
NATURAL HISTORY, CLASSIFICATION, RECONSTRUCTED PHYLOGENY, AND GEOGRAPHIC HISTORY OF *PYTHO* LATREILLE (COLEOPTERA: HETEROMERA: PYTHIDAE)

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NATURAL HISTORY, CLASSIFICATION, RECONSTRUCTED PHYLOGENY, AND GEOGRAPHIC HISTORY OF *PYTHO* LATREILLE (COLEOPTERA: HETEROMERA: PYTHIDAE)

DARREN A. POLLOCK

Abstract

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The classification of the nine world species of *Pytho* Latreille is reviewed by study of adult, larval, and pupal stages. Keys are provided for separation of species in these three life stages. Taxonomic changes (senior synonym in brackets) include synonymy of *P. fallax* Seidlitz 1916 [=*P. niger* Kirby 1837]; *P. americanus* Kirby 1837 [=*P. planus* (Olivier 1795)]; *P. deplanatus* Mannerheim 1843 is transferred from a junior subjective synonym of *P. depressus* (Linnaeus 1767) to a junior subjective synonym of *P. planus* (Olivier 1795). Lectotype designations are provided for the following: *P. seidlitzi* Blair 1925; *P. nivalis* Lewis 1888; *P. niger* Kirby 1837; *P. fallax* Seidlitz 1916; *P. abieticola* J. Sahlberg 1875; and *P. americanus* Kirby 1837. Eight larval stage, and 12 adult stage characters were selected for cladistic analysis. Lacking out-group material, pupal characters were not analysed. Character states were polarized using a generalized out-group composed of the three other genera of Pythinae (all monobasic). Phylogenetic analysis based on these 18 characters suggests four monophyletic species-groups: *P. seidlitzi* group (*P. seidlitzi* Blair — North America); *P. kolwensis* group (*P. strictus* LeConte - North America, *P. kolwensis* C. Sahlberg — Fennoscandia and the U.S.S.R., *P. nivalis* Lewis — Japan); *P. niger* group (*P. niger* Kirby — North America, *P. abieticola* J. Sahlberg — Europe, *P. jezoensis* Kôno — Japan); *P. depressus* group [*P. planus* (Olivier, 1795) — North America, *P. depressus* (Linnaeus, 1767) — Europe and the U.S.S.R.]. Larval stage synapomorphies are relatively more important in defining the species-groups than are those of the adult stage. The ancestor of Pythidae may have been associated with Coniferae as early as the Jurassic. The common ancestor of Northern Hemisphere Pythinae became isolated upon Laurasia once separation from Gondwanaland occurred near the end of the Jurassic. Two of the species-groups have similar disjunctions in North America, Europe, and Japan. The relatively eastern distributions of the North American member of each suggests that the ancestor of each species-group was Euramerican, and underwent vicariance with the opening of the North Atlantic in the Middle Cretaceous. The present distribution of both species-groups is thought to have been caused by the same vicariant event. The ancestor of the *P. depressus* group, which is presently circumboreal, was probably widespread and could have been Asiamerican in distribution. In the middle to late Tertiary, evidence suggests that Beringia was covered with coniferous forest, and the ancestor of the *P. depressus* group probably extended across this land bridge. Final separation between any North American and European/Asian species occurred in the Late Miocene or Pliocene, when a cooling climate made possible the evolution of treeless tundra in the north.

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Résumé

Le classement des neufs espèces mondiales de *Pytho* Latreille a été révisé en étudiant les stades d'adulte, de la larve et de la pupe. Les clés sont fournies pour séparer les espèces de ces trois stades de la vie. Les changements taxinomiques (le synonyme aîné entre parenthèses) comprennent la synonymie de *P. fallax* Seidlitz 1916 [=*P. niger* Kirby 1837]; *P. americanus* Kirby 1837 [=*P. planus* (Olivier 1795)]; *P. deplanatus* Mannerheim 1843 à été muté d'un synonyme subjectif cadet de *P. depressus* (Linnaeus 1767) à un synonyme subjectif cadet de *P. planus* (Olivier 1795). Les nominations lectotypes sont données en ce qui concerne les suivants: *P. seidlitzi* Blair 1925; *P. nivalis* Lewis 1888; *P. niger* Kirby 1837; *P. fallax* Seidlitz 1916; *P. abieticola* J. Sahlberg

1875; et *P. americanus* Kirby 1837. Huit caractères larvaires et 12 caractères d'adultes ont été choisis pour des analyses de clades. À cause de la pénurie de matériels de groupe, les caractères des pupes n'ont pas été analysés. Les états des caractères ont été polarisés, en utilisant un groupe d'en dehors généralisé composé de trois autres genres de Pythinae (tous monobasiques). Les analyses de phylogenèse basées sur ces 18 caractères suggèrent l'existence de quatre groupes-espèce monophylétiques: le groupe *P. seidlitzi* (*P. seidlitzi* Blair en Amérique du nord); le groupe *P. kolwensis* (*P. strictus* LeConte en Amérique du nord, *P. kolwensis* C. Sahlberg en Finnoscandie et en l'U.R.S.S., *P. nivalis* Lewis au Japon); le groupe *P. niger* (*P. niger* Kirby en Amérique du nord, *P. abieticola* J. Sahlberg en Europe, *P. jezoensis* (Kôno au Japon); le groupe *P. depressus* [*P. planus* (Olivier, 1795) en Amérique du nord, *P. depressus* (Linnaeus, 1767) en Europe et en l'U.R.S.S.]. Les synapomorphies du stade larvaire sont relativement plus importantes pour définir les groupes-espèce que celles du stade adulte. L'ancêtre des Pythidae aurait pu être associé avec les Coniferae aussi tôt qu'au Jurassique. L'ancêtre commun des Pythinae de l'hémisphère du nord s'était isolé en Laurasie, une fois que la séparation de Gondwanalande a eu lieu vers la fin du Jurassique. Deux des groupes-espèces ont des disjonctions semblables en Amérique du nord, en Europe et au Japon. Les distributions quasi-orientales du membre nord-américain de chacun suggèrent qu'un ancêtre de chaque groupe-espèce a été Euraméricain et qu'il a subi une modification vicariante à la création de l'océan nord-atlantique à la mi-crétacé. La distribution actuelle des deux groupes-espèce se croît d'avoir été occasionnée par le même événement vicariant. L'ancêtre du groupe *P. depressus*, qui actuellement se trouve circumboréal, a été probablement fort étendu et aurait pu avoir une distribution Asiaméricaine. Du milieu à la dernière partie de la période Tertiaire, l'évidence suggère que Beringie a été couverte d'une forêt conifère et que l'ancêtre du groupe *P. depressus* a été trouvé tout au long de ce pont terrestre. La séparation ultérieure parmi toutes espèces nord-américaines et européennes/asiatiques a eu lieu à la dernière partie du Miocène ou au Pliocène, quand un climat refroidissant a fait possible l'évolution de tundra sans arbres au nord.

INTRODUCTION

The genus *Pytho* Latreille 1796 occurs in North America, Europe, the U.S.S.R., and Japan. Although considered to be a boreal taxon, 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. 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 18th, and early part of the 19th centuries, was due to two species which exhibit great colour and size variations. This fact, and the scattering of descriptions of the various species, caused 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 about the problems encountered with the small number of North American species of *Pytho*.

CONSTITUENTS AND SYSTEMATIC PLACEMENT OF PYTHIDAE

Included herein is a fairly detailed account of the entire family Pythidae, and specifically the subfamily Pythinae. In addition to illustrating the unstable characters of the classification of this, and closely related families of Heteromera, this section introduces the other pythine genera, which are used below for out-group analysis. Also, a recent paper by Watt (1987) is very relevant to the present study; it is discussed and evaluated.

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 lato) 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) accepted 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 reliance upon adult stage characters only. 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, as I believe it should. This, in turn, has increased the number of available characters for taxonomic and phylogenetic analyses. Second, because cladistic methods are used, it is easy to follow Watt's (1987) analysis. Because the rationale for his choice of synapomorphies is provided, the classification is testable.

Watt's (1987) classification 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 1964), and Pythidae (Watt 1987). Nikitsky (1986) proposed the family Pilipalpidae for these taxa, which are known from Chile, Australia, New Zealand, eastern Palearctic, and possibly from the western United States.

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.

The genus *Pytho*, being the nominal genus of the subfamily, has remained relatively unaltered in family position since being described. 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*, known from western North America, is a member of Pythidae.

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 not been demonstrated, although originally described in Pythidae by Horn (1888). This species, known only from Arizona, is thought to have affinities with Trictenotomidae (Crowson 1955). Crowson (1980), like Watt (1987), believes that *Trimitomerus* belongs in Pythidae. However, once the larva is associated and described, the true systematic position of this species may become clearer.

The concept of Pythinae used in this treatment follows that of Watt (1987), except that I have excluded *Trimitomerus*. Because the larva is unknown, and the adult is so aberrant structurally, inclusion of *Trimitomerus* in Pythinae is unsubstantiated, compared with the other pythine taxa with adequately described larvae. Until the larva is described, it may be best to regard *Trimitomerus riversii* as a member of Heteromera incertae sedis.

Historically, Pythidae has been placed near a number of other families, including Mycteridae, Boridae, Trictenotomidae, Pyrochroidae, Salpingidae, and Elacatidae (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 Pilipalpinae + Pythinae is an adult procoxal character. No larval character supports Watt's (1987) hypothesis. Probably taxa included by Watt (1987) in Pilipalpinae are deserving of independent family status (Nikitsky 1986). Although the classification of Watt (1987) is 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.

HISTORICAL REVIEW OF THE TAXONOMY OF PYTHINE LARVAE

In this section, I limit discussion to the historical use of larvae in the taxonomy and classification of *Pytho*, and other members of the subfamily Pythinae as defined in this study. A very detailed treatment of all early literature pertaining to the family Pythidae (sensu lato) is found in Seidlitz (1916) and Blair (1928).

As with many taxa of Coleoptera, work on the immature stages of Pythidae proceeded at a slower rate than that of the adults. The first published account of the natural history of *Pytho*, including larvae, was Degeer (1775) (as cited in Blair 1928). The larva of *Pytho depressus* (L.) was redescribed several times during the early to late 19th century, but these accounts were isolated and not comparative. Westwood (1839) was atypical of this period of heightened work on larval Coleoptera, in that an analysis of larvae was incorporated into the traditional adult classification. In 1875, Sahlberg described the last of the European species of *Pytho*, and included descriptions of the larvae of all three species. Thus the larval stages of European species of *Pytho* were in a relatively advanced state of knowledge comparatively early. Larvae of the two Japanese species of *Pytho* were described by the 1960s (Hayashi et al. 1959; Hayashi 1969). The first key distinguishing larvae and pupae of the three European species was presented by Burakowski (1962). In his revision of Palearctic pythids, Iablokoff-Khnzorian (1985) gave a key to larvae of the five Palearctic species; this key was largely adapted from Burakowski (1962, 1976). Again, the state of knowledge of larvae of Palearctic species of *Pytho* was much advanced compared with those in North America.

Although all four North American *Pytho* species were described by 1866, no larval descriptions appeared until Böving and Craighead (1931), and this consisted only of several figures of *P. niger* Kirby. A similar situation existed with the other two North American pythines, *Priognathus monilicornis* Horn and *Sphalma quadricollis* Horn, described in 1838 and 1872, respectively, whose larvae were not identified until the 1980s. Although Peterson (1951) actually described the larva of *P. monilicornis*, it was misidentified as *Lecontia discicollis* (LeConte). Young (1985) stated that the larva figured in Peterson (1951) must be that of *Priognathus* and not of *Lecontia*. My own rearing trials have confirmed this. The larval stage of *Sphalma quadricollis* was described by Young (1976), and the characters of the larva facilitated convincingly the placement of this species in Pythidae. Compared with European species, a much greater lag time existed between description of adults and larvae of North American pythids. Recently, descriptions of immature stages of all Coleoptera have progressed from being nonanalytical and comparative to being incorporated into classifications.

The final species in Pythinae, *Synercticus heteromerus* Newman, has not been formally described in the larval stage. One specimen of the supposed larva of this species was obtained from J.F. Lawrence (ANIC).

No treatment examining larvae from more than one genus of Pythidae had been done until Watt (1987) revised the New Zealand fauna of Pilipalpinae. An important component of this study was a phylogenetic analysis of the salpingid group of families. In his cladogram, Watt (1987) used several larval characters to define the major lineages, or families in the salpingid group.

It is evident that during the 150 years since the first description of *Pytho depressus* was published, the study of larval stages of Pythidae and Coleoptera in general has progressed greatly. Once regarded as imperfect stages in the insects' life cycle, larvae and pupae have become integral parts of many classifications; this is certainly true of Pythidae.

MATERIAL

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 codens used in the text. The codens 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 and UASM.

AMNH: Department of Entomology, American Museum of Natural History, New York, NY, USA 10024; L.H. Herman.
ANIC: Australian National Insect Collection, CSIRO Division of Entomology, PO Box 1700, Canberra City, ACT 2601, Australia; J.F. Lawrence.
BCPM: Entomology Division, British Columbia Provincial Museum, Victoria, B.C., 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, UT, USA 84602; R. Baumann.
CARR: J.L. and A.F. Carr, 24 Dalrymple Green, Calgary, Alta., Canada T3A 1Y2.
CAS: Department of Entomology, California Academy of Sciences, San Francisco, CA, USA 94118; D.H. Kavanaugh.
CDAS: Canada Department of Agriculture, Research Station, 107 Science Crescent, Saskatoon, Sask., Canada S7N 0X2; P. Mason.
CMP: Section of Entomology, Carnegie Museum of Natural History, Pittsburgh, PA, USA 15213; R. Davidson.
CMSC: Entomological Museum, Department of Entomology, Fisheries and Wildlife, Clemson University, Clemson, SC, USA 29631; M.W. Heyn.
CNCI: Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ont., Canada K1A 0C6; A. Smetana.
CU: Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, NY, USA 14853; J.K. Liebherr and E.R. Hoebeke.
DAPC: Darren A. Pollock, Department of Entomology, University of Alberta, Edmonton, Alta., Canada T6G 2E3.
DBTU: Department of Biology, University of Turku, SF-20500 Turku, Finland; S. Koponen.

DEUM: Department of Entomology, Deering Hall, University of Maine, Orono, ME, USA 04469; E.S. Osgood.

DLGC: Daniel J. Gustafson, Department of Biology, Montana State University, Bozeman, MT, USA 59717.

DKYC: D.K. Young, Department of Entomology, University of Wisconsin-Madison, Madison, WI, USA 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, PA, USA 16802; T.A. Miller.

FMNH: Division of Insects, Field Museum of Natural History, Chicago, IL, USA 60605; A.F. Newton, Jr.

FPMI: Forest Pest Management Institute, Great Lakes Forest Research Centre, PO Box 490, Sault Ste. Marie, Ont., Canada P6A 5M7; P. Syme.

FSCA: Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, FL, USA 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, IL, USA 61820; K. McGiffen.

ISUI: Insect Collection, Department of Entomology, Iowa State University, Ames, IA, USA 50011; R.E. Lewis.

JBWM: J.B. Wallis Museum, Department of Entomology, University of Manitoba, Winnipeg, Man., Canada R3T 2N2; R.E. Roughley.

LACM: Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA, USA 90007; R. Snelling.

LEMC: Lyman Entomological Museum and Research Laboratory, Macdonald College, McGill University, Ste. Anne de Bellevue, Qué., Canada H9X 1C0; F. Génier.

MAIC: M.A. Ivie, Department of Entomology, Montana State University, Bozeman, MT, USA 59717.

MCZ: Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA 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, WI, USA 53233; G.R. Noonan.

MSUC: Entomological Museum, Department of Entomology, Montana State University, Bozeman, MT, USA 59717; M.A. Ivie.

NDSU: Department of Entomology, North Dakota State University, Fargo, ND, USA 58102; E.J. Balsbaugh, Jr.

