.J. Weselake, under bark of Pinus banksiana, (2, DAPC)

9.0 km. S. East Braintree (Prov. Rd. 308), 26.ix.1985, D.A. Pollock, under bark of Picea, (1, DAPC)

4.x.1986, W.J. Weselake, (3, WJWC)

23.x.1986, W.J. Weselake, (3, WJWC)

- 5.iv.1987, D.A. Pollock and L.A. Reichert, under bark of Pinus banksiana, (3, DAPC)
- 11.0 km. S. East Braintree (Prov. Rd. 308), 12.viii.1986, D.A. Pollock and W.J. Weselake, under bark of Pinus banksiana, (6, DAPC)
- 4.x.1986, D.A. Pollock and W.J. Weselake, under bark of Pinus banksiana in pupal cells, (2, DAPC)
- 23.x.1986, W.J. Weselake, under bark of Picea mariana, (6, WJWC)
- 26.x.1986, W.J. Weselake, under bark of Picea mariana, (12, WJWC)
- 15.iv.1987, D.A. Pollock and W.J. Weselake, in pupal cells under bark of Abies, (26, DAPC)
- 13.0 km. S. East Braintree (Prov. Rd. 308), 5.x.1986, D.A. Pollock and W.J. Weselake, under bark of Pinus banksiana in pupal cells
- 18.5 km. S. East Braintree (Prov. Rd. 308), 23.x.1986, W.J. Weselake, (2, WJWC)
- 8.0 mi. S. East Braintree (Prov. Rd. 308), 26.x.1986, W.J. Weselake, under bark of Picea mariana, (8, DAPC)
- Gillam, 11.vii.1950, J.F. McAlpine, (1, CNC)
- Goose Creek Road, 3 km S. Jct. Goose Crk. Rd. & Launch Rd., 4 km SW Churchill, 24.vii.1988, D.A. Pollock and L.A. Reichert, coll. as pupa under bark of Picea, (1, DAPC)
- Grass River Prov. Pk., 16 km. W. Iskwasum Lk., 25-30.vi.1981, Ashworth, Schwert and Keller, window trap in Picea-Populus woodland, (1, NDSU)
- 2 mi. W. Julius, 25.x.1986, W.J. Weselake, (4, WJWC)
- The Pas, 2.vi.1953, W. Krivda, (1, JBWM)
- Victoria Beach, 24.v.1928, L.H. Roberts, (1, JBWM)
- Winnipeg, no date or collector, (1, BCPM)

larvae

9.0 km. S. East Braintree (Prov. Rd. 308), 26.ix.1985, D.A. Pollock,
under bark of Picea, (4, DAPC)

Goose Creek Road, 3 km S. Jct. Goose Crk. Rd. & Launch Rd., 4 km SW
Churchill, 24.vii.1988, D.A. Pollock and L.A. Reichert, coll. under
bark of Picea, (2, DAPC)

Grand Rapids Wayside Park Campground, 2 km S. Grand Rapids on Hwy # 6,
20.vii.1988, D.A. Pollock and L.A. Reichert, coll. under bark of Pinus
banksiana, (2, DAPC)

13.0 km. SSW Hadashville, Jct. Prov. Rd. 505 and Whitemouth River,
12.viii.1986, D.A. Pollock and R.E. Roughley, (15, DAPC)

pupae

7 mi. S. East Braintree (Prov. Rd. 308), 12.viii.1986, D.A. Pollock and
W.J. Weselake, coll. as pupa, (1, DAPC)
Prov. Rd. 503, 4.9 mi. W. Hwy #1, 12.viii.1986, D.A. Pollock and W.J.
Weselake, coll. as pupae, (3, DAPC)

Ontario**adults**

E. Ont., no date or collector, (1, CNC)

Madsen, 28.vii.1986, W.J. Weselake, ex. reared pupae, (2, DAPC)

Maynooth, 30.v.1963, J.E.H. Martin, (2, CNC)

Ottawa, 192_, no collector, (1, CNC)

192_, no collector, under bark of spruce, (1, CNC)

27 mi. S. Pickle Lk., 22.vi.1973, Campbell and party, (1, CNC)

Sioux Lookout, 28.vi.1947, W.Y. Watson, (1, ROMC)

larvae

Madsen, 28.vii.1986, W.J. Weselake, (4, DAPC)

pupae

Madsen, 28.vii.1986, W.J. Weselake, (1, DAPC)

Prince Edward Island**larvae**

Summerside, 22.iv.1980, L. Corbin, found in plywood shipment to Italy,
(1, DKYC)

Quebec**adults**

Bonaventure Island, no date, C.H. Young, (1, CNC)

Dosquet, J.-C. Aubé, 20.v.1972, (1, DKYC); 17.v.1977, (1, DKYC)

Duparquet, G. Stace Smith, 15.v.1934 (2, CAS), 27.v.1934 (1, CAS),
30.v.1934 (2, CAS), 11.vi.1934 (1, CAS), 24.vi.1935 (1, CAS),
5.vii.1935 (1, CAS), 9.v.1936, host Abies (4, CAS), 10.v.1936, host
Abies (3, CAS), 16.v.1936 (1, CAS), 2.vi.1936 (2, CAS), 3.vi.1936, (1,
CAS), 6.vi.1936, lake shore (1, CAS), 30.v.1938 (1, CAS), 1.vi.1938
(2, CAS), 3.vi.1938 (1, CAS), 15.vi.1938 (1, CAS), 9.vi.1939 (1, CAS),
27.v.1940 (2, CAS), 28.v.1940 (2, CAS), 30.v.1940 (3, CAS), 31.v.1940
(1, CAS), 9.vi.1940 (2, CAS), 16.vi.1940 (1, CAS), 22.vi.1940 (2,
CAS), 16.vii.1940 (1, CAS), 31.v.1941 (1, CAS), 13.vi.1941 (1, CAS),
23.v.1943 (1, CAS), 21.v.1944 (1, CAS)

Gaspé Co., 1.vii.1934, E.B. Watson, (1, CNC)

Gaspé Park, 3500', 26.vii.1971, E.C. Becker, (1, CNC)

Laniel, 26.vii.1933, (1, CNC)

18.vi.1935 (1, CNC)

24.vi.1935, H. Fleming, (1, CNC)

29.viii.1935, H. Fleming, (1, CNC)

Mistassini Lk., 20 mi. N. Mistassini Post, 16.vi.1955, J.R. McGillis,
(7, CNC)

Mt. Lyall, 1500 ft., 24.vi.1933, W.J. Brown, (1, CNC)

3000 ft., 28.vi.1933, W.J. Brown, (1, CNC)

Roberval, 27.v.1940, S. Dumont, (2, CNC)

St. Foy, 29.iv.1961, J.-C. Aubé, (1, DKYC)

30.iv.1961, J.-C. Aubé, pris sur le pin, (1, NMDC)

larvae

Long Lake, F.C. Craighead, white pine, (10, NMNH)

Newfoundland

adults

Labrador, Goose Bay, 23.vi.1948, W.E. Beckel, (1, CNC)

Nova Scotia

adults

C. Breton, White Point, 23.vi.1983, Y. Bousquet, (1, CNC)

Saskatchewan

adults

Saskatoon, no data, (1, CDAS)

4.5 km. S. Twoforks River on Hwy 2, 16.v.1987, D.A. Pollock and L.A.

Reichert, under bark of Pinus banksiana, in pupal cells, (2, DAPC)

White Fox, 6.vii.1950, L.A. Konotopetz, (1, CDAS)

larvae

3.2 km. E. on Rd. 3.5 km. N. Prince Albert on Hwy 2, 15,18.v.1987, D.A.

Pollock and L.A. Reichert, under bark of Pinus banksiana, (50, DAPC)

7.4 km. N. White Gull Creek off Hwy 120, 17.v.1987, D.A. Pollock and

L.A. Reichert, (12, DAPC)

Northwest Territories

adults

Aklavik, 25.v.1931, lot 217, O. Bryant, (1, CAS)

Yukon Territory

adults

Mayo, 5.vii.1955, lot 3, B.F. and J.L. Carr, (1, CARR)

McQuesten, 29.vi.1979, lot 3, B.F. and J.L. Carr, (1, CARR)

Ross River 3000', 21.vi.1960, J.E.H. Martin, (1, CNC)

UNITED STATES OF AMERICA

Alaska

adults

Kenai, 8,14.vi.1974, M.M. Furniss, "in flight", (2, UIM)

Savage Riv. Mt. McKinley Distr. snowfields 5100-6000 ft., 28.vi.1926, G.
Wright, (1, CAS)

larvae

McKinley Park, nr. Supt. Headquarters, 2.vi.1931, F.W. Morand, (6, NMNH)

McKinley Park, 6.vi.1931, F.W. Morand, (7, NMNH)

Maine

adults

Aroostook Co.

Island Falls, 1-23.v.1977, W.P. Kemp, sticky trap, (2, CU)

Oxford Co.

Norway, 6.5.1925, (1, MCZ)

Penobscot Co.

Bradford, no data, (2, AMNH)

Springfield, 14.vi., (1, UNH)

Piscataquis Co.

Kineo, June, (2, CAS)

Mt. Katahdin, 2.vii.1932, (1, CMP)

17.vi.1934, (1, FSCA)

larvae

Lincoln Co.

county record only, 7-4-50, D.J. Borrer, under bark, (10, OSU)

Massachusetts

adults

Berkshire Co.

Lenox, no data, (23, AMNH)

Lenox "Auction", 22.iv.1896, (1, AMNH)

Bristol Co.

Dartmouth, 8.xi.1906, (1, MCZ)

Fall River, 15.v.1906, N.S. Easton, (1, MCZ)

Middlesex Co.

Billerica, 2.4.1924, (2, MCZ)

Camb[ridge]., no data, (1, UVCC)

Natick, 25.iv.1944, C.A. Frost, under bark pine logs, (1, CAS)

2.iv.1944, C.A. Frost, under bark pine logs

Tewkesbury, no data, (4, CMP), (4, SMEK)

Tyngsboro, 1898, (1, MCZ)

Wayland, 31.i.1925, (1, MCZ)

31.i.1925, Darlington, bark of P. strobilus, (1, CU)

3.ii.1925, Darlington, bark of P. strobilus, (2, CU), (2, MCZ)

4.xi.1928, C.A. Frost, under bark, (1, OSUC)

Norfolk Co.

Cohasset, 6.4.1917, A.M. Wilcox, (1, MCZ), (1, CAS)

state records, (2, MCZ), (2, CMP), (3, INHS), (1, FMNH)

larvae

Hampden Co.

Holyoke, Holly's Ledge, 12.xi.1903, under decaying bark of Pinus
strobus, (3, NMNH)

Michigan

adults

Mackinac Co.

St. Helena Island, 26.v.1922, S. Moore, (1, OSU)

St. Ignace, 31v.1921, S. Moore, (1, UMAA)

Marquette Co.

Van Riper St. Pk., 12-14.vii.1972, D.K. & D.C. Young, reared ex. larva
from Pinus strobus, (1, DKYC)

larvae

Marquette Co.

Marquette, vi.1928, (4, NMNH)

pupae

Marquette Co.

Van Riper St. Pk., 12-14.vii.1972, D.K. & D.C. Young, under loose bark
of P. strobus, (2, DKYC)

Minnesota

adults

Isanti Co.

county record, 24.iv.1948, (1, UMSP)

St. Louis Co.

Duluth, Daggett, (3, CAS), (6, LACM)

larvae**Clearwater Co.**

Itasca State Park, 1.vii.1954, under bark, (3, UMSP)

7/2/55, R.M. Andrews, (1, OSU)

7.vii.1956, under bark, (1, UMSP)

13.vi.1957, F.W. Stehr, (4, DKYC)

24.vi.1957, F.W. Stehr, (3, UMSP)

2.vii.1960, K.C. Kim, (3, UMSP)

17.vi.1965, R.M. Andrews, cut logs, (1, MCZ)

Itasca, Bohall Trail, 7/8/55, R.M. Andrews, under bark, (10, OSU)

New Hampshire**adults****Belknap Co.**

Barnstead, 1929, (1, CAS)

Carroll Co.

2 mi. NW Wonalancet, 8-14.vi.1984, D.S. Chandler, window trap, (1, UNH)

1 mi. N. Wonalancet, E. Fk. Spring Brk 23.v-4.vi.1985, D.S. Chandler,
malaise trap 1900', (1, UNH)

Coos Co.

Mt. Washington, no data, (1, AMNH)

1.0 mi. S. Jefferson Notch 2700', 7.ix.1975, A. Newton and M. Thayer,
(1, FMNH)

Grafton Co.

Franconia, no data, (3, AMNH)

Rockingham Co.

Exeter, 21.ix.1922, P.J. Darlington, (1, UNH)

Hampton, 31.iii.1899, S.A. Shaw, (1, UNH)

Newton, 29.iv.1951, A.R. Lewis, (1, UNH)

Strafford Co.

Durham, 24.iv.1907, (3, INHS)

2.v.1906, (1, INHS)

5/12/1941, (1, UNH)

larvae**Coos Co.**

Jefferson Notch 3000', 7.vi.1975, A. Newton and M. Thayer, under bark
and in logs, (4, MCZ)

Mount Washington Auto Road, 3000', 10.vi.1986, D.A. Pollock and R.E.
Roughley, (10, DAPC)

Hwy #2, 1.1 mi. W. Jct. Hwy #16, 9.vi.1986, D.A. Pollock, (10, DAPC)

Grafton Co.

Kancamagus Pass 2800', 24.vii.1974, A. Newton, under conifer bark, (6,
MCZ)

Sawyer R. 1600' nr. Bartlett, 6.ix.1975, A. Newton and M. Thayer,
under spruce and fir bark, (3, MCZ)

New York**adults****Erie Co.**

Buffalo, no data, (1, AMNH)

Essex Co.

Mt. Marcy, Indian Falls, 15.vi.1944, H. Dietrich, (4, CU)

Tompkins Co.

Caroline, Cen., 15.iv.1961, M.A. Dayrup, (2, AMNH)

Dryden, Ringwood, 8.v.1951, H. Dietrich, under bark of white pine, (31,
CU)

Ithaca, F.C. Fletcher, 28.iii.1915, (1, CU); 8.xi.1924, (2, CU);
5.v.1928, (1, CU)

Coy Glen Ithaca, H. Dietrich, 8.i.1922, H. Dietrich, (1, CU)

larvae

Essex Co.

Mt. Marcy, nr. Indian Falls, 3700', 3.vi.1986, D.A. Pollock and R.E.
Roughley, (25, DAPC)

pupae

Essex Co.

Mt. Marcy, nr. Indian Falls, 3700', 3.vi.1986, D.A. Pollock and R.E.
Roughley, ex. reared larva, (1, DAPC)

Pennsylvania

Cook Forest, 1x.15, (11, CMP)

Cook Woods, X,2, (1, CMP)

Vermont

adults

state record only, no data, (1, INHS) **larvae**

Bennington Co.

N. of Peru 1700', 26.ix.1976, A. Newton and M. Thayer, under bark
conifer logs, (5, MCZ)

Wisconsin

Ashland Co.

Copper Falls St. Pk., 7.vii.1972, D.K. Young, reared from larva, (1,
DKYC)

Oneida Co.

Minocqua, 3.viii.1962, S. Earnshaw, (1, MCZ)

Vilas Co.

Nicolet Nat. For., T41N, R11E, Sec.12, 23.viii.1984, Pinus, (8, DKYC)

state record only, no data, (2, MPM)

larvae

Bayfield Co.

Madeline Island, 15.viii.1985n, D.K. Young, P. strobilus, (6, DKYC)

Vilas Co.

Nicolet Nat. For., T41N, R11E, Sec.12, 23.viii.1984, Pinus, (38, DKYC)

Wood Co.

Port Edwards, 24.iv.1948, R. Schenefelt, spruce, (1, NMNH)

pupae

Vilas Co.