NFRC: Newfoundland Forest Research Centre, PO Box 6028, St. John's, Nfld., Canada A1C 5X8; A.G. Raske.

NMDC: N.M. Downie, 505 Lingle Terrace, Lafayette, IN, USA 47901.

NMNH: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA 20560; D. Anderson and T. Spilman.

NSMC: Nova Scotia Museum, Halifax, N.S., Canada B3H 3A6; B. Wright.

OSU: Department of Entomology, Ohio State University, Columbus, OH, USA 43210; C.A. Triplehorn.

OSUC: Entomological Museum, Department of Entomology, Oregon State University, Corvallis, OR, USA 97331; C. Parsons.

ROMC: Department of Entomology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont., Canada M5S 2C6; G.B. Wiggins.

SMEK: Snow Entomological Museum, Department of Entomology, University of Kansas, Lawrence, KA, USA 66045; J. Pakaluk.

SMF: Forschungs-Institut und Natur-Museum Senckenberg der Senckenbergishen Naturforschenden Gesellschaft, 6 Frankfurt 1, Senckenberganlage 25, W. Germany; R. zur Strassen.

TMB: Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary; O. Merkl.

TMDZ: Tromsø Museum, Department of Zoology, N-9000 Tromsø, Norway; A. Fjellberg.

UASM: Strickland Museum, University of Alberta, Edmonton, Alta., Canada T6G 2E3; G.E. Ball, D. Shpeley.

UBCZ: Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver, B.C., Canada V6T 1W5; S.G. Cannings.

UCD: R.M. Bohart Museum of Entomology, Department of Entomology, University of California, Davis, CA, USA 95616; R.O. Schuster.

UCR: Department of Entomology, University of California, Riverside, CA, USA 92521; S.I. Frommer.

UGA: Museum of Natural History, University of Georgia, Athens, GA, USA 30602; C.L. Smith.

UIM: Entomology Section, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID, USA 83843; F. Merickel.

UMAA: Museum of Entomology, Division of Insects, University of Michigan, Ann Arbor, MI, USA 48109; M.F. O'Brien.

UMSP: Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, MN, USA 55101; P.J. Clausen.

UNH: Entomological Museum, Department of Entomology, University of New Hampshire, Durham, NH, USA 03824; D.S. Chandler.

USUC: Department of Biology, Utah State University, Logan, UT, USA 84322; W.J. Hanson.

UVCC: Department of Zoology, University of Vermont, Burlington, VT, USA 05405; R.T. Bell.

UWL: College of Agriculture, Department of Plant, Soil and Insect Sciences, University of Wyoming, Laramie, WY, USA 82071; J.C. Burne.

UZIL: Museum of Zoology and Entomology, Lund University, Helgonavägen 3, S-223 62 Lund, Sweden; R. Danielsson.

VPI: Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA 24061; M. Kosztarab and J.R. Voshell, Jr.

WJWC: William J. Weselake, Department of Plant Science, University of Manitoba, Winnipeg, Man., Canada R3T 2N2.

WSU: James Entomological Collection, Department of Entomology, Washington State University, Pullman, WA, USA 99164; R.S. Zack.

ZMH: Entomologiska Avdelningen, Universitetets Zoologiska Museum, N. Järnvägsgatan 13, SF-00100 Helsingfors 10, Finland; H. Silfverberg.

ZMHB: Ausstellung Zoologie, Museum für Naturkunde der Humboldt-Universität, Invalidenstrasse 43, 1040 Berlin, East Germany; F. Hieke.

ZMMU: Zoological Museum of the Moscow State University, Moscow, U.S.S.R.; N.B. Nikitsky.

ZSM: Zoologische Staatssammlung München, Münchenhausenstrasse 21, D-8000 München 60, West Germany; G. Scherer.

METHODS

COLLECTING

Initially, areas of coniferous forest in Manitoba were investigated for possible *Pytho* habitat. Once a suitable site was found, i.e. one with a number of large, felled, dead coniferous trees, trees were sampled for larvae, pupae, adults, or all three stages. The presence of large numbers of scolytids, and dead needles still on the branches, were indications that the tree was dead too recently to be suitable habitat for *Pytho*. 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 prsent.

REARING

Representative 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 identity of the larval and pupal stages of all four Nearctic species of *Pytho*. Rearing was undertaken 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. Larvae and pupae of the Palearctic species were studied sufficiently to enable identification from publications.

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 patent-lip 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. Tops of vials were 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 accurately; (2) 3-dram vials are conveniently stored in large numbers; (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 reared larvae to pupal and adult stages of *P. seidlitzi, P. strictus, P. niger*, and *P. planus*. No parasitoids were observed during these trials. Once I had reared and associated specimens of all four North American species, larvae and pupae collected in the field or present in borrowed material were readily identified.

PREPARATION AND PRESERVATION OF SPECIMENS FOR STUDY

In field collecting, larvae were often present in large numbers. At most sites, some of the larvae were preserved immediately in 70% ethanol. If the larvae were fairly large, or presumed 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 to the lab for rearing, which was carried out as described above. Careful records of the dates of prepupation, pupation, and eclosion were kept for each vial. Individuals to be killed in the pupal stage were immersed in near boiling water for several minutes. They were stored in 70% ethanol along with the last-instar larval exuviae, including normal label data supplemented with dates of prepupation, pupation, and termination. It was noted that if pupae that have only recently (less than 2 or 3 days) become pupae are killed and preserved by the above method, they turn dark within a day of being placed in the 70% ethanol. Therefore, pupae were given a minimum of 3 days before being killed and preserved. Several methods have been published for the preservation or storage, or both, of Coleoptera larvae and pupae (e.g. Perkins 1980). Larvae first killed in recently boiling water and then stored in ethanol tend to be straighter and easier to manipulate. These larvae also tend to be more opaque than larvae killed in ethanol. For many ethanol-killed larvae, the layers of cuticle separate, with the outer layer becoming almost transparent.

Those specimens that were to be reared through to the adult stage were allowed up to 2 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 the adults while they were still fresh and relaxed. The reared adults were stored in two different ways. The adult, along with the associated exuvium, was placed in 70% ethanol in a glass patent-lip vial. Some of the reared adults were pinned, with the larval exuviae 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.

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).

Several larval and adult specimens were prepared for scanning electron micrographs. Mandibles of larvae and adults were dissected, sonicated in ammonium hydroxide for several minutes, placed in ethanol of 70%, and then, finally, 98% ethanol. These structures were mounted on bent minuten pins, coated with gold, then photographed using a Cambridge Stereoscan 250. Entire larvae were critical point dried after cleaning and dehydration in increasing concentrations of ethanol. These also were then examined and photographed.

MEASUREMENTS

The following measurements were made of adult specimens, selected from as widely separated localities as sample size permitted: total length, greatest elytral width, and the ratio of pronotal width to pronotal length. Included are the ranges, means, and standard deviations for these various body measurements. Where possible, at least 10 specimens from each locality were chosen, with as equal as possible representation of both sexes. 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. 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. Only GPW/PL (ratio of greatest pronotal width to pronotal length) was used as a taxonomic character. The other two measurements are meant to be a supplement to the descriptions. These measurements and their abbreviations are as follows:

total length (TL) = sum of HL + PL + EL;
greatest width of elytra (GEW) = greatest transverse width across both elytra; and
ratio of pronotal width of length (GPW/PL)

where HL = linear distance from anterior margin of pronotum to anterior margin of labrum, along midline; PL = linear distance from anterior to posterior margins of pronotum, along midline; GPW = greatest transverse distance of pronotum; and EL = linear distance from posterior tip of scutellum to apex of elytron.

ILLUSTRATIONS

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.

LOCALITY DATA

Distribution and locality records were obtained both from publications 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 published locality records were obtained. For the European species, anecdotal accounts of the distributions are mentioned in my treatment of the distribution for each species; no localities from previous publications are included on the distribution maps for any European species. Published records are included on the maps of the two Japanese species.

In the lists of localities, 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 coden of the collection from which the specimens were borrowed. For most specimens, 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. Information in square brackets was added by me.

TAXONOMIC METHODS

General methods. For detailed taxonomic study, adult male and female specimens of the individual taxa were selected from widely separated localities within their respective ranges to analyse any geographic variation. For examination of genitalia, dried specimens were softened for several hours in warm water, to which was added a small amount of detergent. Once sufficiently softened, the elytra were spread slightly, and a hooked insect pin was used to extract the genitalia through an incision in the last visible tergum (as in Lindroth 1969: 30–31). 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.

Species definitions and criteria. 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 microsympatric on a habitat level. Individuals of 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. Obviously, species separated by oceans or other impassible barriers would be essentially reproductively isolated. I believe *Pytho* has limited dispersal ability, at least from one area of coniferous forest to another such area across a barrier without such forest.

The species definition applied to *Pytho* is a combination of several of the modern definitions in the literature. A biological species can also be an evolutionary species, or a phylogenetic species, or vice versa. This combination of species definitions has been used by Askevold (1988) who invokes both the biological species definition and evolutionary species definition to delimit species of *Neohaemonia* (Coleoptera: Chrysomelidae). By using a morphological, or phenetic species definition, 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 definition of Donoghue (1985). These units eventually represented the terminal taxa on the cladogram depicting the reconstructed phylogeny.

Species-groups in *Pytho* are recognized on the basis of structure of the larval urogomphal plate (Fig. 14), and parabasal ridge processes (Fig. 13). 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 species-group.

Association of immature stages with adults. Immatures were associated with adults by two methods of rearing. By far the most convenient rearing method was that of ex evolutione imaginis, 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. Details of the methods used to associate larval and pupal stages with their respective adult counterparts are given above.

NATURAL HISTORY OF *PYTHO* SPECIES

All stages of *Pytho* species occur under the bark of dead coniferous trees in the genera *Pinus, Larix, Picea, Tsuga,* and *Abies*, as given in Table 1. I believe that host selection is associated more closely with stage of decay of the tree rather than with the actual host tree genus or species, based on numerous field observations, published and specimen label data, and attempts at rearing larvae.

Pytho larvae live under the bark of trees within a fairly narrow range of decay and such trees are suitable probably only for 4–10 years duration. Most host trees are dead for 3–4 years before being used by larvae of *Pytho*. Individuals of 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 positioned horizontally near or on the ground. A few were collected from inclined logs, and only very few specimens from dead, standing 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 analysed 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 overlap in generations in the field. One species, *P. kolwensis*, has a fairly well-documented life cycle (Burakowski 1962). 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 this act. 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 most pupate after 3 years but may extend this to 5 years if conditions are not optimal. The larvae build pupal cells between July and August. The pupal stage lasts 2–3 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 Nearctic *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 using 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. Adults of *Pytho* may behave similarly, except that perhaps horizontal objects would be sought preferentially 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 3 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 *Pytho*. DeLeon (1934) states that one female of *P. planus* laid 41 eggs between 29 June and 1 July 1930. However, the oviposition process is not discussed. Matings were observed in the laboratory, most of which were less than 1 min 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. In the laboratory studies, many young larvae died 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 have attained maximum size by August of the second year, but some individuals 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 various 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 nonfunctional, and pupal tubercles become visible beneath the larval cuticle. This prepupal stage, which has a duration of 4 days in the laboratory, 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 1 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 do not pupate. Both adults and all stages of larvae are capable of overwintering. Cold-hardiness studies for *P. depressus* by Zachariassen (1977, 1979, 1980) and for *P. planus* by Ring (1981, 1982) and Ring and Tesar (1980, 1981) indicate 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 subzero 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 may be a consequence of its predominantly boreal distribution.

Based on my fieldwork, subcortical insect co-inhabitants of species of *Pytho* in the province of Manitoba include members of the families Staphylinidae, Elateridae, Cleridae, Tenebrionidae, Boridae, Cerambycidae, and Scolytidae (Coleoptera), and Sciaridae and Xylophagidae (Diptera). No predators of *Pytho* larvae were observed, 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 1988). No parasitoids were discovered in my numerous larval rearing trials of Nearctic species.

Adult *Pytho* vary considerably in size, as is common in other groups of insects using 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.

TAXONOMIC CHARACTERS AND TERMS

In this section, an explanation is provided for character systems used in the taxonomy of adults, larvae, and pupae of species of *Pytho*. Included are only those characters that merit further discussion due either to confusion historically, or to being of relatively new use. Familiar characters, especially those of the adult stage, are omitted.

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 (Fig. 5C, D). Females possess no such pit. Extending ventrally from the base of the pit are a number of setae, twisted together (Fig. 5D). 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*.

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* (Fig. 3), and 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. 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 the apicale, shape of median lobe, and relative lengths of accessory lobes. Most species have basale and apicale subequal in length, except for males of *P. seidlitzi* (Fig. 3B) and

P. depressus (Fig. 3F), 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 toward the apex, with the lateral margins straight. In male *P. seidlitzi*, the lateral margins are sinuate and the apex of the apicale is broadly expanded (Fig. 3C).

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

LARVAL STAGE

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 terga. *Pytho* larvae have terga with well-developed, raised, sclerotized lines near their anterior margins. These are similar and analogous to those structures in pyrochroid larvae. Young (1975) terms these structures the parabasal ridges (Fig. 10A). In *Pytho*, these lines are bent posteriorly and raised, where they reach the medial portion of the tergum. These posterior projections are herein termed the parabasal ridge processes (Fig. 10A). These processes vary from being small, triangular structures, to being very slender and parallel-sided (Fig. 13).

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 (Fig. 13B). 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 analogous 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 (Fig. 10). On each urogomphus, there are two or three small teeth, which either project inwardly or (in particular the apical tooth) ventrally. These teeth are herein called the inner urogomphal teeth (Fig. 10B). 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 (Figs. 10, 14D), but in the remainder of species the reverse is true. Larvae of some species have the third, or apical, inner tooth well-developed, but in others, it is absent. At the base of, and between, the urogomphi is the urogomphal lip (Fig. 10A), which is a heavily pigmented, shelflike structure. This feature has some taxonomic value. The urogomphal lip may be narrow and protruding (Fig. 14A) or wide and not protruding (Fig. 14C, D); the posterior margin may be almost truncate, quite arcuate, or trapezoidal (Fig. 14B). On the dorsal surface of the urogomphal plate, there are a various number of heavily pigmented protuberances which are here called tubercles (Figs. 10A, 14) (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 various to a certain degree, is diagnostic of at least the major groups of *Pytho* species as larvae (Fig. 14). The setal arrangement on the apical tubercle can be used to separate larvae of the *P. kolwensis* group (Fig. 14B). 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 (Fig. 14D). Ventrally, the double arch of asperities (Figs. 10B, 12E) may be taxonomically important. Again, this character exhibits some intra-specific 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.

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. Because size is sexually dimorphic in adults, the same is probably also true for pupae, although this was not measured.

Abdomen. The terms used for the dorsal abdominal tubercles on segments 1–6 follow that of Rozen (1959) and Young (1975), and are illustrated in Fig. 15C, D. 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 segments 7–9, the 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 (Fig. 15C), and the number is species specific. The posterior marginal tubercles (Fig. 15C) 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 (Fig. 15C) are, in most species, two per side, but in pupae of *P. seidlitzi* there may be up to six per side. Pupae of all species except three have only one large, pleural tubercle (Fig. 15D). Pupae of *P. planus*, *P. depressus*, and *P. seidlitzi* 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 *P. strictus* and *P. kolwensis* pupae are distinct in that all dorsal abdominal tubercles are spade-shaped with a swollen basal portion.

The tubercles on the abdominal sterna of pupae (Fig. 15D) 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.

SYSTEMATICS

GENUS *PYTHO* LATREILLE

Pytho Latreille 1796: 23 (justified emendation of *Tytho*, Pythe); Blair 1928: 5; Hansen 1945: 20 and 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 Füessly 1782 (Blair 1928: 6)]. Fixation: Latreille (1810: 429) by subsequent designation.

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 and 29).

Pytholus Rafinesque 1815: 114. Type species: *Cucujus coeruleus* Fabricius 1792. Fixation: Rafinesque, by proposing *Pytholus* as a new name for *Pytho* whose type was *coeruleus* (Spilman 1954: 91).

Enoptes Gistel 1848. Type species: *Cucujus coeruleus* Fabricius 1792. Fixation: by Gistel, by proposing *Enoptes* as a new name for *Pytho* whose type was *coeruleus* (Spilman 1954: 88).

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. Because *P. coeruleus* was one of the originally included species of *Pytho* (Fabricius 1801), and Latreille (1810) was the first author subsequently to designate it as type species, *P. coeruleus* is the valid type species. This is in agreement with Spilman (1954), and contradicts Blackwelder (1946, 1947).

ADULT STAGE

Diagnosis. Pythinae (as in Lawrence 1982; Watt 1987) with the following combination of characters: pronotum with smooth lateral margins, and paired, longitudinal discal depressions (Fig. 2); elytra with variably convex intervals, separating linear rows of punctures (Fig. 9B).

Description. Body form (Fig. 1) elongate, flattened to moderately convex dorsally; TL 5.6–16.2 mm; GEW 1.9–5.9 mm; body evenly and slightly sclerotized, with setiferous punctures covering body and appendages.

Colour. Specimens from light testaceous to black, with or without metallic lustre; elytra contrasted or not in colour to head and prothorax.

Head (Fig. 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 distinct and transversely ridged or wrinkled; gular sutures arcuate and divergent posteriorly from deep posterior tentorial pits; eyes protruded, coarsely faceted.

Antennae (Fig. 1). Slender, of 11 articles, approximately twice length of head; setose from robust scape; antennomere 3 longest; antennomeres 2–7 subfiliform, 8–11 submoniliform; extra fine, sensory hairs distally, on antennomeres 5- or 6–11 (Fig. 5A), which are slightly clavate.

Mouthparts. 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 (Fig. 6A–C) large, extended beyond labrum by almost half their lengths; lateral margins evenly arcuate to apex, or abruptly bent subapically (two species); incisor lobe apically bicuspate with three or four smaller, inner marginal teeth (Fig. 6A); ventral surface with oblique row of setae inserted near inner margin (Fig. 6B); mandibles punctate and pubescent on dorsolateral surface; left mandible slightly longer with apex extended anterior of apex of right mandible; mandibles only moderately asymmetrical. Cardo one-fifth length of stipes; stipes elongate, triangular; lacinia apparently without digitus; galea and lacinia fringed with long, dense setae at apex (Fig. 6F); galea slightly widened distally; lacinia with setae along medial margin; palpifer present; palpus of 4 articles; 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; palpomere 4 flattened and moderately to markedly securiform (Fig. 5B); digitiform sensillae present on anterolateral area (Fig. 6D); apex hollow, with sensilla (Fig. 6E); all four articles with moderately long setae, not extended to apex of palpomere 4. Mentum (Fig. 5C) trapezoidal, widest basally with slightly sinuate lateral margins; posteromedial area of mentum of male with subcircular pit (Fig. 5C, D), approximately one-quarter width of mentum; margin of pit slightly to markedly elevated above mentum surface; pit with ventrally protruded group of setae (Fig. 5D); 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 three-segmented; palpomere 3 widest apically, concave, with sensilla; palpi with scattered, moderately long setae; medial area of ligula with several long setae.

Prothorax. Pronotum (Fig. 2) subquadrate or trapezoidal, dorsal surface flattened with two longitudinal, discal depressions; lateral margins of disc smooth and subparallel, evenly arcuate, or somewhat angulate near middle; carina between pronotal disc and hypomeron absent; pronotum uniformly punctate, each puncture with inconspicuous seta; punctation in most specimens 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 markedly developed along ventrolateral margin. Prosternum trapezoidal, narrowest posteriorly, surface transversely wrinkled; anterior margin with long setae, projected 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 extended posterior of procoxae; apex blunt to acute, elevated as part of bead (Fig. 7A), or not; lateral margins variably sinuate.

Pterothorax. Mesosternum (Figs. 7C, 8B, C) subtriangular in shape with moderately well-developed mesosternal intercoxal process surrounded by bead; bead widened posterolaterally (Fig. 8B), or indistinct (Fig. 7A); 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 (Fig. 7D); lateral bead present; posterior margin extended 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 subquadrate to rounded posteriorly, with various number of small, setiferous punctures; impunctate in some specimens; length approximately one-third length of pronotum, slightly longer than wide in most specimens. Metepisternum subrectangular, elongate; length approximately four times width at anterior margin; widest apically; uniformly punctate and pubescent. Metasternum large, slightly convex, and trapezoidal, widest posteriorly; width at posterior margin approximately 1.5-fold length along midline; anterolaterally, almost extended to anterior edge of mesocoxae; anterior bead present; sides straight or slightly sinuate; antecoxal groove prominent; antecoxal piece narrower medially; median groove visible in posterior quarter to fifth 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.

Elytra (Fig. 1). Elongate, covering all but perhaps last visible abdominal tergum (in mature specimens); widest near or slightly posterad midlength; elytra in most specimens 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 10 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 sloped with or without extra pubescence; epipleuron indistinctly developed, extended posteriorly to first abdominal sternum.

Metendosternite (Fig. 4C). With stalk subparallel-sided, laminae well-developed.

Hind wing. Normally developed; venation as shown in Figure 4B.

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 sterna; terga slightly sclerotized; sternum 8 and tergum 9 densely covered with setae; sternum 9 of males with anteriorly extended lateral sclerites articulating with tergum 9.

Male genitalia (Fig. 3). Aedeagus of typical heteromeroid type; tegmen elongate, oriented dorsally, in two pieces; apicale grooved ventrally for reception of elongate median lobe (Fig. 3E); median lobe with no discernible internal sac armature; accessory lobes inserted near base of apicale, extended near or beyond apex of the apicale.

Female genitalia (Fig. 4A). Ovipositor elongate, with four elongate baculi; coxites densely covered with setae; styli elongate, cylindrical.

LARVAL STAGE

Diagnosis. Pythinae (as in Lawrence 1982; Watt 1987) with the following combination of characters; meso- and metathoracic, and abdominal terga 1–8 with distinctly developed parabasal ridges (Fig. 13); abdominal terga 1–8 mesally with paired, raised, parabasal ridge processes (Fig. 13); urogomphal plate (Fig. 14) with at least four tubercles per side; urogomphal lip (Fig. 14) distinctly developed.

Description. Body form (Fig. 10) elongate, parallel-sided; body markedly to slightly flattened dorsoventrally; mature larvae with lengths of 20–40 mm, and maximum widths of 3–5 mm; body slightly sclerotized, thickest on urogomphal plate, parabasal ridges, and parabasal ridge processes; colour in life from light yellow to dark rufous, nearly black in areas of heaviest sclerotization; body with pattern of scattered setae of various lengths; body surface smooth except on urogomphal plate, and parabasal ridge processes.

Head (Fig. 10). 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; five pigmented stemmata per side (Fig. 12B), 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 lateral margin variably sinuate; antennomeres 2 and 3 cylindrical; antennomere 2 with small, dome-shaped sensory process at apex.

Mouthparts. Labrum symmetrical, with convex anterior margin; labrum with 8–10 marginal, and two or four discal setae; frons fused with clypeus; mandibles (Fig. 11A–K) retracted, thickly sclerotized, distinctly asymmetrical; apex of left mandible extended anterad apex of right mandible; left mandible with large molar tooth (Fig. 11A); left and right mandibles with mola, more extensive on right mandible (Fig. 11G); dorsal surface of mola with variously sized microtrichiae (Fig. 11E); on ventral surface of mola, rows of small, sharp tooth-like structures (Fig. 11D); mandibles with two or three apical teeth and several teeth on inner, subapical margin; lateral margin of mandible evenly arcuate to apex; maxilla with cardo appearing two-segmented because of internal fold; mala cleft apically with three-toothed uncus on inner distal margin (Fig. 12A).

Thorax. With lateral margins subparallel; cervicosternum (Fig. 10B) in 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 on abdominal terga 2–8; thoracic spiracle between pro- and mesothorax, large, annular (Fig. 12D); legs (Fig. 12C) with five articles distinctly developed; all leg articles with many short, stout spinelike setae in addition to several more slender setae; all three pairs of legs subequal in size and similar in shape; single tarsungulus distinctly developed.

Abdomen. Ten-segmented, elongate, with lateral margins subparallel; abdominal terga 1–9 with transverse parabasal ridges near anterior margin (Fig. 10A); parabasal ridges on terga 1–8 with mesal, posteriorly directed, slightly raised parabasal ridge processes (Fig. 13); parabasal ridge processes on tergum 1 shorter than those on terga 2–8; tergum 9 more thickly sclerotized than remainder of abdomen, extended ventrally to form urogomphal plate; urogomphal plate (Fig. 14) dorsally with transverse truncate, to semicircular row of 7–28, uniform or variably sized tubercles (detail — Fig. 12F); 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); immovable, paired urogomphi (Figs. 10, 14) with outer margins subparallel, slightly angulate above level of tergum 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 variously protruded urogomphal lip (Fig. 14); posterior margin of urogomphal lip truncate to markedly arcuate; sternum 9 with 13–30 small, dentiform asperities in double arch arrangement (Figs. 10B, 12E); asperities uniform or greatly various in size, with or without conspicuous longitudinal ridges; sternum 9 divided into six peripheral plates; segment 10 small, surrounding opening of anus.

PUPAL STAGE

Diagnosis. 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 of *Pytho* pupae should probably serve as a diagnostic character. 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 (Fig. 15A, B) similar to adults; colour milky-white, almost pure white at pupation and darkened with development. Length various, 12–25 mm from anterior pronotal margin to apex of abdomen; maximum widths 3–5 mm across pronotum.

Head and mouthparts. Deflexed ventrally, almost completely concealed dorsally by pronotum (Fig. 15B); tubercles as follows — one conspicuous pair near inner margin of each eye, one smaller pair medially and toward 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; mandibles apically bifurcate.

Antennae. Extended dorsally over meso- and metafemur and laterad wings and elytra (in well-preserved pupae); with several minute denticles on each of antennomeres 3 to apex at widest point of each antennomere.

Pronotum (Fig. 15B). Similar in shape to adults, with paired, longitudinal depressions visible; tubercles as follows — various number of large tubercles around dorsal pronotal margin, several pairs of small tubercles on pronotal disc.

Pterothorax. 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, extended to anterior margin of abdominal segment 2; wings and elytra close against body (in inadequately preserved specimens, wings and elytra 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 (Fig. 15C, D). Segments wider than long; tubercles as follows — posterolateral margins of terga with four or five tubercles, posterior margins of terga with two or three tubercles, discal area of terga with various number of tubercles, pleural region with one or two tubercles, posterolateral margins of sterna with one or two tubercles; abdominal tubercles roughly triangular, with single seta inserted subapically.

Keys to Species of the Genus *Pytho* Latreille

ADULTS

1. Lateral margins of pronotal disc subparallel or slightly convergent, without distinctly developed anterior or posterior beads (Fig. 2A); mesepimeron impunctate or at least markedly less punctate than mes- and metepisternum (Fig. 7D); aedeagus of male with apicale broadly expanded subapically (Fig. 3C) .... *P. seidlitzi* group
.... 1. *P. seidlitzi* Blair

— Lateral margins of pronotal disc variably arcuate, with posterior and with or without anterior beads (Fig. 2B–I); mesepimeron as densely punctate as mes- and metepisternum; aedeagus of male with apicale gradually narrowed subapically (as in Fig. 3D) 2

2. Lateral margins of pronotal disc weakly to strongly angulate at greatest width (Fig. 2B, 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 .... *P. kolwensis* group
.... 3

— Lateral margins of pronotal disc evenly arcuate at greatest width (Fig. 2E–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. Pronotum in most specimens with lateral margins of disc interrupted by transverse grooves near middle, and elevated above level of pronotal disc; mandibles abruptly bent near apex; prosternal process long and slender, extended almost to posterior margin of procoxae; distribution — Palearctic 4

— Lateral margins of pronotal disc complete, without transverse grooves near middle, and at same level as pronotal disc; mandibles evenly arcuate to apex; prosternal process blunt, extended only half the length of the procoxae; distribution — eastern Nearctic ....
.... 2. *P. strictus* LeConte

4. Elytra piceous, with distinct brassy or violaceous metallic lustre, lighter in colour than head and pronotum; mesoscutellum impunctate; appendages rufous; distribution — eastern Palearctic (Japan) .... 4. *P. nivalis* Lewis

— 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; appendages piceous to black; distribution — Palearctic .... 3. *P. kolwensis* C. Sahlberg

5. Elytron various in colour from light testaceous to dark piceous, with slight to marked metallic lustre; pronotum widest anterad middle, with sides not constricted anteriorly (Fig. 2H, I) .... *P. depressus* group 6

— Elytra constant in colour from piceous to black, with no metallic lustre; pronotum widest near middle, with sides constricted anteriorly (Fig. 2E, F, G) .... *P. niger* group 7

6. Male aedeagus with apicale and basale subequal in length (Fig. 3D); distribution — Nearctic .... 8. *P. planus* (Olivier)

— Male aedeagus with apicale approximately 1.5 times length of basale (Fig. 3F); distribution — Palearctic .... 9. *P. depressus* (Linnaeus)

7. 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 .... 6. *P. abieticola* J. Sahlberg

— 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 piceous or black; distribution — Nearctic and eastern Palearctic (Japan) 8

8. Prosternum with bead of posterior margin thickened near apex of prosternal process (medial portion of process elevated) (Fig. 7A); pronotum coarsely and uniformly punctate; mesosternum with posterior bead expanded, visible to lateral margin of mesosternum (Fig. 8B); antennomeres 8–10 with sensillar region on apices; metasternum with intercoxal process acute apically; distribution — Nearctic .... 5. *P. niger* Kirby

— Prosternum with bead of posterior margin of uniform thickness around apex of prosternal process (medial portion of process not elevated) (as in Fig. 7B); 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) .... 7. *P. jezoensis* Kôno

MATURE LARVAE

This key has been constructed to disciminate among mature larvae only. The criteria for a mature larva are as follows: clearly 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 12–28 variously sized tubercles, arranged in a semicircular pattern (Fig. 14A); terga 2–7 with parabasal processes short, and inwardly curved (Fig. 13A), each process with six or more medial setae; sternum 9 with 13–17 asperities .. *P. seidlitzi* group .... 1. *P. seidlitzi* Blair

— Urogomphal plate with 7–16 more uniformly sized tubercles, arranged in an elliptical to semicircular pattern (Fig. 14B, C, D); terga 2–7 with parabasal processes various in length (Fig. 13B, C, D), each process with less than six medial setae; sternum 9 with 18–30 asperities 2

2. Urogomphal plate (Fig. 14D) with 11–16 small tubercles with the tips anteriorly directed; urogomphus with the middle, inner tooth larger than or subequal in size to the basal, inner tooth; terga 2–7 with parabasal processes long, length of terga three to four times length of processes (Fig. 13D) .... *P. depressus* group .... 9. *P. planus* (Olivier) (Nearctic) and 10. *P. depressus* (Linnaeus) (Palearctic)

— Urogomphal plate with 7–13 larger tubercles with the tips posteriorly directed; urogomphus (Fig. 14B, C, D) with the middle, inner tooth smaller than the basal, inner tooth; terga 2–7 with parabasal processes shorter, length of terga at least five times length of processes (Fig. 13C, D) 3

3. Urogomphal plate (Fig. 14B) with 10–13 large tubercles, various in size on some specimens; apical urogomphal tubercle with more than two setae of equal or greater length as the apical tubercle; urogomphal lip with trapezoidal or markedly arcuate posterior margin; terga 2–7 with parabasal processes short, length of terga at least seven times length of processes (Fig. 13B); terga 2–7 with four medial setae, subequal in size, in most specimens arranged linearly .... *P. kolwensis* group
.... 3. *P. kolwensis* C. Sahlberg (Palearctic), 2. *P. strictus* LeConte (Nearctic), and 4. *P. nivalis* Lewis (Japan)

— Urogomphal plate (Fig. 14C) with seven to nine smaller tubercles, uniform in size on most specimens; apical urogomphal tubercle with one seta of equal or greater length as the apical tubercle; urogomphal lip with weakly arcuate posterior margin; terga 2–7 with prabasal processes long, length of terga five to six times length of processes (Fig. 13C); terga 2–7 with more than four medial setae, various in size, with no distinct pattern of arrangement .... *P. niger* group
.... 5. *P. niger* Kirby (Nearctic), 6. *P. abieticola* J. Sahlberg (Palearctic), and 7. *P. jezoensis* Kôno (Japan)

KNOWN PUPAE

Names of the various tubercles important in the identification of the pupal stage of *Pytho* are illustrated in Figure 15. Pupae of the two Japanese species, *P. nivalis* and *P. jezoensis*, are not known.