Nicolet Nat. For., T41N, R11E, Sec.12, 23.viii.1984, Pinus, (1, DKYC)

A.6 PYTHO ABIETICOLA

AUSTRIA

Langbath-Tal, O. Oesterreich, 6.09, (1, SMF)

FINLAND

Etelä-Häme

adults

Jämsä, no data, U. Sahlberg, (1, ZMH)

Korpilahti, no data, J. Sahlberg, (1, SMF)

Kuru, no data, J. Sahlberg, (1, ZMHB)

Ruovesi, no data, U. Saalas, (1, ZMH)

no data, J. Sahlberg, "ind. typ.", (1, TMB)

no data, J. Sahlberg, "type", (1, ZMH)

no data, J. Sahlberg, (1, TMB)

Teisko, no data, J. Sahlberg, (1, TMB)

Fenn. Med, no data, (1, ZMHB)

no data, (1, SMF)

larvae

Ruovesi, 21.ix.1902, U. Saalas, Picea excelsa, (2, NMNH)

Pohjois-Häme

adults

Saarijärvi, 20.viii.1944, Stockmann, (2, ZMH)

larvae

Saarijärvi, Pyhähäkki 697: 42, O. Biström and R. Väisänen, 1.vii.1984, (1, ZMH); 22.iv.1984, (7, ZMH)

POLAND

Glatz [=Kłodzko], 5.10, (2, SMF); 6.1897, (1, SMF)

SWEDEN

Ångermanland

larvae

Torrbole, 12.v.1985, R. Pettersson, (4, DAPC)

Långrumpskogen, 12.v.1985, R. Pettersson, (6, DAPC)

Jämtland

regional record only, Strömsund, 5.9.1960, (1, ZMHB); 17.1961, (1, ZMHB)

"Jmt. Fors. sn. Palm", 10.6.1946, T. Palm, (1, ZMHB)

Norrbotten

Överkalix, S. Lundberg, 22.vii.1957, (1, ZMHB); 22.vii.1958, (2, ZMHB)

Västerbotten**adults**

RN 21J4g 4-2-: Kulbäcksliden: Reservatet, 18.v.1985, R. Pettersson,
(12, DAPC)

pupae

RN 21J4g 4-2-: Kulbäcksliden: Reservatet, 18.v.1985, R. Pettersson, (2,
DAPC)

A.7 PYTHO JEZOENSIS**JAPAN****adults**

Ehime Pref., Mt. Shiratsue nr. Komenono, 24.i.1965, S. Hisamatsu, under
bark of Tsuga sieboldi Carrière, (3, EUM; 2, DAPC)

Gifu Pref., Hirayu, 28.viii.1959, M. Sâto, (1, BLNU)

Gifu, Takayama, 31.iii.1955, H. Torigai, (3, BLNU)

Takayama, Hida Honshu, 31.iii.1955, H. Torigai, (1, BLNU)

Hokkaido, Jozankei, VI/2, 1935, H. Kôno, Picea jezoensis, (2, HUS)

larvae

Ishikawa-ken, Mt. Hakusan, 1.viii.1977, (1, DAPC)

literature references

Takinozawa, near Sapporo (Iablokoff-Khnzorian 1985)

nr. Hakutaisan, Okuchichibu (Hayashi 1969: 7)

nr. Oze, Okunikko (Hayashi 1969: 7)

Yumoto, Nikko, Tochigi-ken (Hayashi 1969: 7)

A.8 PYTHO PLANUS**CANADA****Alberta****adults**

- Banff, 2.iii.1927, O. Bryant, under spruce bark, (1, UASM)
- Banff, Mt. Edith Trail, 6000 ft., 2.iii.1927, O. Bryant, in cells of
cerambycids?, under bark of spruce, (17, CAS)
- Edmonton, 2.vi.1917, F.S. Carr, (1, UASM)
- Exshaw, 23.ii.1963, lot 1, B.F. and J.L. Carr, spruce, (1, CARR)
- Canmore, 30.viii.1959, lot 2, B.F. and J.L. Carr, (1, CARR)
- 16.x.1977, lot 1, B.F. and J.L. Carr, (2, CARR)
- Ghost Dam, 4.vi.1975, lot 1, B.F. and J.L. Carr, (1, CARR)
- 27.v.1983, lot 1, B.F. and J.L. Carr, (1, CARR)
- Fort McMurray, 6.x.1929, O. Bryant, (1, CAS)
- 12 mi. N. Fox Creek, 11.vii.1969, A.G. Raske, Pinus contorta, (1, CNC),
(1, NFRC)
- 5 mi. N. Strachan, 20-22.ix.1967, A.G. Raske and B.M. Dahl, (1, NFRC)
- 6 mi. S. Seebe, 6.ix.1968, A.G. Raske and B.M. Dahl, (1, NFRC)
- Tp. 40, r. 10, W. 5 Mer., 20.v.1962, lot 2, B.F. and J.L. Carr, (1,
CARR)
- Tp. 29, r. 5, W. 5 Mer., 10.v.1984, lot 2, B.F. and J.L. Carr (1, CARR)

larvae

- Edmonton, 10.v.1924, O. Bryant, (6, NMNH)

British Columbia**adults**

- Aspen Grove, 14.vi.1933, K. Graham, (1, UBCZ)
- 11.vi.1933, K. Graham, (2, CAS)

- 14.vi.1933, H. Richmond, (1, CAS)
- 1.vii.1933, H. Richmond, (1, CNC)
- 12.vi.1933, H. Richmond, ponderosa pine, (1, CNC)
- 22.v.1934, H.B. Leech, under bark of ponderosa pine (1, AMNH)
- Barkerville, Antler Mtn., 24.vii.1947, M. Stace Smith, (1, UBCZ)
- Barkerville, Quartz Crk, 1.vii.1946, A.W. Ludditt, 4200 ft., (1, UBCZ)
- 1.x.1928, Stace Smith, Pinus contorta stump, (1, CAS)
- Engineer, 24.vi.1934, (1, AMNH)
- Errington, V.I., 15.i.1939, G.H. Larnder, (1, CNC)
- Forbidden Plat., V.I., 13.vii.1935, J.D. Gregson, (1, CNC)
- Golden, no data, (1, CAS)
- G. Central L., 29.v.1942, M.L. Prebble, (1, CNC)
- Indian Meadows, 10.v.1920, R. Hopping, (1, CNC)
- Kingsvale, 28.v.1921, (1, MCZ)
- 28.v.1921, R. Hopping, Pinus ponderosa, (1, CAS)
- 2.vi.1921, R. Hopping, (1, CAS)
- Kleena Kleene, Tatler Lake, Oct./Dec. 15, S.J. Caldwell, (1, CNC)
- Lorna, 5.vi.1925, (1, INHS)
- Merritt, Midday Valley, v.1925, (1, INHS)
- 11.v.1925, J. Stanley, Pinus ponderosa, (1, CAS)
- 19.v.1925, J. Stanley, Pinus ponderosa, (1, CAS)
- Mt. Benson, S. Vancouver Island, J. Chapman, (1, UBCZ)
- Princeton, 25.ix.1914, R.H. Chrystal, (5, CNC)
- 24.ix.1914, G.H. Larnder, (1, CNC)
- 25.x.1914, T. Wilson, (14, CNC)
- Princeton, S. Wash Ck., 22.vii.1983, Lindgren Funnel Trap, (1, MAIC)
- Radium, 4.vi.1953, lot 6, B.F. and J.L. Carr, (10, CARR)
- 5.vi.1953, lot 3, B.F. and J.L. Carr, (1, CARR)

Salmon Arm, 14.iv.1928, H.B. Leech, from pupal cell under pine bark, (2, UBCZ)

11.iv.1928, H.B. Leech, (1, BCPM)

11.iv.1928, H.B. Leech, Pinus monticola, (1, AMNH)

Stanley, 10.vi.1932, K. Graham, (1, UBCZ), (1, CAS)

Terrace, 1925, W.W. Hippiusley, (1, UBCZ), (8, UASM)

M.E. Hippiusley, (2, MCZ)

Mrs. Hippiusley, (1, MCZ), (4, MCZ)

Trinity Valley, J.R. Howell, 7.ix.1927, (1, CNC), (1, OSU); 4.ix.1927,

(2, CNC); 15.ix.1927, (1, CNC); 8.v.1928, (1, CAS); 13.v.1928, (1,

CNC); 14.v.1928, (1, OSU); 19.v.1928, Pinus monticola, (1, CNC);