1. Abdominal terga 2–6 each with five lateral, marginal tubercles; dorsal abdominal tubercles not markedly dilated basally, evenly tapering to their apices .... *P. depressus* group 2

— Abdominal terga 2–6 each with four lateral, marginal, tubercles; dorsal abdominal tubercles markedly dilated basally, or evenly tapering to their apices 3

2. Abdominal sterna 2–6 each with two large, lateral, marginal tubercles subequal in size; distribution — Palearctic .... 9. *P. depressus* (Linnaeus)

— Abdominal sterna 2–6 each with one large, lateral, marginal tubercle (on some specimens, a second lateral marginal tubercle present, but much smaller); distribution — Nearctic .... 8. *P. planus* (Olivier)

3. Abdominal terga 2–6 each with more than three discal tubercles on most specimens; labrum with anterior margin truncate; pronotum with lateral margins parallel-sided .... *P. seidlitzi* group
.... 1. *P. seidlitzi* Blair

— Abdominal terga 2–6 each with two discal tubercles on most specimens; labrum with anterior margin variably emarginate; pronotum with lateral margins arcuate 4

4. Abdominal terga 2–6 each with tubercles spade-shaped, dilated basally; most abdominal segments with one large, pleural tubercle; labrum with anterior margin deeply emarginate .... *P. kolwensis* group 5

— Abdominal terga 2–6 each with tubercles evenly tapered to their apices; most abdominal segments with two unequally sized pleural tubercles; labrum with anterior margin only slightly emarginate .... *P. niger* group
..................5. *P. niger* Kirby (Nearctic) and 6. *P. abieticola* J. Sahlberg (Palearctic)

5. Most of abdominal terga 2–6 each with five lateral, marginal tubercles; abdominal sterna 2–6 with three posterior, marginal tubercles; pronotum with more than 20 tubercles per side .... 3. *P. kolwensis* C. Sahlberg

— Most of abdominal terga 2–6 each with four lateral, marginal tubercles; abdominal sterna 2–6 with one posterior, marginal tubercle; pronotum with seven or eight tubercles per side .... 2. *P. strictus* LeConte

1. *P. SEIDLITZI* GROUP

ADULT STAGE

Diagnosis. Adults of this species-group may be recognized by the following characters: pronotum with lateral margins of disc subparallel, with neither anterior nor posterior beads; paired depressions shallow, oval; mesepimeron impunctate in most specimens; aedeagus with apex of apicale broadly expanded.

Description. TL 9.3–14.8 mm; GEW 3.5–5.8 mm. Colour little varied, uniformly non-metallic piceous to black dorsally; lateral areas of frons, mouthparts, antennae, coxae, and tarsi rufopiceous (lighter than dorsal colouration). Sensilla on antennomeres 8–10. Lateral margins of mandibles near apices evenly arcuate. Pronotum with neither anterior nor posterior beads; lateral margins of disc subparallel or slightly convergent anteriorly; paired pronotal depressions shallow, oval; areas laterad depressions at same level as disc; prosternal process short. Mesoscutellum with 15–25 setigerous punctures; mesepimeron impunctate in most specimens; in few individuals, several punctures along lateral margin only; mesosternum with posterior bead impressed laterally to inner margin of mesotrochantin; punctation reduced posteriorly and absent laterally. Elytra slightly convex, each elytron with nine moderately to markedly convex intervals; 10th interval visible posterad midlength; posterolateral elytral margin without long pubescence. Male genitalia with apicale approximately two times length of basale; apicale expanded, spatulate apically; apicale narrowest near middle with sinuate lateral margins.

LARVAL STAGE

Diagnosis. Larvae of the *P. seidlitzi* group are recognized by the following characters: parabasal ridge processes short, inner margins convergent anteriorly; apical urogomphal tooth absent; urogomphal tubercles various in size, arranged in semicircle; urogomphal lip with posterior margin strongly arcuate.

Description. Abdominal terga 2–6 with parabasal ridge processes (Fig. 13A) short, extended only slightly anterad parabasal ridge; inner margins arcuate, convergent anteriorly; distance from anterior tip of processes to posterior margin of terga 2–7 approximately 10 times length of process. Parabasal setae (Fig. 13A) various in size, at least six per side, majority posterior of parabasal ridge processes; on some specimens and terga, pattern of four linearly arranged setae present with extra, smaller setae. Urogomphus (Fig. 14A) 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 sloped posteriorly to urogomphal lip. Urogomphal lip (Fig. 14A) with posterior margin markedly arcuate, in some specimens slightly trapezoidal; ratio of urogomphal lip width at base to length along midline approximately 1:0.6. Urogomphal tubercles (Fig. 14A) various 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 13–17 in number, large, with conspicuous longitudinal ridges.

PUPAL STAGE

Diagnosis. Pupae of *P. seidlitzi* group may be distinguished by the following characters: anterior margin of labrum truncate; pronotum with lateral margins subparallel; abdominal terga 2–6 each with four lateral marginal tubercles and more than three discal tubercles.

Description. Single ocular tubercle; anterior margin of labrum truncate. Pronotum with shape as in adult, lateral margins subparallel; 12–13 large marginal tubercles per side. Abdominal terga 2–6 with four lateral marginal tubercles, some specimens with five on a single side; three to six discal tubercles; two posterior marginal tubercles, the outer larger; two pleural tubercles, the anterior smaller; dorsal tubercles evenly tapered to apex, not widened basally. Abdominal sterna 2–6 with two posterior marginal tubercles, the inner tubercle larger.

INCLUDED TAXA AND GEOGRAPHICAL DISTRIBUTION

The *P. seidlitzi* group contains a single species, *P. seidlitzi* Blair, which has a range extending across North America, north to treeline and south to about 42°N latitude (Map 1).

1. Pytho seidlitzi Blair

(Figs. 1, 2A, 3A, B, C, 4C, 5A, 6D, E, F, 7B, C, D, 9B, 11A–K, 12A–F, 13A, 14A, 15C, D; Map 1; Table 2)

Pytho seidlitzi 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).

ADULT STAGE

Notes on type specimens and taxonomic notes. Seidlitz (1916) presented a key to adults of *Pytho* species, 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. seidlitzi*. 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 by 7 mm] "147 or 546 Pytho niger"/[rectangular det. label] "P. niger Seidl. (nec Kirby) det K.G. Blair"/[small det. label] "Pytho seidlitzi Blr"/[large red label] "LECTOTYPE Pytho seidlitzi Blair 1925 design. D.A. Pollock 1987". The lectotype 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.

Diagnosis. See diagnosis for *P. seidlitzi* group.

Description. See description for *P. seidlitzi* group; measurements given in Table 2.

LARVAL STAGE

The larva of *P. seidlitzi* was previously undescribed.

Diagnosis. See diagnosis for *P. seidlitzi* group.

Description. See description for *P. seidlitzi* group.

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.

PUPAL STAGE

Diagnosis. See diagnosis for *P. seidlitzi* group.

Description. See description of *P. seidlitzi* group.

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.

NATURAL HISTORY

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 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 4 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. seidlitzi* has an average prepupal duration of about 4 days and a pupal stage of about 10 days (based on all reared pupae). *Pytho seidlitzi* has a wide host acceptability throughout its range (Table 1).

DISTRIBUTION

Pytho seidlitzi occurs across North America from British Columbia and the Northwest Territories to Nova Scotia (Map 1). The northern extent of its range probably closely coincides with treeline; the southern range extent is not well delimited. The southeast corner of Idaho is the most southerly record. I interpret the absence of *P. seidlitzi* 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. seidlitzi* should occur in Saskatchewan. This gap does not have biogeographic significance.

MATERIAL EXAMINED

I examined 185 adults, approximately 300 larvae, and 16 pupae of this species, from the following localities:

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, USAM); 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 mi 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). **Québec:** 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. ESE 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. NE Harvard, Laird Park, 15.v.1976, F.M. Tessitore, (1, WSU); 6 mi. NE 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). **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 and 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. and D.C. Young, reared larva ex *Pinus strobus*, (1, DKYC). **LARVAE**. Keweenaw Co., Isle Royal, 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 and Minong Ridge, 16–23.viii.1974, (9, DKYC). **Minnesota: LARVAE**. Clearwater Co., Itasca St. Park, data and collection unknown. **Montana: ADULTS**. Mineral Co., 6 mi. W Saltese, ca. 4000′, 25.vii.1975, A. Newton and M. Thayer, under conif. bark, (1, MCZ); Gallatin Co., Bozeman Cr., 6000′, 4.vi.1987, D.L. Gustafson, (2, MSUC), (1, DLGC); Gallatin Co., Blackmore Cr., funnel trap, 17.vi.1988, D.L. Gustafson, (1, DLGC); Gallatin Co., Hyalite Reservoir, ca. 12 km S Bozeman, 14.viii.1990, D.A. Pollock and R.E. Roughley, ex. pupa, (1, DAPC). **LARVAE**. Gallatin Co., Hyalite Reservoir, ca. 12 km S Bozeman, 14.viii.1990, D.A. Pollock and R.E. Roughley, (20, DAPC); Glacier Co., Hwy 89, 8 km S St. Mary, 16.viii.1990, D.A. Pollock and R.E. Roughley, (10, DAPC). **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 2700′, 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); Wasco Co., Mt. Hood National Forest, Forest

Service Road 4310 at Clear Creek Campground, 3.vi.1989, E. Fuller, in flight (1, DAPC); 2.vi.1989, D.A. Pollock, reared from larvae ex *Pseudotsuga menziesii*, (2, DAPC); 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); Wasco Co., Mt. Hood National Forest, Forest Service Road 4310 at Clear Creek Campground, 2–3.vi.1989, D.A. Pollock, ex *Pseudotsuga menziesii*, (25, DAPC). **Washington.** **ADULTS**. Klickitat Co., Blockhouse, 11.vi.1941, M.C. Lane, (1, OSUC); Skagit Co., 2 mi. NW Rainy Pass, 13.vii.1982, R. Baranowski, (2, UZIL). LARVAE. Kittitas Co., Wenatchee National Forest, Mineral Springs Campground ~10 km N Virden on Hwy 97, 12.vi.1989, D.A. Pollock, ex *Pseudotsuga menziesii*, (20, DAPC). **Wisconsin:** **ADULTS**. 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).

2. *P. KOLWENSIS* GROUP

ADULT STAGE

Diagnosis. Adults of the *P. kolwensis* group may be recognized by the following characters: pronotum with anterior and posterior beads; lateral margins of disc angulate at greatest width; paired depressions deep and often subdivided; elytra markedly convex.

Description. TL 10.9–16.2 mm; GEW 4.0–5.9 mm. Colour varied, from uniformly rufous to black, with or without metallic lustre. Sensilla on apices of antennomeres 7–10. Lateral margins of mandibles near apices evenly arcuate or abruptly bent. Pronotum with anterior and posterior beads, anterior bead in some specimens only slightly impressed; lateral margins of disc variously angulate at widest point, near midlength; paired pronotal depressions deep, linear, in some specimens extended onto lateral margins of pronotum or otherwise subdivided; areas laterad depressions elevated above, or at same level as disc. Mesoscutellum impunctate or with small setigerous punctures; mesepimeron uniformly punctate; mesosternum with posterior bead impressed laterally to inner margin of mesotrochantin; punctation reduced laterally and along midline. Elytra markedly convex, each elytron with nine convex intervals; 10th interval visible posterad midlength; posterolateral elytral margins without long pubescence. Male genitalia with apicale and basale subequal in length; apicale tapered evenly to apex; apicale narrowest apically with straight lateral margins.

LARVAL STAGE

Diagnosis. Larvae of species in the *P. kolwensis* group may be recognized by the following characters: parabasal ridge processes short, with inner margins arcuate; group of four large parabasal setae; urogomphal lip with posterior margin trapezoidal; urogomphal tubercles with apices directed posteriorly; apical urogomphal tubercle plurisetose.

Description. Abdominal terga 2–6 with parabasal ridge processes (Fig. 13B) short, extended anterad parabasal ridge by half their lengths; inner margins arcuate, convergent anteriorly; distance from anterior tip of processes to posterior margin of terga 2–7 approximately seven times length of process. Parabasal setae (Fig. 13B) 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 Fig. 14B) 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 sloped posteriorly to urogomphal lip; urogomphal lip (as in Fig. 14B) with posterior margin trapezoidal, in some specimens nearly arcuate; urogomphal tubercles (as in Fig. 14B) 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 16–18 in number, small, with inconspicuous longitudinal ridges.

PUPAL STAGE

Diagnosis. Pupae of the *P. kolwensis* group (the pupa of *P. nivalis* is unknown) may be recognized by the following characters: anterior margin of labrum deeply emarginate; pronotum with lateral margins variously angulate near widest point; dorsal abdominal tubercles broadly expanded basally.

Description. Single ocular tubercle; anterior margin of labrum deeply emarginate. Pronotum with shape as in adult, angulate near midlength; 7–20 variously sized tubercles per side. Abdominal terga 2–6 with four or five lateral marginal tubercles; one to three large, discal tubercles; two posterior marginal tubercles; one pleural tubercle; dorsal tubercles spade-shaped, broadly expanded basally. Abdominal sterna 2–6 with one to three posterior marginal tubercles.

INCLUDED TAXA

The *P. kolwensis* group includes three species: *P. strictus* LeConte, *P. kolwensis* C. Sahlberg, and *P. nivalis* Lewis.

GEOGRAPHICAL DISTRIBUTION

This group is Holarctic, with a range extending from eastern North America, across eastern Europe, U.S.S.R., and into Japan.

2. *Pytho strictus* LeConte 1866

(Figs. 2B, 13B; Map 2; Table 2)

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).

ADULT STAGE

Notes about type material. 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 1987". The specimen has the following identifying features: right antenna with only two basal antennomeres; large pin hole through right elytron extended through to venter; left middle leg broken off near apex of femur; left metatarsus with two basal tarsomeres only, right metatarsus with three only; colour of body uniformly rufous.

Diagnosis. Adult *P. strictus* may be recognized by the following characters: pronotum (Fig. 2B) with short, basal, parallel-sided portion; lateral margins of disc angulate and widest near midlength; elytra nonmetallic rufous or piceous, markedly convex dorsally; distribution — eastern Nearctic.

Description. Character states of the *P. kolwensis* group and the following: TL 13.4–16.2 mm; GEW 4.9–5.8 mm; measurements given in Table 2. Colour of two forms: most specimens examined, including holotype, uniformly dark rufous with femora darker than tibiae and tarsi; other specimens piceous, with sutural interval and epipleuron of elytra lighter in colour; mouthparts, antennae, trochanters, tibiae, and tarsi dark rufous (lighter than dorsal colour). Mandibles with lateral margins evenly arcuate to apices. Pronotum with basolateral margins forming parallel-sided collar; areas laterad depressions at same level as middle of disc; prosternal process short, extended to about half length of procoxae. Mesoscutellum with more than 10 setigerous punctures in most specimens.