21.v.1928, (1, CNC); 8.vi.1928, Pinus monticola, (1, CAS); 29.vi.1928,

Pinus monticola, (1, CNC); 13.viii.1928, Pinus monticola, (1, UBCZ)

E.A. Rendell, 4.vi.1927, (1, MCZ); 14.ix.1927, (1, CAS); 5.v.1928, (1, LEMC); 10.v.1928, (1, UBCZ), (2, CAS)

H. Richmond, 15.v.1930, (1, UBCZ); 16.v.1930, (1, UBCZ)

R.T. Turner, 1.vi.1928, (1, CNC); 23.v.1928, (1, CNC)

Vermillion Pass, 31.vi.1953, lot 2, B.F. and J.L. Carr, (1, CARR)

larvae

Glacier, 9.vi.1892, fir bark, (20, NMNH)

Riske Creek, 8.viii.1984, C. Macdonald, under bark of Pinus contorta (latifolia) felled in 1983 (6, DAPC)

Manitoba

adults

9 km. S. East Braintree on Prov. Rd. 308, 5.x.1986, D.A. Pollock and

W.J. Weselake, under bark of standing dead Pinus banksiana (2, DAPC)

Prov. Rd. 210, 15.7 km. N. Woodridge, 16.viii.1987, D.A. Pollock and L.A. Reichert, in pupal cells under bark of Pinus banksiana, (12, DAPC)

Prov. Rd. 304, 5 km. E. Bissett, 3.viii.1987, D.A. Pollock and L.A. Reichert, under bark of P. banksiana, (5, DAPC)

Prov. Rd. 304, 4.7 mi. E. Bissett, 22.viii.1987, L.A. and E.M. Reichert, under bark of P. banksiana, (11, DAPC)

Winnipeg, 14.v.1984, D.A. Pollock, found on driveway, (2, DAPC)

9.vi.1910, J.B. Wallis (1, CNC)

vii.20, N. Pankiw (1, CNC)

F. Dalman, no data, (1, CNC)

no data, (1, BCPM)

larvae

Island on Rice Lake, nr. Bissett, 19.viii.1985, L.A. Reichert, under bark of jack pine (10, DAPC)

9 km. S. East Braintree, 4.x.1985, D.A. Pollock, under bark (6, DAPC)

5.x.1986, D.A. Pollock and B. Weselake, under bark of standing dead jack pine (1, DAPC)

Gillam, 9.vi.1950, J.F. McAlpine, (1, DKYC)

Grand Rapids Wayside Park Campground, 2 km S. Grand Rapids, on Hwy #6, 20.vii.1988, D.A. Pollock and L.A. Reichert, coll. under bark of dead Pinus banksiana, (2, DAPC)

Julius, 17.vii.1985, D.A. Pollock, under bark of Pinus banksiana, (5, DAPC)

13 km. SSW Hadashville, Jct. Prov. Rd. 505 and Whitemouth River, 26.vi.1986, D.A. Pollock, under spruce bark, (2, DAPC)

Jct. Prov. Rd. 505 & 503, 12.ix.1985, D.A. Pollock and R.E. Roughley,
under bark (prob. spruce), (1, DAPC)

Caribou Lake, nr. Bissett, 13.x.1986, E.M. Reichert, under bark of Pinus
banksiana, (15, DAPC)

pupae

Prov. Rd. 304, 5 km. E. Bissett, 3.viii.1987, D.A. Pollock and L.A.

Reichert, under bark of P. banksiana, (11, DAPC)

11 km. S. East Braintree, 5.iv.1987, D.A. Pollock and L.A. Reichert,

ex. reared larvae coll. under bark of P. banksiana, (4, DAPC)

forest nr. Julius, 15.vii.1985, D.A. Pollock, ex. reared larvae, (3,
DAPC)

Ontario

adults

Blind River, 27.ix.1945, red pine, (2, FPMI)

Credit, no data, (2, ROMC)

Dymont, 29.vi.1951, spruce, (1, FPMI)

Flying Thor Lake, Aug-Sept. 1926, H.S. Fleming, (1, CNC)

Frater, 14.vii.1925, H.S. Fleming, (1, CNC)

Kanata, A. Smetana, (2, CNC)

Kenora, (1, CNC)

Lk. Opasatika, 2.vi, J.N. Knull, (1, CAS)

Maynooth, 2.vii.1950, J.F. McAlpine, (1, CNC)

Mcdiarmid, 6.vi.1921, N.K. Bigelow, (1, ROMC)

Ottawa, 12.ix.1957, R. de Ruelle, (1, CNC)

no data, (1, ROMC)

Poplar Lodge, Lk. Nipigon, 21.vi.1921, N.K. Bigelow, (1, ROMC)

Rainy River Dist., 27.ix.1924, J.F. Brimley, (1, CNC)

Ridgeway, no data, (2, CMP)

Sioux Lookout, W.Y. Watson, 21.vi.1947, (1, ROMC) 2.vii.1947, (1, ROMC)
 3.viii.1947, (1, ROMC)
 Sudbury, no data, (3, FMNH), (1, CNC), (4, CU), (2, USUI), (3, LEMC), (3,
 ROMC) 1889, (1, CNC); 1893, (1, CNC); J.D. Evans, (1, CNC)
 Timagami, 9.vi.1932, A.W.A. Brown, (1, UNH)
 Toronto, 10.x.1896, R.J. Crew (6, CU)
 vii.1930 (2, CMP); 29.iv.1964 (1, UMAA), (2, CAS);
 11-10-96, (15, ROMC); 3-7-1887, (1, ROMC); 9-5-1899, (1, ROMC)
 no data, (1, ROMC)
 Windsor, 7.i.1907, W.E. Britton, (2, CU)
 Hastings Co., 1.vi.1937, J.F. Brimley, (2, UCD) Evans, (1, UCD), (1,
 ROMC)
 Prince Edward Co., 31.v.1923, J.F. Brimley (1, CNC)
 3.vi.1914,)
 25.v.1919, J.F. Brimley, (1, CNC)
 E. Ont., no data, (1, CNC) W. Couper (3, LEMC);

larvae

Sudbury R.M., 0.4 km. S. Noelville, 8.viii.1985, R.E. Roughley, Pinus
strobus, (4, DAPC)
 11.viii.1986, R.E. Roughley, pre-pupae, (15, DAPC)

pupae

Sudbury R.M., 0.4 km. S. Noelville, 11.viii.1986, R.E. Roughley, Pinus
strobus, (15, DAPC)

New Brunswick

adults

Tabusintac, 20.vi.1939, W.J. Brown, (1, CNC)

Nova Scotia

adults

Halifax Co., Armdale, 19.v.1959, D.C. Ferguson (1, NSPM)

Quebec

adults

Aylmer, Queen's Park, 24.x.1923, C.B. Hutchings, (1, CNC)

Bristol Pont, 21.x.1974, C. Chantal, (1, DKYC)

Cantley Touraine, 14.ix.1973, R. Sexton, under bark of Pinus strobus,
(7, CNC)

6.iv.1974, R. Sexton, under bark of Pinus strobus, (27, CNC)

Duparquet, G. Stace Smith, 14.x.1934, (25, CAS); 25.xi.1934, (1, CAS);

29.x.1935, (2, CAS), (1, AMNH); 10.v.1936, (1, CAS); 2.vi.1936, (1,

CAS); 4.vi.1936, (1, CAS); 1.vi.1938, (1, CAS); 27.v.1940, (3, CAS);

28.v.1940, (1, CAS); 30.v.1940, (2, CAS); 3.vi.1940, (1, CAS);

16.vii.1940, (1, CAS); 17.vii.1940, (1, CAS); 21.v.1944, (1, CAS)

Ft.-Coulogne, 4.vi.1918, J.I. Beaulne, (1, CNC)

Hull, 16.v.1912, (1, ROMC)

18.v.1914, (1, ROMC); 1914, (4, ROMC)

P.S.P. Station, Lake Edward, Champlain Co., 5.x.1923, H.S. Fleming, (1,
CNC)

L. du Chevalier Champl., 2.x.1969, C. Chantal, (3, DKYC)

Laniel, 13.vi.1932, (1, CNC); 2.vi.1933, (1, CNC); 5.vi.1933, (4, CNC);