LARVAL STAGE

Diagnosis. At present, larvae of *P. strictus* are inseperable from both *P. kolwensis* and *P. nivalis*, except by geographical distribution. Therefore, see the diagnosis for *P. kolwensis* group.

Description. See description for larvae of *P. kolwensis* group.

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

PUPAL STAGE

Diagnosis. The pupa of *P. strictus* is most similar to that of *P. kolwensis*, but may be separated by the following characters: pronotum with seven or eight tubercles per side; terga 2–6 with four lateral marginal tubercles; sterna 2–6 with one posterior marginal tubercle.

Description. Character states of the *P. kolwensis* group and the following: pronotum with seven or eight marginal tubercles per side. Abdominal terga 2–6 with four lateral marginal tubercles; two discal tubercles; two posterior marginal tubercles, the outer larger. Abdominal sterna 2–6 with one posterior marginal tubercle.

Association method. 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 exuviae from a pupa that died before emerging was examined and was found to be *P. strictus*.

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 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).

DISTRIBUTION

Pytho strictus is apparently restricted to eastern North America (Map 2) with the westernmost record being Clingman's Dome in the Great Smoky Mountains, Tennessee. Additional records of specimens not seen by me include Mt. McIntyre, New York; Camp Caribou, and near Lincoln Pond, Maine. 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.

MATERIAL EXAMINED

Eleven adults, four larvae, two larval exuviae, and one pupa of this species were examined, from the following localities:

CANADA. New Brunswick: ADULTS. 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: ADULTS. 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:** **ADULTS**. 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:** **ADULTS**. Sevier Co. Gt. Smoky Mtns. N. Park, Clingman's Dome, 6000′, 16.v.1946, H. Dietrich, (1, CU).

3. *Pytho kolwensis* C. Sahlberg 1833

(Figs. 2C, 14B; Map 3; Table 2)

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.

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

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

ADULT STAGE

Notes about type material. Requests for type specimens of *P. kolwensis* were sent to ZMH and DBTU. Two specimens of *P. kolwensis* were received from DBTU, both of which are from the type locality, but collected by J. Sahlberg. It is probable that the original types were destroyed or were not designated as such by C. Sahlberg. According to ICZN (1985), Article 75 (b), a neotype is to be designated only in exceptional circumstances when it 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. If so, the appropriate type dsignations may be made.

Taxonomic notes. *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 taxonomic notes for *P. nivalis* for additional information about *P. kolwensis*.

Diagnosis. Adult *P. kolwensis* can be distinguished on the following combination of characters: pronotum (Fig. 2C) with lateral margins of disc 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, nonmetallic piceous to black; distribution — known from Fennoscandia, Poland, and Siberia.

Description. Character states of the *P. kolwensis* group and the following: TL 10.9–15.9 mm; GEW 4.0–5.9 mm; measurements given in Table 2. No variation in colour noted among specimens examined; uniform nonmetallic piceous to black dorsally; on some specimens, elytra lighter than head and pronotum; mouthparts, antennae, coxae, trochanters, apices of tibiae, and tarsi lighter than dorsal colour. Mandibles with lateral margins arcuate, abruptly bent near apex. Pronotum with basolateral margins forming short, parallel-sided collar, distinctly shorter than that in *P. strictus*; areas laterad depressions elevated above middle of disc; prosternal process long, extended past half length of procoxae. Mesoscutellum with less than 10 setigerous punctures in most specimens; in some individuals impunctate.

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).

Diagnosis. See diagnosis for *P. strictus*.

Description. See description for larvae of *P. kolwensis* group.

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

PUPAL STAGE

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

Diagnosis. The pupa of *P. kolwensis* most resembles that of *P. strictus* but has the following diagnostic features: pronotum with at least 20 variably sized tubercles per side; terga 2–6 with five lateral marginal tubercles; sterna 2–6 with three posterior marginal tubercles.

Description. Character states of the *P. kolwensis* group and the following: pronotum with 20 tubercles of various sizes per side. Abdominal terga 2–6 with five lateral marginal tubercles, in some specimens four or six on a single side; one to three discal tubercles; two posterior marginal tubercles, subequal in size. Abdominal sterna 2–6 with three posterior marginal tubercles: inner tubercle minute, middle large, outer tubercle small.

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

NATURAL HISTORY

According to Pettersson (1983), *Pytho kolwensis* 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). *Pytho kolwensis* requires sun-exposed habitat, but the inner bark of the host tree must be very moist and without fungal growth for 5–10 years. 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 above in the section on natural history of the genus.

DISTRIBUTION

Pytho kolwensis is known from Finland, Sweden, and the U.S.S.R. according to label data of specimens examined in this study (Map 3). More detailed information about the Fennoscandian distribution of this species is provided by Grill (1896), Saalas (1917), Lindroth (1960), and Silfverberg (1979). Many of the older collection localities no longer support populations of *P. kolwensis* (Pettersson 1983). Iablokoff-Khnzorian (1985) described the distribution of this species as being Poland, Baltic countries, Scandinavia, and Siberia. Information about the distribution in Poland of *P. kolwensis* is given by 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 the 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.

MATERIAL EXAMINED

Twenty-six adults, 19 larvae, and a single pupa were examined from the following localities:

FINLAND. Etelä-Häme: ADULTS. 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, (2, 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 20I5e, Sammtratten, 15.viii.1985, R. Pettersson, *Picea abies* (L.), (1, DAPC). LARVAE. Locksta. Vandatberget, 3.ix.1981, R. Pettersson, (1, DAPC); RN 20I5e, Sammtratten, 15.viii.1985, R. Pettersson, (1, DAPC). PUPAE. RN 20I5e, Sammtratten, 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.: ADULTS. Ust Kut, Lena Super, no date, B. Poppius, (1, ZMH); S. Primore, Kamenumka, bl. Ussurijsk, 29.VI.1982, Nikitskij, (1, ZMMU).

4. *Pytho nivalis* Lewis 1888

(Fig. 2D; Map 4; Table 2)

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).

ADULT STAGE

Notes about type material. 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 × 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.

Taxonomic notes. Seidlitz (1916) did not treat *P. nivalis* in his key to species of *Pytho*. As a note, however, he suggests correctly 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 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. Because 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 nonmetallic piceous colour. According to my concept of *P. nivalis*, 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*.

Diagnosis. Adult *P. nivalis* may be separated from its congeners by the following characters: lateral margins of pronotal disc (Fig. 2D) slightly 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 the Japanese Archipelago only.

Description. Characters of the *P. kolwensis* group and the following: TL 11.8–15.0 mm; GEW 4.3–5.5 mm; measurements in Table 2. No variation in colour noted among specimens examined; head piceous to black dorsally; pronotum lighter, especially along lateral margins; elytra rufopiceous with distinct brassy or violaceous lustre; pterothorax except lighter metasternum, piceous; coxae and femora piceous; mouthparts, antennae, tibiae, and tarsi light rufous. Mandibles with lateral margins arcuate, abruptly bent near apex. Pronotum without distinct basolateral collar; areas laterad depressions elevated above level of middle of disc; prosternal process long, extended almost entire length of procoxae. Mesoscutellum impunctate.

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.

Diagnosis. See diagnosis for the larval stage of *P. strictus*.

Description. See description for larvae of *P. kolwensis* group.

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).

PUPAL STAGE

The pupa of *P. nivalis* in unknown.

NATURAL HISTORY

Exceedingly little is known about the habits of this species. Lewis (1888) mentions that he collected the first specimens of *P. nivalis* in a dense forest of "pines" (*Abies*) at about 2100 m 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.

DISTRIBUTION

The range of this species is difficult to define because of the very few specimens examined (Map 4). *Pytho nivalis* is 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 known also from the U.S.S.R., but this was not substantiated by me (see Taxonomic notes).

MATERIAL EXAMINED

Only seven adults and one larva of this species were available for examination, from the following localities:

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). **Published references**: Oze, Ozunikko (Hayashi 1969: 7); Yumoto, Nikko, Tochigi-ken (Hayashi 1969: 7); Hokkaido, Berg Daisetsu, Sounkei (Kôno 1936).

3. *P. NIGER* GROUP

ADULT STAGE

Diagnosis. Adults of the *P. niger* group may be distinguished by the following characters: pronotum widest at midlength, disc with markedly arcuate lateral margins; pronotal depressions shallow, oval.

Description. TL 5.6–13.7 mm; GEW 1.9–5.5 mm. Colour uniform, varied from light piceous to black, without metallic lustre. Sensilla present on antennomeres 7– or 8–10. Lateral margins of mandibles evenly arcuate. Pronotum with posterior bead only, slightly impressed anterior bead in few individuals; lateral margins of disc evenly and markedly arcuate, widest at midlength; paired pronotal depressions shallow, oval; areas laterad depressions at same level as disc; prosternal process of varied length. Mesoscutellum with various number of setigerous punctures; mesepimeron uniformly punctate, in some specimens, punctures restricted to lateral margin; mesosternum with posterior bead impressed to, or laterad inner margin of mesotrochantin; punctation uniform or markedly reduced. Elytra depressed to slightly convex, each elytron with nine slightly convex intervals; posterolateral elytral margins without long pubescence. Male genitalia with apicale and basale subequal in length; apicale tapered evenly to apex; apicale narrowest apically with straight lateral margins.

LARVAL STAGE

Diagnosis. Larval of the *P. niger* group are recognized by the following characters: parabasal ridge processes elongate, parallel-sided; urogomphal lip with slightly arcuate posterior margin; urogomphal tubercles in two groups of four, separated by medial gap; urogomphal tubercles with apices directed posteriorly.

Description. Abdominal terga 2–6 with parabasal ridge processes (as in Fig. 13C) long, extended anterad parabasal ridge by a third their lengths; inner margins subparallel; distance from anterior tip of processes to posterior margin of terga 2–7 approximately five times length of process. Parabasal setae (as in Fig. 13C) various in size, two large setae per side, posterad parabasal ridge processes; four or five smaller setae laterad processes. Urogomphus (Fig. 14C) 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 various, smaller but well developed in most specimens; barely present and oriented ventrally in other individuals; urogomphal plate sharply sloped posteriorly to urogomphal lip. Urogomphal lip (Fig. 14C) with posterior margin slightly arcuate; ratio of urogomphal lip width at base to length along midline approximately 3:1. Urogomphal tubercles (Fig. 14C) 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 20–30 in number, small, with inconspicuous longitudinal ridges.

PUPAL STAGE

Diagnosis. Pupae of the *P. niger* group (the pupal stage of *P. jezoensis* Kôno is unknown) may be recognized by the following characters: anterior margin of labrum slightly emarginate; pronotum with evenly arcuate lateral margins, widest at or near midlength; abdominal terga 2–6 each with four lateral marginal tubercles.

Description. One or two ocular tubercles; anterior margin of labrum slightly emarginate. Pronotum with shape as in adult, lateral margins markedly arcuate, widest near midlength; 7–10 uniformly sized marginal tubercles per side. Abdominal terga 2–7 with four lateral marginal tubercles; two to four discal tubercles; two posterior marginal tubercles; one pleural tubercle; dorsal tubercles not widened basally, evenly tapered to apex. Abdominal sterna 2–6 with two posterior marginal tubercles.

INCLUDED TAXA

The *P. niger* group includes three species: *P. niger* Kirby, *P. abieticola* J. Sahlberg, and *P. jezoensis* Kôno.

GEOGRAPHICAL DISTRIBUTION

The *P. niger* group is Holarctic in distribution, with a range extended across North America, to north and central Europe, and to Japan.

5. *Pytho niger* Kirby 1837

(Figs. 2E, 4A, B, 6A, B, C, 7A, 8B, 9A, 14C; Map 5; Table 2)

Pytho niger Kirby 1837: 164, plate 7, fig. 2 [Type area — 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 area — Pennsylvania. Type repository — ZMHB] **New synonymy**; Blair 1928: 7.

ADULT STAGE

Notes about type material. 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 × 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 × 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] ''Summlung Cl. Müller''/[large label, 18 × 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 × 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.

Taxonomic notes. In Seidlitz's (1916) key to species of *Pytho*, his *P. niger* was in fact an undescribed species, *P. seidlitzi* Blair (see notes on type specimens and taxonomic notes for *P. seidlitzi*). As Blair (1925: 211) suggests, specimens of the true *P. niger* Kirby key 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 various 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 probably not have been proposed and described.

Diagnosis. Adults of *P. niger* may be recognized on the combination of the following characters: lateral margins of pronotal disc (Fig. 2E) strongly arcuate, widest near midlength; apex of prosternal, intercoxal process (Fig. 7A) incorporated into posterior bead of prosternum; posterior bead of mesosternum (Fig. 8B) visible laterad mesotrochantin; distribution — trans-Nearctic.

Description. Character states of the *P. niger* group and the following: TL 7.2–13.7 mm; GEW 2.6–5.5 mm; measurements given in Table 2. Colour with little variation among specimens examined, uniformly nonmetallic 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). Antennae with sensilla on antennomeres 8–10. Prosternal process (Fig. 7A) extended to half length of procoxae; process with bead thickened near apex, bead at same level as entire apex of process. Mesosternum with posterior bead impressed to lateral margins; punctation reduced along midline and laterally.

LARVAL STAGE

The larva of this species was illustrated by Böving and Craighead (1931). 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).

Diagnosis. Larvae of *P. niger* are at present indistinguishable from larvae of both *P. abieticola* and *P. jezoensis*, except by geographical distribution.

Description. See description for the *P. niger* group.

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

PUPAL STAGE

Diagnosis. 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 terga 2–6; most specimens with two discal tubercles on terga 2–6; abdominal tubercles not spade-shaped.

Description. See description for pupae of the *P. niger* group.

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

NATURAL HISTORY

Very little is published about the natural history of *Pytho niger*. Label data has furnished some information, as has personal observation. Records of flight, from label data, occur in May and June. 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 extended 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 pattern exhibited by all *Pytho* species (at least those in North America). Known hosts are listed in Table 1.

DISTRIBUTION

Pytho niger occurs across North America without significant gaps longitudinally (Map 5). The northern limit of the range probably follows treeline 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. However, the predominantly eastern distribution may reflect an eastern North American origin or refugium.

MATERIAL EXAMINED

Four hundred adults, approximately 450 larvae, and 15 pupae were examined, from the following localities:

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); Edmonton, Whitemud Creek, 16.x.1988, D.A. Pollock and E. Fuller, under bark of *Picea*, (7, DAPC); 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. Edmonton, Whitemud Creek, 16.x.1988, D.A. Pollock and E. Fuller, under bark of *Picea*, in pupal cells, (7, DAPC); Sibbald Flats (Jumping Pound Creek), 23.viii.1984, D.A. Pollock and J.L. Carr, (2, DAPC). **British Columbia:** ADULTS. 15 mi. NW 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. and 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. and 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.v.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). **Québec:** 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, (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. Borror, 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. strobus*, (1, CU), 3.ii.1925, Darlington, bark of *P. strobus*, (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, 31.v.1921, S. Moore, (1, UMAA); Marquette Co., Van Riper St. Pk., 12–14.vii.1972, D.K. and 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. and 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:** ADULTS. Cook Forest, 1.x.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:** ADULTS. 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.1985, D.K. Young, *P. strobus*, (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).

6. Pytho abieticola J. Sahlberg 1875

(Figs. 2F, 8A, C, D, 13C, 15B; Map 6; Table 2)

Pytho abieticola J. Sahlberg 1875: 222 [Type locality — Ruovesi, Finland. Type repository — ZMH]; Blair 1928: 4; Burakowski 1962: 193 and 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).

ADULT STAGE

Notes about type material. In the original description, Sahlberg states that four adults were collected from a fir tree on the margin of a fen called Sükaneva, in the "district" of Ruovesi. Also he 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 obtained subsequently 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.", but 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. Because all three specimens examined were collected at the type locality, and no clear designation of a type specimen is presented 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. Poillock 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).