7.vi.1933, (1, CNC); 8.vi.1933, (1, CNC); 10.vi.1933, (3, CNC);

12.vi.1933, (1, CNC); 16.vi.1933, (1, CNC); 17.vi.1933, (1, CNC);

19.vi.1933, (4, CNC); 20.vi.1933, (2, CNC); 5.vii.1933, (1, CNC);

16.ix.1933, (1, CNC); 5.x.1933, (1, CNC); 31.v.1934, (2, CNC);

1.vi.1934, (6, CNC); 2.vi.1934, (9, CNC); 4.vi.1934, (2, CNC);

- 5.vi.1934, (3, CNC); 6.vi.1934, (1, CNC); 11.vi.1934, (1, CNC);
 13.vi.1934, (2, CNC); 14.vi.1934, (2, CNC); 15.vi.1934, (4, CNC);
 28.viii.1935, (1, FPMI)
- H.S. Fleming, 13.vi.1935, (1, CNC); 14.vi.1935, (1, CNC); 15.vi.1935,
 (1, CNC)
- 13.vi.1932, D. Gray, (1, FPMI)
- J.B. Thomas, 1951, (5, FPMI); 30.v.1950, (1, FPMI); 22.vi.1950, (1,
 FPMI); 4.vii.1950, (1, FPMI)
- Limbour, Gatineau, 13.vi.1975, C. Chantal, (2, DKYC)
- Mistassini Lk. 20 mi. N. Mistassini Post, 16.vi.1955, J.R. McGillis, (1,
 CNC)
- Montreal, coll. nat. Hist. Soc., no data, (3, LEMC)
- Old-Chelsea, 16.v.1934, (3, CNC)
- Trois Rivières, 16.v., F. Germain, (1, UASM)
- Wakefield, 24.ix.1973, R. Sexton, under bark of Pinus strobus, (31, CNC)
- larvae**
- West Brome, 24.iv.1981, S. Laplante, Pinus strobus, (2, CNC), (2, DKYC)

Saskatchewan

adults

- Hwy #2, 4.5 km. W. Jct. Twoforks River & Hwy #2, 16.v.1987, D.A. Pollock
 and L.A. Reichert, under bark of Pinus banksiana, (1, DAPC)
- 3.5 km. N. Prince Albert on Hwy #2 and 3.2 km. E., 15.v.1987, D.A.
 Pollock and L.A. Reichert, ex. larvae coll. under bark of Pinus
banksiana, (19, DAPC)

larvae

- 3.5 km. N. Prince Albert on Hwy #2 and 3.2 km. E., 15, 18.v.1987, D.A.
 Pollock and L.A. Reichert, under bark of Pinus banksiana, (150, DAPC)

Hwy #55, 20.7 km. N. Jct. of Hwy #55 and 793, 17.v.1987, D.A. Pollock
and L.A. Reichert, under bark of Pinus banksiana, (2, DAPC)

Jct. Hwy #165 & 100, in gravel pit, 16.v.1987, D.A. Pollock and L.A.
Reichert, under bark of Pinus banksiana, (15, DAPC)

7.4 km. N. White Gull Creek off Hwy #120, 17.v.1987, D.A. Pollock and
L.A. Reichert, under bark of Pinus banksiana, (10, DAPC)

Hwy #55, 7.2 km. N. Jct. Hwy #55 & 240, nr. Canwood, 17.v.1987, D.A.
Pollock and L.A. Reichert, under bark of Pinus banksiana, (10, DAPC)

pupae

3.5 km. N. Prince Albert on Hwy #2 and 3.2 km. E., 15.v.1987, D.A.

Pollock and L.A. Reichert, ex. reared larva coll. under bark of Pinus
banksiana, (1, DAPC)

Northwest Territories

adults

Fort Smith, J.B. Wallis, 10.vi.1950, (4, CNC); 13.vi.1950, (2, CNC)
12.vi.1950, W.G. Helps, (1, CNC)

Aklavik, O. Bryant, 16.ix.1929, lot 6, (4, CAS); 5.ix.1930, lot 120, (3,
CAS); 27.iv.1931, lot 206, (4, CAS); iv.1931, lot 201, (8, CAS);
18.v.1931, lot 213, (11, CAS); 25.v.1931, lot 217, (1, CAS);
24.vi.1931, lot 241, (1, CAS); 29.vii.1931, lot 312, (2, CAS)

larvae

N. of Inuvik, McKenzie River, viii.1979, R.A. Ring, Picea, (4, CNC)

Yukon Territory

Vangora Crk. 3500', 12.vi.1960, E.W. Rockburne, (1, CNC)

UNITED STATES OF AMERICA

Alaska

adults

Ketchikan, vii.1916, (1, CAS)

Skagway, vi-viii.1923, L.L. Muchmore, "J. Aug. Kusche", (3, LACM)

Alaska, vi-viii.1923, L.J. Muchmore, "J. Aug. Kusche," (2, UMAA), 7
(LACM)

larvae

Porcupine R., 100 mi. N. Ft. Yukon, 2.vi.1911, J. Jessup, (10, NMNH)

New Rampart House, 10.ix.1911, J.M. Jessup, dead spruce, (3, NMNH)

nr. Rampart House, 1912, J.M. Jessop, (6, NMNH)

state record only, no data, (6, NMNH)

Arkansas

Southwest Ark., (1, AMNH)

California

Tulare Co.

Kaweah, R. Hopping, (1, MCZ)

Colorado

adults

Conejos Co.

Valley Upper San Juan, 13-15.viii.1885, 7-10,500 ft., 1 (MCZ).

larvae

Larimer Co.

Glendevy 8500', H.E. Evans, under bark, (4, VPI)

State record only, in yellow pine, (3, NMNH)

Connecticut

Litchfield Co.

Cornwall, K.F. Chamberlain, 18.xi.1918, (4, CAS), (2, CU) 13.iv.1922,
(2, CU) 29.v.1922, (2, SMEK), (2, CAS); 24.v.1924, (2, FMNH)

Idaho

adults

Bear Lake Co.

12 mi. W. Montpelier, ex. larva coll. 22.vii.1985, J.B. Johnson, under
bark of down spruce, (7, UIM)

Latah Co.

Laird Pk., 4 mi. NE Harvard, 24.iii.1973, S.D. Berkencamp, (2, WSU)

Twin Falls Co.

Magic Mtn. Ski Area, 8.v.1976, A. Allen, under bark of Abies, (2, DKYC)

larvae

Bear Lake Co.

12 mi. W. Montpelier, 22.vii.1985, J.B. Johnson, under bark of wind
thrown spruce, (1, UIM)

Idaho Co.

Lolo Pass, 16.viii.1982, J.B. Johnson, under bark of Pinus log, (1,
DKYC)

Latah Co.

12 mi. N.E. Potlatch nr. Big Ck and Hope Ck., 12.v.1976, L. Chin, (2,
WSU)

5 mi. N.E. Harvard, 15.v.1976, F.M. Tessitore, under bark, (1, WSU)

Big Meadows, 7 mi. N. Troy, 19.vi.1986, J.B. Johnson, under loose bark
of moist fir log, (5, UIM)

State record only, Pinus monticola, (1, NMNH)

Twin Falls Co.

Magic Mtn. Ski Area, 8.v.1976, A. Allen, under bark of Abies, (7, DKYC)

Maine**adults****Bangor Co.**

Orono, 1.v.1912, H.M. Parshley, (1, CAS)

13.v.1914, Biol. 8, (2, CAS)

19.vi.1967, (4, DKYC)

Passadunkeag, 26.v.1944, A.E. Brower, recently cut Pinus resinosa, (1, UNH)

Kennebe Co.

Monmouth, 24.vi.1909, C.A. Frost, (1, FMNH)

24.vi.1910, C.A. Frost, (1, MCZ)

25.vi.1910, slab piles, (1, MCZ)

Sidney Bog, 8.vi, A.E. Brower, (1, UNH)

Oxford Co.

Paris, 24.vi.1922, C.A. Frost, 1 (MCZ)

16.vi.1910, C.A. Frost, (1, UMAA), (1, UCR)

Penobscot Co.

Old Town, University Forest, R. Dearborn, 8.vi.1961, (1, DEUM)

28.vi.1961, (1, DEUM) 6.vii.1961, (1, DEUM); 2.viii.1961, (4, DEUM);

14.viii.1961, (1, DEUM) 15.viii.1961, (3, DEUM); 16.viii.1961,

D.C. Allen and D.B. Shibles, 16.vi.1964, (1, DEUM) 18.vi.1964, (2, DEUM) 22.vi.1964, (1, DEUM)

5.vi.1962, no collector, (2, DEUM)

Piscataquis Co.

Mt. Katahdin Summit, 17.vi.1934, J.N. Belkin, (1, FSAC)

Somerset Co.

Detroit, 31.iii.1959, (1, DKYC)

Jackman, 27.viii.1939, (1, NMDC), (3, FSCA)

larvae

Lincoln Co.

county record only, 20.vi.1956, D.J. Borrer, under bark, (2, OSU)

Maryland

adults

Montgomery Co.

3 mi. E. Takoma Pk., 17.xii.1949, G.H. Nelson, under bark of dead pine,
(1, UCR)

Prince Georges Co.

College Park, 7.iii.1942, G.B. Vogt, (1, CAS)

Greenbelt, 30.xii.1950, B.K. Dozier, under pine bark, 1 (FSCA)

state record only, (3, CMP)

larvae

Prince Georges Co.

College Park, 21.ii.1948, H.F. Howden, dead standing pine # 2, (1, CNC)

Massachusetts

adults

Berkshire Co.

Lenox, no data, (1, AMNH)

Bristol Co.

Taunton, G.W. Pepper, (1, MCZ)

Franklin Co.

Wendell, 9.vi.1974, R.P. Webster, on white pine log, (1, CU)

Hampden Co.

Springfield, 7.vi.1917, E.A. Chaplin, (3, FMNH)

Hampshire Co.

Amherst, 20.iv.1919, (1, MCZ)

28.v.1925, (3, UASM), (1, CAS)

Belchertown, 20.ix.1941, A.R. Lewis, (1, UNH)

Northampton, 7.iv.1915, D.L. Merchant, pine, (3, CAS)

7-4-19, D.L. Merchant, 2 (CAS)

Middlesex Co.

Concord, 9.iii.1925, pine bark, (2, MCZ), (1, FSCA)

Concord, Estabrook Woods, 1.xi.1975, A. Newton & M. Thayer, (2, DAPC)

Tyngsboro, 14.x.1894, (7, MCZ)

25.iii.1900, (1, MCZ)

Waltham, 30.xii.1924, (1, UASM)

Wayland, 31.i.1925, P.J. Darlington, Pinus strobus, (3, MCZ)

Worcester Co.

Harvard Forest, Petersham, 8.v.1969, J.F. Lawrence, (2, MCZ)

state record only, (4, FMNH), (1, CAS)

larvae**Middlesex Co.**

Concord Field Stn., 2.vi.1973, under bark, conifer log, (5, MCZ)

Pickman Area, Bedford, 23.vii.1974, J.F. Lawrence, under conif. bark,
(2, MCZ)

Michigan**adults****Chippewa Co.**

Whitefish Point, 28.vii.1914, A.W. Andrews, (2, UMAA)

no data, det. as P. deplanatus by Seidlitz, (1, ZMHB)

Mackinac Co.

St. Ignace, 30.v.1922, S. Moore, (3, UMAA)

Marquette Co.

T 44N-R 28W-Sec. 15, Blk. Riv. Dr., 23.vii.1982, D.K. Young, beneath
bark of Pinus, (1, DKYC)

Huron Mountain Club, D.C.L. Gosling, 18.vi.1983, (1, DKYC); 24.vi.1984,
(1, DKYC)

Marquette, 28.vi, (1, UMSP), (1, ZMHB)

2.7, 1 (UVCC)

Van Riper St. Pk., 12-14.vii.1972, D.K. & D.C. Young, (2, DKYC)

state record only, (1, MPM)

larvae

state record only, in white pine, (3, NMNH)

pupae**Marquette Co.**

T 44N-R 28W-Sec. 15, Blk. Riv. Dr., 23.vii.1982, D.K. Young, beneath
bark of Pinus, (6, DKYC)

state record only, in white pine, (3, NMNH)

Minnesota**adults****Carlton Co.**

Cloquet, A. Raske, 21.iv.1959, (1, CNC) 2.vi.1959, (1, CNC)

Cass Co.

Estherville, x.1906, W. Schuster, (1, FMNH)

Clearwater Co.

Itasca State Park, summer 1937, student collector, 1 (WSU)

Itasca Park, L.W. Orr, 15.vi.1931, (1, UMSP) 19.v.1932, (3, UMSP)

3.vi.1932, (1, UMSP); 8.vi.1933, (1, UMSP); 11.vi.1933, (4, UMSP)

12.vi.1933, (2, UMSP); 13.vi.1933, (1, UMSP); 15.vi.1933, (2, UMSP);

1935, (6, DKYC)

Itasca Park, nursery, 30.v.1928, B. and L.W. Orr, (1, UMSP)

Itasca Park, 28.vi.1923, S.A. Graham (1, UMSP)

Itasca State Park, 23.viii.1955, T. Daggy, (1, UMSP)

A.C. Ashworth, under pine bark, (9, NDSU)

Lake Itasca, S.A. Graham, 9.vi.1920, (1, UMSP) 1.vi.1923, (1, UMSP)

7.vi.1923, (7, UMSP); 12.vi.1923, (5, UMSP); 20.vi.1923, (1, UMSP)

Crow Wing Co.

Brainerd, A. Raske, reared pupa from jack pine, 15.viii.1951, (1, CNC)

13.ix.1958, (1, CNC)

St. Louis Co.

Duluth, no data, (1, INHS), (3, MCZ), (5, LACM)

Daggett (1, LACM)

state record only, (1, SMEK)

larvae

Anoka Co.

Cedar Creek Bog, 17.iv.1954, H.G. Ewan, (5, UMSP)

Carlton Co.

Cloquet, 8.ix.1936, H.R. Dodge, jack pine windfall (under bark), (3, UMSP)

Clearwater Co.

Itasca State Park, 1935, L. Orr, under bark of dead tree, (12, UMSP)

7.vi.1956, Bohell, under bark, (4, UMSP)

22.vi.1956, R. Piva, under spruce bark, (2, UMSP)

24.vi.1957, F.W. Stehr, (7, UMSP)

27.vii.1960, (3, UMSP)

27.vii.1960, K.C. Kim, ex. Pinus resinosa, (3, UMSP)

Bohall [Trail?], 7.vii.1956, (7, UMSP)

Bohall Trail, Itasca, 7.vii.1956, (10, OSU)

6 mi. N. of Itasca St. Park (Carl Gustafson farm), 6.vi.1954, T. Daggy,
under pine bark, (1, UMSP)

county record only, 7.vi.1954, (4, UMSP)

Itasca Co.

county record only, vii.1957, H. Kulman, under pine bark, (1, VPI)

Lake Co.

near Ely, 10.ix.1936, under bark of Pinus banksiana, (4, UMSP)

Montana

Gallatin Co.

Bozeman, x.1957, R.C. Froeschner, (1, MSUC)

Jefferson Co.

31.v.1982, student collector, (1, MSUC).

New Hampshire

adults

Belknap Co.

Barnstead, 1929, (1, CAS)

Cheshire Co.

Hinsdale, 19.iv.1908, (1, MCZ)

Coos Co.

Randolph, 16.x.1897, (1, MCZ)

Grafton Co.

Franconia, no data, (1, MCZ), (1, AMNH)

Hillsboro Co.

Hollis, 19.iv.1980, N.E. Woodley, Beaver Brook Ass'n, (2, FMNH), 12,
WSU)

Rockingham Co.

Exeter, 21.iv.1923, C.E. White, jr., (2, MCZ)

Hampton, 29.iv.1900, S.A. Shaw, (1, UNH)

28.iv.1968, F. Harshman, (1, UNH)

Nottingham, 30.xi.1962, A.H. Mason and W.J. Morse, coll. on Pinus,
(3, UNH)

Strafford Co.