Taxonomic notes. J. Sahlberg (1892) synonymized informally the names *P. niger* Kirby and *P. abieticola* Sahlberg, after having received and examined specimens of the former species from G.H. Horn. This has been reflected in several contemporary works dealing with *P. abieticola* (e.g. Grill 1896; Saalas 1917). This synonymy was not given, however, by Blair (1928). According to Sahlberg (1892), both the brief description and figure of *P. niger* Kirby (1837) were misleading. The figure is somewhat inaccurate in that the body is wider in proportion to length than is actually the case.

Diagnosis. Adult *P. abieticola* possess the following diagnostic features: lateral margins of pronotal disc (Fig. 2F) strongly arcuate, widest near midlength; mesosternum (Fig. 8C) 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. Character states of the *P. niger* group and the following: TL 5.6–10.6 mm; GEW 1.9–4.2 mm; measurements given in Table 2. Colour exhibiting little variation among specimens examined; uniformly, nonmetallic 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. Antennae with sensilla on antennomeres 8–10. Prosternal process short, extended to less than half length of procoxae; bead not distinctly widened near apex. Mesosternum with posterior bead impressed laterally to inner margin of mesotrochantin; punctation reduced to six or less medial punctures; on some specimens, mesosternum impunctate.

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).

Diagnosis. See diagnosis for *P. niger*.

Description. See description for the *P. niger* group.

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

PUPAL STAGE

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

Diagnosis. See diagnosis for pupae of *P. niger* Kirby.

Description. See description for pupae of *P. niger*.

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

NATURAL HISTORY

Pytho abieticola is exclusively a spruce beetle (Saalas 1917) and requires fairly dry and sun-exposed habitats. Saalas (1917) lists the following preferences for *P. abieticola*: swampy habitats, trees lying horizontally, with trunks 6–25 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 above.

DISTRIBUTION

According to label data, *P. abieticola* is known from Austria, Finland, Poland, and Sweden (Map 6). There is a recent new collection of this species from Czechoslovakia (Maca et al. 1984) and it is probable that the species will be found to be more widespread than originally thought. 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.

MATERIAL EXAMINED

Forty-six adults, 14 larvae, and two pupae of this species were examined, from the following localities:

AUSTRIA. ADULTS. 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. ADULTS. Glatz [=Klodzko], 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). **Jåmtland:** ADULTS. 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:** ADULTS. 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).

7. *Pytho jezoensis* **Kôno 1936**

(Fig. 2G; Map 7; Table 2)

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).

ADULT STAGE

Notes about type material. (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.

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

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

Description. Characters of the *P. niger* group and the following: TL 7.8–13.4 mm; GEW 3.0–5.0 mm; measurements given in Table 2. Colour slightly varied; uniformly nonmetallic 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. Antennae with sensilla on antennomeres 7–10. Prosternal process long, extended to at least half length of procoxae; posterior bead not distinctly widened near apex. Mesosternum with posterior bead impressed laterally to inner margins of mesotrochantin; punctation reduced on extreme lateral regions.

LARVAL STAGE

Diagnosis. See diagnosis for *P. niger*.

Description. See description for *P. niger* group.

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

PUPAL STAGE

The pupa of *P. jezoensis* is unknown.

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 above. Known host trees are given in Table 1.

DISTRIBUTION

Pytho jezoensis is apparently restricted to the Japanese islands (Map 7). Determination of the exact distribution in Japan is difficult because I was unable to locate many of the localities, from both label data and publications, and in atlases. Therefore, this species is undoubtedly more widespread in Japan, than indicated in Map 7. Kôno (1936) collected the original specimens on Hokkaido, and additional localities are given in Hayashi (1969). I have also examined specimens from Honshu.

MATERIAL EXAMINED

I examined 10 adults and a single larva of this species, from the following localities:

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, (2, 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).

4. *P. DEPRESSUS* GROUP

ADULT STAGE

Diagnosis. Adults of the *P. depressus* group are recognized by the following characters: pronotal disc with slightly arcuate lateral margins, widest anterad middle; elytral colour varied, metallic; posterolateral elytral margin with long pubescence.

Description. TL 7.1–14.8 mm; GEW 2.3–6.1 mm. Colour varied, from light rufous to black, with slight to marked metallic lustre on elytra. Antennae with sensilla present on antennomeres 7–10. Lateral margins of mandibles evenly arcuate. Pronotum with posterior bead only; lateral margins of disc slightly arcuate posteriorly, widest distinctly anterad midlength; paired pronotal depressions shallow, oval; prosternal process short. Mesoscutellum impunctate, or with various number of setigerous punctures; mesepimeron uniformly punctate; mesosternum with posterior bead impressed laterally to inner margin of mesotrochantin; punctation reduced along midline and laterally. Elytra depressed, each elytron with nine slightly convex intervals; posterolateral margins with long pubescence. Male genitalia with apicale and basale subequal in length, or length of apicale approximately 1.8 times length of basale; apicale tapered evenly to apex; apicale narrowest apically with straight lateral margins.

LARVAL STAGE

Diagnosis. Larvae of the *P. depressus* group may be recognized by the following characters: parabasal ridge processes very long and parallel-sided; urogomphal tubercles with tips directed anteriorly, arranged in truncate ellipse without medial gap; basal and middle urogomphal teeth subequal in size.

Description. Abdominal terga 2–6 with parabasal ridge processes (Fig. 13A) very long, extended anterad parabasal ridge by one-sixth their lengths; inner margins subparallel; distance from anterior tip of process to posterior margin of terga 2–7 approximately three times length of process. Parabasal setae (as in Fig. 13D) various in size, four to seven per side, arranged posterad and laterad parabasal ridge processes; posterior setae longer than lateral setae. Urogomphus (Fig. 14D) 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 ventral; urogomphal plate sharply sloped posteriorly to urogomphal lip. Urogomphal lip (Fig. 14D) with posterior margin weakly arcuate, straight in some specimens; ratio of urogomphal lip width at base to length along midline approximately 2.9:1. Urogomphal tubercles (Fig. 14D) 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 truncate anteriorly; tubercles 12–18 in number. Ventral asperities 18–25 in number, small, with inconspicuous longitudinal ridges.

PUPAL STAGE

Diagnosis. Pupae of the *P. depressus* group may be distinguished by the following characters: anterior margin of labrum slightly emarginate; pronotum widest anterad midlength; terga 2–6 each with five lateral marginal tubercles; dorsal tubercles evenly tapered to their apices, not expanded basally.

Description. One or two ocular tubercles; anterior margin of labrum slightly emarginate. Pronotum with shape as in adult, lateral margins slightly arcuate, widest anterad midlength; 10–12 marginal tubercles per side. Abdominal terga 2–6 with five lateral marginal tubercles, in few specimens four on single sides; two discal tubercles; two or three posterior marginal tubercles; two pleural tubercles; dorsal tubercles not widened basally, evenly tapered to apex.

INCLUDED TAXA

This species-group is composed of two species: *P. planus* (Olivier) and *P. depressus* (Linnaeus).

GEOGRAPHICAL DISTRIBUTION

The *P. depressus* group is Holarctic and widespread across North America and the Palaearctic Region, south to approximately 40° N latitude.

8. Pytho planus (Olivier 1795)

(Figs. 2H, 3D, E, 5B, D, C, 9C, D, 10A, B, 14D, 15A; Map 8; Table 2)

Tenebrio planus Olivier 1795 (No. 57): 14, plate II, fig. 17 [Type area — "Caroline méridionale". Type repository — unknown, type not seen]; Horn 1886: 138; Blair 1928: 5; Smith 1910: 367.

Pytho americanus Kirby 1837: 165 [Type area — 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, type not seen]; Blair 1928: 5, Lewis 1888: 108; Hamilton 1889: 55; Fauvel 1889: 55; Hamilton 1894*b*: 401; Ring 1982: 605–612 (natural history); Iablokoff-Khnzorian 1985: 205 (revision of Palearctic species). **New synonymy**.

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

Pytho depressus: Blatchley 1910 (nec Linnaeus 1767).

ADULT STAGE

Notes about type material. 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 Pytho americanus Kirby 1837 design. D.A. Pollock 1987". The specimen has the following identifying features: last three left antennomeres missing, last five 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)].

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*. 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).

Historically, there has been much confusion among taxonomists regarding status of *P. deplanatus* Mannerheim, *P. americanus* Kirby, and *P. depressus* (Linnaeus). The latter two species are quite varied in colour, which has led to a number of named varieties of each. The varieties of *P. depressus* were given separate names, but those of *P. americanus* were given merely letters, by Kirby (1837). Kirby (1837) realized that *P. americanus* resembled *P. depressus*, but states 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). Although *P. americanus* and *P. depressus* are very similar, they are not declared conspecific. Hamilton (1890: 44) proposes *P. americanus* Kirby as a variety of *P. depressus* (L.) and in essence synonymizes these two species. Hamilton (1894*a*: 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 (1894*a*) that *P. americanus* is identical to *P. depressus*. In his catalogue of the Coleoptera common to North America, northern Asia, and Europe, Hamilton (1894*b*: 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 varied. Iablokoff-Khnzorian (1985), who also saw the type specimen of *P. deplanatus*, deemed it conspecific 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 (Fig. 3D, F). I have not had the opportunity to examine the type specimen of *P. deplanatus*, apparently a female (Iablokoff-Khnzorian 1985) 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 various 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 is a junior synonym of *P. planus* (Olivier) and not of *P. depressus* (L.) as given by Iablokoff-Khnzorian (1985).

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

Description. Characters of the *P. depressus* group and the following: TL 7.1–14.8 mm; GEW 2.3–6.1 mm; measurements given in Table 2. Colour quite varied among specimens examined; dorsally, head ranging from light rufous to black with palpi and antennae always rufous; pronotum nonmetallic 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 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 then remainder of ventral surface; legs invariably rufous, tibiae and tarsi of most individuals darker than femora. Male genitalia with apicale and basale subequal in length; apicale tapered evenly to apex; apicale narrowest apically with straight lateral margins.

LARVAL STAGE

Diagnosis. Larvae of *P. planus* are inseparable from those of *P. depressus*, except by geographical distribution; see diagnosis for *P. depressus* group.

Description. See description for *P. depressus* group.

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

PUPAL STAGE

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

Description. Characters of the *P. depressus* group and the following: abdominal sterna 2–6 with one large posterior marginal tubercle in most specimens.

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.

NATURAL HISTORY

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). Recorded hosts of *P. planus* are listed in Table 1.

DISTRIBUTION

Pytho planus has an extensive range and occurs across Canada without significant gaps longitudinally (Map 8). To the north, treeline presumably subtends the extent of this species. To the south, *P. planus* does not have a specific range limit, but does not occur further south than about 35° N latitude.

MATERIAL EXAMINED

I examined 1013 adults, approximately 550 larvae, and 63 pupae of this species, from the following localities:

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, *Pinus monticola*, (1, AMNH); Stanley, 10.vi.1932, K. Graham, (1, UBCZ), (1, CAS); Terrace, 1925, W.W Hippisley, (1, UBCZ), (8, UASM), M.E. Hippisley, (2, MCZ), Mrs. Hippisley, (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); Kleanza Creek Provincial Park Campground, ~15 km E Terrace on Hwy 16, 26.vi.1989, D.A. Pollock, ex *Tsuga*, (5, DAPC); 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 and 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); Dyment, 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 Ruette, (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, prepupae, (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). **Québec:** 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 and 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 and 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 and 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:** ADULTS. 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:** ADULTS. Southwest Ark., (1, AMNH). **California.** ADULTS. 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., Glendevey 8500′, H.E. Evans, under bark, (4, VPI); state record only, in yellow pine, (3, NMNH). **Connecticut:** ADULTS. 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. NE Potlatch nr. Big Ck. and Hope Ck., 12.v.1976, L. Chin, (2, WSU); 5 mi. NE 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). **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, FSCA); 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. Borror, 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 and 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. and 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:** ADULTS. Gallatin Co., Bozeman, x.1957, R.C. Froeschner, (1, MSUC); Jefferson Co., 31.v.1982, student collector, (1, MSUC); Gallatin Co., Bozeman Cr., 6000′, 4.vi.1987, D.L. Gustafson, (6, MSUC), (3, DLGC); Gallatin Co., Mystic Lake area, 10 mi. SE Bozeman, 6.x.1986, D.L. Gustafson, (1, DLGC); Gallatin Co., Hyalite Reservoir, ca. 12 km S Bozeman, 14.viii.1990, D.A. Pollock and R.E. Roughley, ex pupa, (1, DAPC); Glacier Co., Hwy 89, 8 km S St. Mary, 16.viii.1990, D.A. Pollock and R.E. Roughley, ex. pupae, (5, DAPC); Judith Basin Co., Little Belt Mtns., 5 mi. S Deadhorse Crk., 6600 ft., FIT, 27.v–1.vii.1988, C.E. Siebert, (2, MSUC). LARVAE. Gallatin Co., Hyalite Reservoir, ca. 12 km S Bozeman, 14.viii.1990, D.A. Pollock and R.E. Roughley, (10, DAPC); Glacier Co., Hwy 89, 8 km S St. Mary, 16.viii.1990, D.A. Pollock and R.E. Roughley, (25, DAPC). **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, 10.iv.1980, N.W. 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.ix.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:** ADULTS. 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.ix.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, Babiy, (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:** ADULTS. 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. SW Ripplebrook, 27.vii.1976, (2, NMDC); Hood River Co., Mt. Hood near Barlow Pass, 29.vi.1974, A. and 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. and 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); country 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:** ADULTS. 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:** ADULTS. 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:** ADULTS. 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:** ADULTS. 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).

9. *Pytho depressus* (Linnaeus 1767)

(Figs. 2I, 3F, 13D; Map 9; Table 2)

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, 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); Yanovskiy and Dmitrienko 1983 (distribution); 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.

ADULT STAGE

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. Thus, *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 varied 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). Because *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 Taxonomic notes for *P. planus* for more information.

Diagnosis. Adult *P. depressus* possess the following diagnostic features: lateral margins of pronotal disc (Fig. 2I) weakly arcuate, widest anterad midlength; elytra with slight to strongly metallic lustre; aedeagus (Fig. 3F) with apicale approximately 1.8 times length of basale; distribution — trans-Palearctic.

Description. Characters of the *P. depressus* group and the following: TL 7.4–13.7 mm; GEW 2.5–5.3 mm; measurements given in Table 2. Colour quite varied 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; some specimens with rufous elytra with violet metallic sheen pronounced on lateral margins and/or entire apical half of elytra (giving bicoloured effect); many specimens with piceous to black elytra with 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. Male genitalia with apicale approximately 1.8 times length of basale; apicale tapered evenly to apex; apicale narrowest apically with straight lateral margins.

LARVAL STAGE

The larval stage of *P. depressus* has been described previously by many authors. Earlier references are listed in Seidlitz (1916: 123–124). The larva has been redescribed by more recent authors, including Burakowski (1976).

Diagnosis. See diagnosis for *P. planus*.

Description. See description for *P. depressus* group.

Association methods. All of the larval specimens of *P. depressus* were previously determined. However, I confirmed the identifications by study of published descriptions.

PUPAL STAGE

Diagnosis. Pupae of *P. depressus* can be separated from those of *P. planus* on the basis of the former possessing two large, subequal, posterior marginal tubercles on sterna 2–6.

Description. Characters of the *P. depressus* group and the following: abdominal sterna 2–6 with two posterior marginal tubercles, subequal in length.

Association methods. The previous identifications of the pupae of this species were confirmed by study of published descriptions.

NATURAL HISTORY

Because this species is very widespread, and because it is Palearctic, *P. depressus* has had a comparatively large amount written about 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* are in Seidlitz (1916) and Blair (1928). Host trees are found in dry forests, swamps, and on hills (''Fjeldabhängen''), and can be standing, lying, or stumps (Saalas 1917). Size of host tree trunk can range from 6 to more than 35 cm in diameter. *Pytho depressus* prefers trees that are decayed, but still fresh and without fungal attacks. Known host trees of *P. depressus* are given in Table 1.

DISTRIBUTION

Pytho depressus is the most widespread Palearctic species, and is known from Scotland (locality not mapped) to the far eastern U.S.S.R. (Map 9). Kôno (1934) lists this species as inhabiting Sachalin. The large gap in the 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.

MATERIAL EXAMINED

I examined 290 adults, 33 larvae, and three pupae of this species, from the following localities:

AUSTRIA. ADULTS. 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: ADULTS. München, 3.5.81, (1, ZMHB); Pressath opf Germania, 23.ix.71, G. Uhmann, ex. larva, (1, ZMHB); Schliersee, 5.7.1909, (1, ZMHB). **Erfurt:** ADULTS. Nordhausen, no date, Reitter, (1, SMF). **Hamburg:** ADULTS. Hamburg, no date, W. Meier, (4, FMNH), 4.87, (2, SMF); 1917, Berghorst, (1, ZMHB), no data, (1, SMF), (1, TMB), (2, ZMHB). **Niedersaschen:** ADULTS. 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:** ADULTS. 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:** ADULTS. Berlin (u. Umg.), no data, (1, SMF); country record only, no data, (6, TMB), (4, MPM), (2, UMAA).

FINLAND. Etelä-Häme: ADULTS. 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:** ADULTS. Kajaani, no data, J. Carpelan, (2, ZMH), (1, TMB), (2, SMF); Suomussålmi, 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:** ADULTS. Sammatti, 24.viii.1917, H. Lindberg, (2, ZMH); Wichtis [= Vihti], 18.viii.1917, H. Lindberg, (2, ZMH), no data, A.G. Helenius, (1, ZMH). **Lappland:** ADULTS. No data, (1, SMF), (3, ZMHB), (1, TMB); country record only, "Al. Smolka", (1, TMB), no data, (6, TMB).

FRANCE. ADULTS. Allier, no data, (2, CMP); Champagne bei Reims, ii.18, (2, ZMHB).

GERMAN DEMOCRATIC REPUBLIC. ADULTS. Luckau, vi.1962, W. Nadolski, (1, ZMHB).

NETHERLANDS. Noord-Brabant: ADULTS. Chaam. 8.iv.1971, P. Kanaar, (1, ROMC). **Noord-Holland:** ADULTS. Hilversum, no data, (4, SMF).

NORWAY. Buskerud: ADULTS. Kongsberg, (2, ZMHB). **Troms (I):** ADULTS. 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. ADULTS. Beuthen [= Bytom] Silesia, no data, M. Nowotny, (1, ZMHB); Bialowies [= Bialowieski Park?], no data, (1, ZMHB); Danzing [= Danzig (Gdansk)?], no data, (1, TMB); Jaroslaw, 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. ADULTS. Galicia, no data, coll. Geitner, (8, TMB).

SCOTLAND. ADULTS. nr. Green Loch (L. Maxlich), 27.ix.1951, D.K. Keven, Sr., (2, LEMC).

SWEDEN. Närke: ADULTS. 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.: ADULTS. Przewalsk [= Przevalsk] Almasy Turkestan, no data, (1, TMB). **Latvijskaja S.S.R.:** ADULTS. Curonia, Libau [= Liepaja], 14.iv.1913, (1, ZMHB). **Rossijskaja S.F.S.R.:** ADULTS. 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.:** ADULTS. 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. ADULTS. Bosna i Hercegovina Zavidovic [= Zavidici], 10.v.1905, Kendi, (1, TMB).

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 in the modern sense of this genus.

PHYLOGENY

This section deals with the relationships among the genera of Pythinae and the reconstructed phylogeny of the species of *Pytho*. The genus *Pytho* is demonstrably monophyletic, but monophyly of the genera of Pythinae, as supported by Watt (1987), is not conclusive. The methods, both theoretical and practical, used to reconstruct the phylogeny of members of *Pytho* are given. Characters and character states relevant to the phylogenetic analysis of *Pytho* are discussed in detail, below.

METHODS

To postulate phylogenetic relationships among species of *Pytho*, cladistic methods described by Hennig (1966), Kavanaugh (1972, 1978), Wiley (1981), and others were used. 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 10 years of the journal *Systematic Zoology* to appreciate the depth of these arguments.

The methods by which a group of organisms is analysed using cladistics are basically similar among workers involved in phylogenetics. It is uncommon for an author to list in detail the steps used, but this has been done by Marshall (1987: 380) who examined the systematics of *Bitheca* (Diptera: Sphaeroceridae), to "clarify the method by which information was incorporated into this cladogram". 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.

TAXA EXAMINED

In addition to studying larvae, pupae, and adults of all species of *Pytho* (except for pupae of *P. nivalis* and *P. jezoensis*), various other species were also examined. Included are 30 adults and approximately 50 larvae of *Priognathus monilicornis*, 12 adults and five larvae of *Sphalma quadricollis*, and 15 adults and one (presumed) larva of *Synercticus heteromerus*. The larva of *Synercticus heteromerus* was identified as such by J.F. Lawrence. Although not included in the phylogenetic analysis, I examined also specimens of the following taxa: 12 adults of *Trimitomerus riversii*, adults and larvae of *Boros unicolor* Say, and adults of *Lecontia discicollis* (LeConte).

PYTHINAE AS A MONOPHYLETIC UNIT

The subfamily Pythinae (Watt 1987) is composed of four genera: the monobasic Australian *Synercticus* Newman; the monobasic, western North American *Sphalma* Horn; the monobasic, trans-North American *Priognathus* LeConte; and the more diverse *Pytho*. In terms of inclusiveness, 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* Winkler, which is restricted to southeastern Europe (Lawrence 1982).

The monophyly of the four pythine genera is based on a single, larval-stage synapomorphy, the presence of a transverse row of tubercles on tergum 9 (Watt 1987). This character occurs also in the genus *Elacatis* (Othniidae) and could have arisen twice, or more, within Pythinae independently. Because the pythine group of genera was not analysed 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 monophyly of Pythinae has direct impact upon the hypotheses regarding the zoogeography of *Pytho* and of the entire subfamily.

PYTHO AS A MONOPHYLETIC UNIT

Several autapomorphic 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; Fig. 2); (2) raised carinae (intervals) on elytra (character 15; Fig. 9B). *Pytho* larvae possess clearly developed parabasal ridge processes on the abdominal terga (character 1; Fig. 13). 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.

ANALYSIS OF CHARACTERS AND RECONSTRUCTED PHYLOGENY OF *PYTHO*

Paramount in phylogenetic analysis is character analysis; relative polarities of the character states in a given morphocline or transformation series affect directly 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 general similarity and geographical distribution, *Priognathus* may be the sister-taxon to *Pytho*. Therefore, 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* not represented in the other genera, in-group comparisons were used to determine the relative polarities of these character states. Character polarities are given in Table 3. Distribution of apomorphic and plesiomorphic character states among species of *Pytho* and the three genera of Pythinae used as the out-group are listed in Table 4.

All characters of both larval and adult stages were initially given equal weight in reconstructing the phylogeny (Fig. 16). 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 eight characters included from the larval stage were effective in defining the species-groups in the relationship. The 12 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-group or toward the terminal ends of the cladogram. Therefore, even though the characters selected were given equal weight at the outset, they developed eventually a different relative weight once they were interpreted and used to reconstruct the phylogeny of *Pytho*. Character states that were polarized by simple out-group analysis, or are autapomorphic for the genus *Pytho*, are not discussed further. These include characters 01, 02, 03, 05, 06, 09, 16, 18, 20. Explanations are provided for the phylogenetic interpretation of states of characters 04, 07, 08, 10, 11, 12, 13, 14, 15, 17, 19.

Relative sizes of the basale and apicale (character 04). In most species of *Pytho*, and in *Sphalma* and *Priognathus*, the basale of male genitalia is subequal in length to the apicale. In *P. seidlitzi* (Fig. 3C) and *P. depressus* (Fig. 3F), 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*.

Apical urogomphal tooth (character 07). An apical, or third, inner urogomphal tooth is developed in larvae of all species of *Pytho* except *P. seidlitzi* 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 (Fig. 14B, 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 (Fig. 14D). 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*.

Punctation of mesepimeron (character 08). The mesepimeron of adults of all species of *Pytho* (except *P. seidlitzi*) is equally as punctate/pubescent as the metepisternum. In *P. seidlitzi*, punctation of the mesepimeron is either entirely absent, or restricted to the lateral margin of the sclerite (Fig. 7D). In either case, the mesepimeron strongly contrasts the metepisternum with respect to degree of punctation. Restricted (or absent) mesepimeral punctation also occurs in *Priognathus*. For *Synercticus* and *Sphalma*, it is difficult to assess this character because of an overall reduction in ventral punctation, but it appears that the punctation of the mesepimeron is not significantly different from that of the metepisternum in these two genera. Due to the restriction of mesepimeral punctation in *Priognathus*, this state is deemed plesiomorphic, with uniform punctation of the mesepimeron as the apomorphic state in *Pytho*.

Shape of pronotal depressions (character 10). Two states are thought to exist, with respect to shape and depth of these depressions. Species in the *seidlitzi, niger*, and *depressus* groups possess pronotal depressions which are elliptical or oval in shape, and quite shallow. In members of the *P. kolwensis* group (Fig. 2B, 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.

Anterior pronotal head (character 11). An anterior pronotal bead, well-developed medially, is present in all three species of the *P. kolwensis* group (Fig. 2B, 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.

Extent of annular, antennal sensilla (character 12). Adults of *Pytho* possess annular sensilla surrounding the apex of the last four or five antennomeres (Fig. 5A). 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, but the remaining two species of the *P. niger* group and *P. seidlitzi* have these sensilla on antennomeres 8–11. *Synercticus, Sphalma*, and *Priognathus* have sensilla on antennomeres 11, 6–11, and 9–11, respectively. Because a variety of conditions exist 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.

Length of parabasal ridge processes (character 13). Among members of *Pytho*, three states are present. *Pytho seidlitzi* has short processes (Fig. 13A) as do members of the *P. kolwensis* group (Fig. 13B). In both of these groups, the length of the processes is approximately one-ninth the length of the terga on which the processes are situated. *Pytho niger* group larvae have processes more elongate (Fig. 13C), approximately one-fifth the length of the terga. The *P. depressus* group larvae possess the highly derived state, in which these processes are very elongate (Fig. 13D), about one-third or greater the length of the terga.

Shape of parabasal ridge processes (character 14). Two distinctive shapes of parabasal ridge processes are present among species of *Pytho*. The plesiomorphic state is exhibited in members of the *P. seidlitzi* and *P. kolwensis* groups, in which the processes have the inner margins arcuate (Fig. 13A, B). The *P. niger* and *P. depressus* groups possess the derived state, in which the inner margins of the processes are subparallel throughout their lengths.

Orientation of medial urogomphal tubercle apices (character 15). Among species of *Pytho*, all species-groups except the *P. depressus* group have mesal urogomphal tubercles with apices directed posteriorly. In the *P. depressus* group, these are directed anteriorly. Among the out-group taxa, the larva of *Priognathus monilicornis* possesses also the anteriorly directed urogomphal tubercles. Presumably this feature is important in some aspect of locomotion beneath the bark, and within the rotting sapwood of dead trees. The derived condition is deemed to have evolved twice, once in the *P. depressus* group and once in *Priognathus*.

Shape of adult mandible (character 17). 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*.

Number of asperities on venter of urogomphal plate (character 19). Two character states are hypothesized to exist, with a reduced number of asperities, less than 20 being plesiomorphic and greater than 21 apomorphic. Larvae of both *Synercticus* and *Sphalma* along with all *Pytho* species except the *P. niger* group possess the primitive state. *Priognathus* larvae have an average of 30 ventral asperities, but members of the *P. niger* group have from 23 to 28. The derivation of the apomorphic state occurred independently in both lineages. This is admittedly subjective, and possibly a weak character.

Table 5 lists apomorphic character states and the number of times each has evolved among species of *Pytho*. Most of the character states have evolved only once, but three character states have multiple derivations. The derived states of characters 04 (apicale of greater length than basale) and 18 (metallic colour of elytra) were deemed to have evolved twice independently within the genus. The apomorphic state of character 12 (sensilla on antennomeres 7–10) has arisen independently three times among species of *Pytho*. Two character states involved reductions or losses: character 06^- (absence of posterior pronotal bead) and 20^- (reduction in size of the basal, inner urogomphal tooth).

ZOOGEOGRAPHY

SUBFAMILY PYTHINAE

Distribution patterns. 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, and *Sphalma quadricollis* Horn is restricted to the western United States and adjacent Canada (Hatch 1965). *Pytho* is Holarctic with nine species worldwide. In the Nearctic Region, the genus ranges 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 hemisphere member of Pythinae, *Synercticus heteromerus* Newman, is known only from eastern Australia.

Geographic history. 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 origin of Pythinae is 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 Mid-continental 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 Region. This sympatry is probably the result of subsequent dispersal following the vicariant event that 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 Region. 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, because, according to Matthews (1979), the Miocene coniferous forest was Holarctic in expanse. If this is so, then *Priognathus* subsequently has gone extinct in the Palearctic Region, or it never reached there. 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 subsequently have 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. He 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 that 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 that 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 less developed legs. It is not known whether the habitat divergence occurred more-or-less simultaneously with the vicariance event that 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*.

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 using the same habitat, the latter of which may be better competitors than the former. The fact that *Sphalma* lives beneath bark of dead deciduous trees (Young 1976) may account for the lack of diversity within that genus. *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 that 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.

Fossils. Wickham (1913) described *Pythoceropsis singularis* from the Florissant shales, Colorado. It was placed in the family Pythidae, but both the description and figures are insufficient to place *Pythoceropsis* at the family level. Wickham (1913) states that the fossil has characters of both *Lecontia* or *Boros*, and *Pytho*. This is difficult to determine by reference to the figures provided. It is probable that fossils of the ancestor of Pythidae + Boridae may be found in North America, but earlier than the Miocene.

GENUS *PYTHO*

Four species-groups, or clades, have been proposed among world species of *Pytho* (Fig. 16). 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 limited ability of adults of *Pytho* to disperse, because relatively short distances exist between Alaska and the 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 as follows: (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 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.

Fossils. *Pytho niger* is listed in Morgan and Morgan (1980) as being present in samples dating from the Late Pleistocene of New York and Ontario. A single pronotum was kindly provided by J. Pilny, University of Waterloo, from the Late Wisconsinan of Lockport Gulf, New York (10 920 ± 160 ^{14}C years B.P.). This specimen falls within the range of variation exhibited by modern specimens of *P. niger* from eastern North America.

***P. seidlitzi* group**. This lineage consists of one species, *P. seidlitzi*, 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. seidlitzi* failed to disperse across the Beringian land bridge in the Miocene when this area was covered with coniferous forest (Matthews 1979, 1980). Alternatively, *P. seidlitzi* may have been more widespread in the Holarctic Region, with subsequent extinction in the Palearctic.

***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, but *P. niger* is more widespread. Although considerably more widespread than *P. strictus*, there is evidence that *P. niger* originally may have 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 *kolwensis* and *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 *kolwensis* and *niger* groups exhibit a North American, European, and Japanese distribution. This pattern 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 *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 *kolwensis* group may be conspecific. As indicated in the cladogram depicting the hypothesized phyletic relationships among species of *Pytho* (Fig. 16), there is an unresolved trichotomy among species of the *niger* group. It is possible that these three species have shared a similar geographic history to those in the *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 *kolwensis* and *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 *kolwensis* and *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*.

***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 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.

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 Wisconsinan 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*, similarly it must have been suitable for at least one species of coniferous tree also. 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 2000 km in 1000 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. Because there is no known pre-Pleistocene fossil record for *Pytho*, a minimum age of origin of the genus and of the various lineages is impossible to document. From the evidence available, the larval stage of *Pytho* has maintained some degree of morphological stasis, when compared with the adult. If fossil larvae were available, the zoogeographic and phylogenetic hypotheses discussed above could be critically tested.