1 mi. SW Durham, 16.iv.1982, D.S. Chandler, water tower (1, UNH)

Durham, 19.iv.1957, H.P. Mock (4, UNH)

3.v.1966, (1, UNH)

14.iv.1976, C. Mack, (1, UNH)

2.iv.1986, W.J. Morse, wood pile, (1, UNH)

Barrington, 10.iv.1983, B. Morse, ex. under bark, (2, UNH)

Rochester, 22.iv.1972, P. Auger, (2, UNH).

larvae

state record only, 22.iv.1905, pine, (3, NMNH)

New Jersey

state record only, no data, (1, CAS)

New York

adults

Erie Co.

Buffalo, no data, (8, INHS), (4, FMNH), (4, MCZ), (2, WSU), (3, SMEK),
(3, UMSP)

Onondaga Co.

Syracuse, 19.xi.1913, M.W. Blackman, (1, OSU)

St. Lawrence Co.

Cranberry Lake, 7.vii.1922, (1, OSU)

Rossie, 16.vi.1967, N.M. Downie, (8, NMDC), (2, FSCA)

Schuyler Co.

county record only, 23.iv.1922, M.H. Hatch, (1, OSU)

Tompkins Co.

Groton, 1.vi.1953, N.M. Downie, (1, NMDC)

Ithaca, no data, (5, CAS), (1, AMNH)

9.v.1897, (13, CU) 2.vi.1899, (1, CMSC); x.1912, (1, CU); 28.iii.1915, (3, CU) 7.v.1915, (1, UMSP); 19.iv.1919, (1, CAS); 8.xi.1924, (6, CU) 20.ii., (1, CU)

8.xi.1924, F.C. Fletcher (4, CAS), (3, CU)

18.iv.1897, Knab, (1, CAS), (1, MCZ), (3, CU), (1, FMNH)

31.iii.1915, H.H. Knight, (1, BYU), (2, ISUI)

8.xi.1929, Babiay (2, CU)

H. Dietrich, 27.iii.1915, (1, CU) 1.iv.1915, (1, CU); 10.iv.1915, (1, CU) 17.iv.1915, (5, CU); 28.vi.1917, (1, CU); 19.v.1934, (3, CU)

Six Mile Ithaca, 3.iii.1946, R.M. Schuster, (1, CU)

Cascadilla Cr. Ithaca, 27.v.1922, F.C. Fletcher (1, CU)

Wyoming Co.

Pike, no data, (1, CAS)

11.vi.1901, (1, LACM) 3.vii.1901, (2, LACM)

larvae**Tompkins Co.**

Ithaca, 1880, (2, NMNH)

Ithaca, Six Mile Creek, 3.iii.1946, R.M. Schuster, Pinus strobus, (10, CU)

Ringwood Dryden, 27.x.1949, H. Dietrich, under bark of white pine, (4, CU)

State record only, pine, (2, NMNH)

pupae**Tompkins Co.**

Ithaca, 1880, (2, NMNH)

North Carolina**adults**

state record only, (2, CAS), (3, CMP), (2, CU)

larvae**Polk Co.**

nr. Tryon, short leaf pine, (1, NMNH)

Ohio

il -3;.bd Hamilton Co.

Cincinnati, no data, (1, MCZ)

Lucas Co.

Toledo, no data, (5, CMP)

state record only, (3, MCZ), (1, INHS), (2, CMP), (2, UVCC), (3, UWL),
(1, UMAA), (1, MPM)

Oregon**adults****Clackamas Co.**

Upr Clackamas Riv. 10 mi. s.w. Ripplebrook, 27.vii.1976, (2, NMDC)

Hood River Co.

Mt. Hood near Barlow Pass, 29.vi.1974, A. & D. Smetana (1, CNC)

Mt. Hood, 3000-6000 ft., 22.vi.1925, (5, CAS) 24.vi.1925, (1, CAS)

Jackson Co.

Union Creek, 1-15.ix.1950, B. Malkin, 3100-3500 ft., (9, FMNH), (1,
OSU)

Lake Co.

Lakeview, Willow Cr. Camp, 28.vi.1984, J.L. & B.C. Carr, (3, CARR)

Union Co.

15 mi. SW of La Grande, 15.vi.1951, R. Stevens, (1, OSU)

larvae**Gilliam Co.**

Rock Creek, no data, Pinus ponderosa, (3, NMNH)

Umatilla Co.

20 mi. E. Ukiah, Umatilla N.F., 30.iii.1978, Raffe, under Pinus contorta bark, (1, WSU)

Pennsylvania**adults****Alleghany Co.**

Fair Oaks, 26.iii.1921, (1, CMP)

Pittsburgh, 3.v, (3, CMP)

6.v, (1, CMP)

county records only, (4, CMP)

Centre Co.

Poe Vly St. Pk. 14.ix.1978, D.K. Young, (11, DKYC), (2, UZIL)

State College, 5.ii.1915, (1, CMP)

Dauphin Co.

Halifax, no data, (1, CAS)

Hummelstown , 31.iii.1918, (2, CAS)

J.N. Knull, 1.v, (1, CMP) 20.v, (2, CAS); 1.vi, (1, CMP); 3.vi, (1, CMP) 5.vi, (1, CAS)

county record only, 8.ii.1928, J.N. Knull, (1, CAS)

Huntington Co.

Rothrock St. For. Seeger Nat. Area, 30.v.1985, D.S. Chandler, under bark and fungi 900', (1, UNH)

Luzerne Co.

Rock Glen, 1.iv.1928, (1, FEM)

Tioga Co.

county record only, (2, FMNH)

Warren Co.

Warren, no data, (3, CAS)

Westmoreland Co.

Jeanette, v, (2, CMP)

20.v, (1, CMP)

state record only, (1, CAS), (3, INHS), (1, CAS), (6, MCZ), (1, NMDC),
(1, ZMHB)

larvae**Centre Co.**

Poe Valley St. Pk., 14.ix.1978, D.K. Young, beneath bark of Pinus, (1,
DKYC)

state record only, Pinus strobus, (7, NMNH)

pupae**Centre Co.**

Poe Valley St. Pk., 14.ix.1978, D.K. Young, beneath bark of Pinus, (30,
DKYC)

Rhode Island

state record only, no data, (1, MCZ)

South Carolina**adults****Oconee Co.**

CCC Camp F2, 22.iii.1939, O.L. Cartwright, (2, CMSC)

larvae**Greenville Co.**

Greenville, 12.iii.1913, under bark of dead pine, (3, NMNH)

Oconee Co.

Clemson, Dairy Farm, 6.x.1961, J.A. Payne, under pine bark, (4, CMSC)

Clemson, 7.x.1961, L.E. Priester, pine log, (1, CMSC)

15.x.1961, R.D. Eikenburg, in dead log, (1, CMSC)

7.x.1961, R.E. O'brien, in pine log, (1, CMSC)

25.ix.1965, A. Kalkandelen, host: pine log, (1, CMSC)

6.x.1961, J.A. duRant, dead pine, (2, CMSC)

25.ix.1965, R.C. Fox, host: pine log, (4, CMSC)

7.x.1961, N.H. Anderson, under pine bark, (3, CMSC)

Stumphouse Mtn., 6.x.1969, H. Douglass and T. Hill, in rotten log, (2, CMSC)

pupae**Greenville Co.**

Greenville, 12.iii.1913, under bark of dead pine, (1, NMNH)

South Dakota**larvae****Lawrence Co.**

Cheyenne Crossing, Blk. Hills Natl. For., 13-14.vii.1974, D.K. Young, (30, DKYC)

Tennessee

state record only, no data, (2, CMP)

Utah**adults****Cache Co.**

Little Bear Creek, 1.vii.1939, C.J. Davis, (3, USUC)

Logan Canyon, S.L. Wood, 9.vi.1949, (1, USUC) 11.vi.1949, (1, USUC)

30.vii.1984, T. Eager, (1, USUC)

larvae

State record only, no data, lodgepole pine logs, (1, NMNH)

Vermont**Bennington Co.**

Dorset, 24.x.1973, C.T. Parsons, under bark white pine, (1, MCZ)

Chittenden Co.

Shelburne Pond, Shelburne, 12.x.1955, R.T. Bell, (1, UVCC)

Washington**adults****Stevens Co.**

Northport, 27.iv.1929, W.W. Jones, (14, CAS)

larvae**Spokane Co.**

Spokane S.P. nr. Bald Knob C.G. 5200 ft., 26.vi.1978, R.S. Zack, (12, WSU)

Wisconsin**Bayfield Co.**

Bayfield, no date, Wickham (1, CAS)
(1, MCZ)

Vilas Co.

Nicolet Nat. For. T41N, R11E, Sec.12, 23.viii.1984, D.K. Young,
beneath bark of Pinus, (6, DKYC)

A.9 PYTHO DEPRESSUS**AUSTRIA**

Carinthia, no data, (6, CMP)
 Kärnthen [=Kärnten], no data, (1, SMF)
 Koralpe, 8. 1904, (1, SMF)
 Kuhtal, Tirol, 7.8.87, (2, ZMHB)
 Oetz, Tirol, 1.7.1903, (1, ZMHB)
 Tyrolis, A. Kasper, (3, TMB)
 country record only, no data, (2, TMB)

DENMARK**Sjaelland****adults**

Tisvilde Hegn, Seeland, 24.v.1896, E. Rosenberg, (1, NMNH)

larvae

Tisvilde Hegn, Seeland, 24.v.1896, E. Rosenberg, (1, NMNH)

Tisvild hegn, Fyregrene, 20.x.1934, (10, NMNH)

pupae

Tisvilde Hegn, Seeland, 24.v.1896, E. Rosenberg, (2, NMNH)

FEDERAL REPUBLIC OF GERMANY**Bayern**

München, 3.5.81, (1, ZMHB)

Pressath opf Germania, 23.ix.71, G. Uhmman, ex. larva, (1, ZMHB)

Schliersee, 5.7.1909, (1, ZMHB)

Erfurt

Nordhausen, no date, Reitter, (1, SMF)

Hamburg

Hamburg, no date, W. Meier, (4, FMNH)

4.87, (2, SMF); 1917, Berghorst, (1, ZMHB)

no data, (1, SMF), (1, TMB), (2, ZMHB)

Niedersachsen

Bassum, no data, G. Schnaf, (4, SMF)

no data, (4, MNV)

Elm, no date, Hummler, (3, ZMHB)

Hagen, "Märt W.", no data, (1, ZMHB)

Hildesheim, Hannover, no data, (1, TMB)

Hannover, no date, Reitter, (1, SMF), (5, TMB), (5, MNV)

Nordrhein-Westfalen

Duisburg, no data, (1, FMNH)

Eversberg, 22.ii.91, (4, ZMHB)

Krefeld, no data, Ulbricht, (1, SMF), (1, TMB), (2, ZMHB)

no data, (1, MNV)

Potsdam

Berlin (u. Umg.), no data, (1, SMF)

country record only, no data, (6, TMB), (4, MPM), (2, UMAA)

FINLAND**Etelä-Häme**

Jämsä, no data, U. Sahlberg, (1, TMB)

Korkeakoski, no data, Carpelan, (1, ZMH)

Korpilahti, no data, J. Sahlberg, (1, ZMH)

Juupajoki, no data, J. Carpelan, (2, ZMH)

Ruovesi, no data, E. Elfving, (1, ZMH)

Kainuu

Kajaani, no data, J. Carpelan, (2, ZMH), (1, TMB), (2, SMF)

Suomussalmi, no data, J. Carpelan, (1, ZMH)

Vuolijoki, no data, J. Carpelan, (1, ZMH)

Pohjois-Häme**larvae**

Saarijärvi, 22.ix.1984, O. Biström and R. Vaisänen, (1, ZMH)

Pohjois-Pohjanmaa, eteläosa**adults**

Ranua, 15.vi.1941, F. Fink, (1, SMF)

larvae

Simojoki, 5.vii.1912, V. Bäsänen, (3, ZMH)

Varsinais-Suomi

Sammatti, 24.viii.1917, H. Lindberg, (2 ZMH)

Wichtis [=Vihti], 18.viii.1917, H. Lindberg, (2, ZMH)

no data, A.G. Helenius, (1, ZMH)

Lapland

no data, (1, SMF), (3, ZMHB), (1, TMB)

country record only, "Al. Smolka", (1, TMB)

no data, (6, TMB)

FRANCE

Allier, no data, (2, CMP)

Champagne bei Reims, ii.18, (2, ZMHB)

GERMAN DEMOCRATIC REPUBLIC**Cottbus**

Luckau, vi.1962, W. Nadolski, (1, ZMHB)

NETHERLANDS

Noord-Brabant

Chaam, 8.iv.1971, P. Kanaar, (1, ROMC)

Noord-Holland

Hilversum, no data, (4, SMF)

NORWAY

Buskerud

Kongsberg, (2, ZMHB)

Troms (I)

TRI: Målselv Hogskarhus, Dividal, 25.vi.1986, Fjellerg and Midtgaard,
(1, TMDZ)

unknown localities:

Bjerkeng Norway, 1898, (2, TMDZ)

Norwegen Ranum Ovehalden, 25.viii.03, S. Strand, under Rinde, (2, ZMHB)

Norge: Sydvaranger Bjorsund, 6-1898, A. Wessel, (1, TMDZ)

country record only, no data, (1, TMB), (1, ZMHB)

POLAND

Beuthen [=Bytom] Silesia, no data, M. Nowotny, (1, ZMHB)

Bialowies [=Białowiecki Park?], no data, (1, ZMHB)

Danzing [=Danzig (Gdansk)?], no data, (1, TMB)

Jaroslau, no data, (1, FMNH)

1895, A. Jakowlew, (1, CMP)

Puszcza Kampinoska, 7.ix.1975, B. and H. Malkin, (1, FMNH)

country record only, no data, (1, ZMHB)

SPAIN

Galicia, no data, coll. Geitner, (8, TMB)

SCOTLAND

nr. Green Loch (L. Maxlich), 27.ix.1951, D.K. Kevan, Sr., (2, LEMC)

SWEDEN**Närke**

Örebro, no data, A. Jansson, (2, UMAA)

Västerbotten**adults**

Umeå: Hamriusberget, 9.v.1985, R. Pettersson, (10, DAPC)

RN 21J4d2-4-: Sundö, Åimyrlidens B.-F., 18.v.1985, R. Pettersson, (1,
DAPC)

RN 21J4g4-2-: Kulbäcksliden: Reservatet, 18.v.1985, R. Pettersson, (1,
DAPC)

larvae

Umeå: Hamriusberget, 9.v.1985, R. Pettersson, (4, DAPC)

pupae

Hänäs, Skatan Gohlandsasen (?), 16.viii.1985, R. Pettersson, (1, DAPC)
country record only, Suecia, no data, Sandin, (2, SMF), (1, TMB), (1,
ZMHB)

no data, I.B. Ericson, (12, ZMHB)

U.S.S.R.**Kirgizskaja S.S.R.**

Przewalsk [=Przevalsk] Almasy Turkestan, no data, (1, TMB)

Latvijskaja S.S.R.

Curonia, Libau [=Liepaja], 14.iv.1913, (1, ZMHB)

Rossijskaja S.F.S.R.

Chabarovsk, no data, (1, SMF)

Kavkaz s.-z., Teberda, vi.1941, (1, ZMMU); 5.vii.1940, (1, ZMMU)

Moskau, no data, (1 SMF)

Okr. Moskvi, st. Losinoostr., 12.v.1931, (1, ZMMU)

Burmantowo Indelskij Rajon gebiet Swerdlowsk, 5.vi.1958, Rosnitzin, (2, ZMHB)

Transbaicalia Selenga-Tal, v-vi.1908, (1, ZMHB)

Ukrainskaja S.S.R.

Kiew Russl., no data, (2, TMB)

Konotop, ii.1913, (1, ZMMU)

Unknown localities:

Nikol. gora Mosk, 9.v.1932, S. Nikulin, (1, ZMMU)

Tjumensk. obl., Berezov, I. Telisev, vi.1932, (1, ZMMU)

Yugoslavia**Bosna i Hercegovina**

Zavidovic [=Zavidici], 10.v.1905, Kendi, (1, TMB)