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CHECKLIST OF SPECIES OF *PYTHO* LATREILLE

P. seidlitzi group.
  1. *P. seidlitzi* Blair 1925
P. kolwensis group.
  2. *P. strictus* LeConte 1866
  3. *P. kolwensis* C. Sahlberg 1833
  4. *P. nivalis* Lewis 1888
P. niger group.
  5. *P. niger* Kirby 1837
    P. fallax Seidlitz 1916
  6. *P. abieticola* J. Sahlberg 1875
  7. *P. jezoensis* Kôno 1936
P. depressus group.
  8. *P. planus* (Olivier 1795)
    P. americanus Kirby 1837
    P. deplanatus Mannerheim 1843
  9. *P. depressus* (Linnaeus 1767)
Species Incertae Sedis
  P. erotis Gistel 1857

Table 1. Known hosts of species of *Pytho* Latreille

Host	*seid.*	*stric.*	*kolw.*	*nival.*	*niger*	*abiet.*	*jezo.*	*plan.*	*depres.*
Pinus strobus L.		X			X			X	
P. monticola Dougl.	X							X	
P. ponderosa Laws.								X	
P. resinosa Ait.								X	
P. banksiana Lamb.	X				X			X	
P. contorta Dougl.	X				X				
P. echinata Mill.								X	
P. silvestris L.									X
Larix occidentalis Nutt.	X								
Picea glauca (Moench) Voss	X								
P. mariana (Mill.) B.S.P.	X				X			X	
P. excelsa Link			X						X
P. abies (L.) Karst.						X			
P. jezoensis (Siebold & Zaccarini) Carrière							X		
Tsuga heterophylla (Raf.) Sarg.	X							X	
T. sieboldi Carrière							X		
Pseudotsuga menziesii (Mirb.) Franco	X								
Abies balsamea (L.) Mill.	X				X				
A. grandis (Dougl.) Lindl.	X								
A. sp.				X					

Table 2. Descriptive statistics for species of *Pytho* Latreille. GEW, greatest elytral width; TL, total length; GPW/PL, ratio of greatest pronotal width at pronotal length (explanations of measurements given in "Measurements" section). Species abbreviations: se, *P. seidlitzi*; st, *P. strictus*; ko, *P. kolwensis*; ni, *P. nivalis*; ng, *P. niger*; ab, *P. abieticola*; js, *P. jezoensis*; pl, *P. planus*; de, *P. depressus*. Abbreviations given for geographic locality of sample, and for sex of specimens. If no geographic abbreviation given, than sample taken from various localities

		GEW	TL	GPW/PL
se AB (M)	Range	3.68–4.56	9.76–11.44	1.29–1.55
	Mean	4.15	10.89	1.38
	S.D.(*N*)	0.37 (6)	0.73 (6)	0.09 (6)
se AB (F)	Range	3.92–4.80	11.12–12.56	1.41–1.50
	Mean	4.50	11.98	1.45
	S.D.(*N*)	0.34 (5)	0.61 (5)	0.04 (5)
se PQ (M)	Range	3.68–4.72	9.84–12.96	1.33–1.47
	Mean	4.2	11.25	1.39
	S.D.(*N*)	0.38 (11)	0.94 (11)	0.04 (11)
se PQ (F)	Range	3.52–4.80	9.28–12.96	1.30–1.50
	Mean	4.34	11.29	1.42
	S.D.(*N*)	0.45 (8)	0.99 (8)	0.04 (8)
st (M,F)	Range	4.88–5.76	13.38–16.24	1.39–1.55
	Mean	5.41	14.68	1.48
	S.D.(*N*)	0.33 (10)	0.80 (10)	0.05 (10)
ko (M)	Range	4.00–5.60	10.88–14.24	1.32–1.43
	Mean	4.84	12.56	1.35
	S.D.(*N*)	0.57 (6)	1.22 (6)	0.04 (6)
ko (F)	Range	4.32 –5.92	11.60–15.92	1.24–1.47
	Mean	5.15	13.62	1.36
	S.D.(*N*)	0.59 (13)	1.44 (13)	0.06 (13)
ni (M,F)	Range	4.32–5.52	11.76–15.04	1.25–1.35
	Mean	4.83	13.41	1.32
	S.D.(*N*)	0.44 (6)	1.13 (6)	0.04 (6)
ng MB (M)	Range	3.12–3.52	8.08–9.36	1.35–1.53
	Mean	3.36	8.70	1.42
	S.D.(*N*)	0.20 (5)	0.54 (5)	0.07 (5)
ng MB (F)	Range	3.20–5.52	7.76–12.08	1.29–1.56
	Mean	4.01	9.41	1.44
	S.D.(*N*)	0.89 (7)	1.67 (7)	0.09 (7)
ng MA (M)	Range	3.20–4.16	9.68–11.20	1.35–1.57
	Mean	3.64	10.36	1.49
	S.D.(*N*)	0.33 (12)	0.47 (12)	0.07 (12)
ng MA (F)	Range	3.20–4.48	9.20–12.32	1.48–1.57
	Mean	3.99	11.09	1.54
	S.D.(*N*)	0.35 (12)	0.82 (12)	0.04 (12)
ab FIN (M,F)	Range	2.72–3.76	6.96–9.76	1.35–1.56
	Mean	3.16	8.17	1.49
	S.D.(*N*)	0.31 (10)	0.90 (10)	0.06 (10)
ab SWE (M)	Range	1.92–3.68	5.60–8.96	1.45–1.63
	Mean	2.82	7.38	1.53
	S.D.(*N*)	0.50 (10)	1.06 (10)	0.07 (10)
ab SWE (F)	Range	2.48–4.24	6.72–10.64	1.47–1.67
	Mean	3.23	8.35	1.55
	S.D.(*N*)	0.58 (10)	1.36 (10)	0.07 (10)

Table 2. (*Concluded*)

		GEW	TL	GPW/PL
je (M)	Range	2.96–4.72	7.84–12.08	1.32–1.44
	Mean	3.84	9.90	1.38
	S.D.(*N*)	0.62 (5)	1.51 (5)	0.05 (5)
je (F)	Range	4.56–5.04	12.00–13.36	1.35–1.46
	Mean	4.83	12.91	1.39
	S.D.(*N*)	0.22 (5)	0.53 (5)	0.05 (5)
pl PQ (M)	Range	4.00–4.64	10.32–12.24	1.36–1.55
	Mean	4.22	11.05	1.43
	S.D.(*N*)	0.26 (7)	0.66 (7)	0.07 (7)
pl PQ (F)	Range	4.48–5.44	11.60–14.16	1.44–1.52
	Mean	4.91	12.83	1.47
	S.D.(*N*)	0.29 (7)	0.81 (7)	0.03 (7)
pl NT (M)	Range	2.32–3.52	7.12–10.00	1.33–1.47
	Mean	3.10	8.98	1.40
	S.D.(*N*)	0.36 (10)	0.93 (10)	0.05 (10)
pl NT (F)	Range	2.88–4.64	9.84–12.88	1.45–1.61
	Mean	3.64	11.41	1.51
	S.D.(*N*)	0.48 (10)	0.97 (10)	0.05 (10)
de FIN (M)	Range	2.64–4.40	7.44–11.84	1.39–1.52
	Mean	3.54	9.57	1.45
	S.D.(*N*)	0.64 (10)	1.50 (10)	0.05 (10)
de FIN (F)	Range	3.28–5.28	9.04–13.20	1.33–1.50
	Mean	4.14	10.89	1.45
	S.D.(*N*)	0.65 (10)	1.33 (10)	0.05 (10)
de FRG (M)	Range	2.56–3.92	7.36–10.40	1.33–1.42
	Mean	3.35	9.08	1.38
	S.D.(*N*)	0.42 (10)	0.90 (10)	0.03 (10)
de FRG (F)	Range	3.12–4.24	8.34–11.68	1.35–1.52
	Mean	3.75	10.38	1.43
	S.D.(*N*)	0.45 (10)	1.29 (10)	0.05 (10)

Table 3. Characters and phylogenetic designations of character states for species of the genus *Pytho*

		Character states and designations	
No.	Character	Plesiomorphic	Apomorphic
01	Parabasal ridge processes	Absent	Present
02	Pronotum: paired depressions	Absent	Present
03	Elytra: carinate intervals	Absent	Present
04	Relative sizes of apicale and basale	Apicale = basale	Apicale > basale
05	Apicale: shape of apex	Evenly tapered to apex	Expanded at apex
06	Pronotum: posterior bead	Present	Absent
07	Apical urogomphal tooth	Absent	Present
08	Mesepimeron: punctation	Reduced	Uniform
09	Apical urogomphal tubercle: setation	Unisetose	Plurisetose
10	Pronotal depressions: depth/shape	Shallow, oval	Deep, ± linear
11	Pronotum: anterior bead	Absent	Present
12	Antennae: sensilla	On antennomeres 8–10	On antennomeres 7–10
13	Parabasal ridge processes: length	Processes ~ 1/9 length of terga	1. Processes ~ 1/5 length of terga 2. Processes ~ 1/3 length of terga
14	Parabasal ridge processes: shape	Inner margins arcuate	Inner margins parallel
15	Mesal urogomphal tubercles: orientation of apices	Posterior	Anterior
16	Prosternal process: shape	Shorter	Longer
17	Mandibular apex: shape	Evenly rounded to apex	Abruptly bent near apex
18	Elytra: colour	Unmetallic	Metallic
19	Ventral asperities: number	Reduced	Increased
20	Middle and basal urogomphal teeth: relative sizes	Basal > middle	Middle ≥ basal

Table 4. Characters and distribution of phylogenetically designated character states among species of *Pytho*, and of *Synercticus*, *Sphalma*, and *Priognathus*. Style and format for table taken from Shpeley (1986). Symbols for character states are as follows: a dash (—) represents the plesiomorphic state; for the apomorphic state, a minus sign ($^-$) represents a loss or reduction from the apomorphic state; the letter "a" represents the apomorphic state in a simple two-state transformation series; uppercase letters represent progressive states in a multiple-state transformation series; numerals indicate independent derivations of the apomorphic state; NA = not applicable

Char.	*Pytho seidl.*	*strict.*	*kolw.*	*nival.*	*niger*	*abiet.*	*jezo.*	*plan.*	*depre.*	*Synerc.*	*Sphal.*	*Priog.*
01	a	a	a	a	a	a	a	a	a	—	—	—
02	a	a	a	a	a	a	a	a	a	—	—	—
03	a	a	a	a	a	a	a	a	a	—	—	—
04	1	—	—	—	—	—	—	—	1	1	—	—
05	a	—	—	—	—	—	—	—	—	—	—	—
06	a	—	—	—	—	—	—	—	—	—	—	—
07	—	1	1	1	1	1	1	1	1	1	1	—
08	—	1	1	1	1	1	1	1	1	1	1	—
09	—	a	a	a	—	—	—	—	—	—	—	—
10	—	a	a	a	—	—	—	—	—	NA	NA	NA
11	—	1	1	1	—	—	—	—	—	1	—	—
12	—	1	1	1	—	—	1	1	1	—	2	—
13	—	—	—	—	1	1	1	2	2	NA	NA	NA
14	—	—	—	—	a	a	a	a	a	NA	NA	NA
15	—	—	—	—	—	—	—	a	a	—	a	—
16	—	—	a	a	—	—	—	—	—	—	—	—
17	—	—	1	1	—	—	—	—	—	—	—	2
18	—	—	—	1	—	—	—	1	1	—	—	—
19	—	—	—	—	1	1	1	—	—	—	—	2
20	—	—	—	—	—	—	—	a^-	a^-	—	—	—

Table 5. Character state evolution among species of the genus *Pytho*

Character state number	Number of times character state evolved		
	1	2	3
01	X		
02	X		
03	X		
04		X	
05	X		
06^-	X		
07	X		
08	X		
09	X		
10	X		
11	X		
12			X
13^1	X		
13^2	X		
14	X		
15	X		
16	X		
17	X		
18		X	
19	X		
20^-	X		

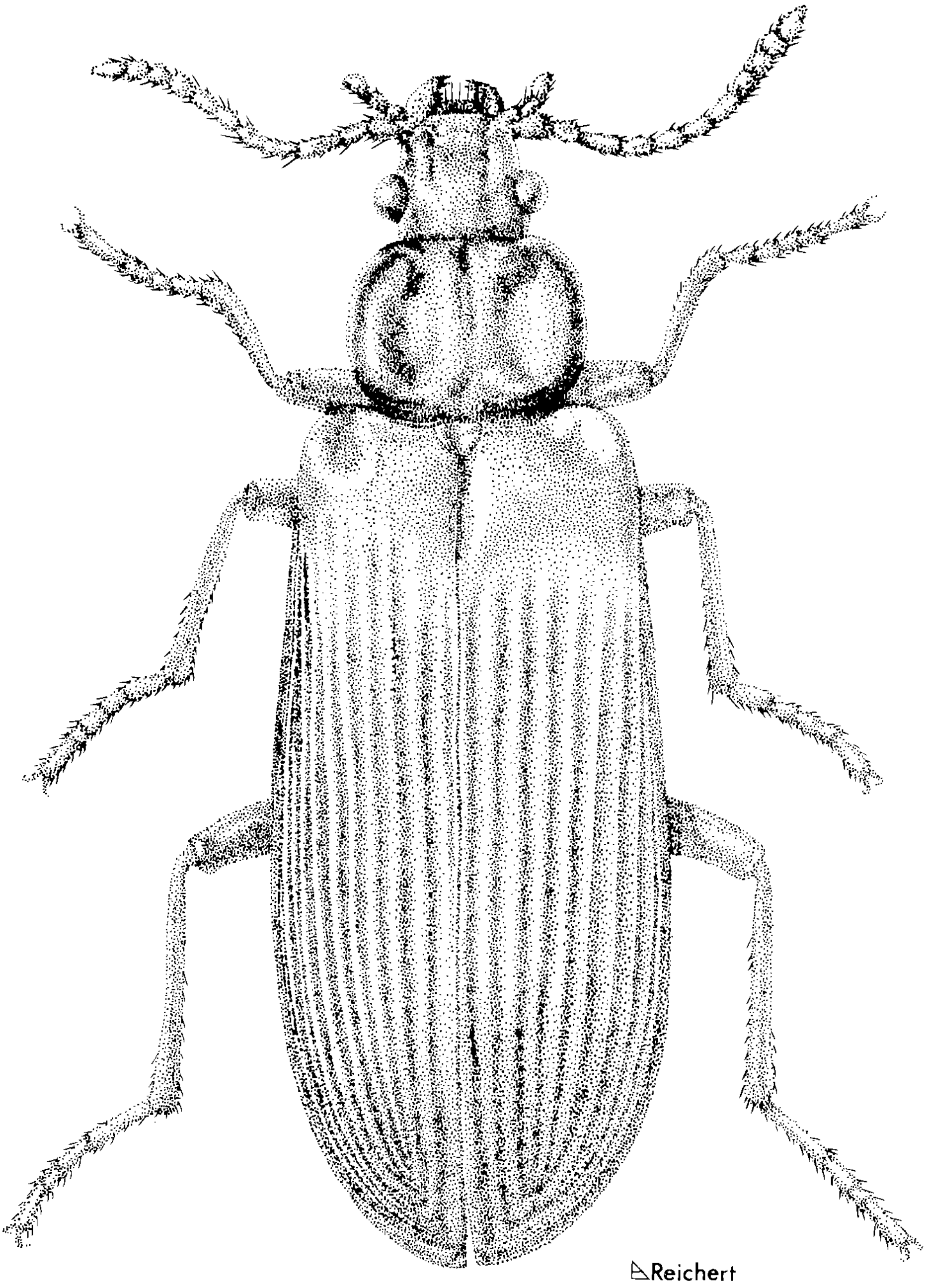


FIG. 1. Dorsal habitus of the adult stage of *Pytho seidlitzi* Blair [total length of specimen = 14.1 mm].

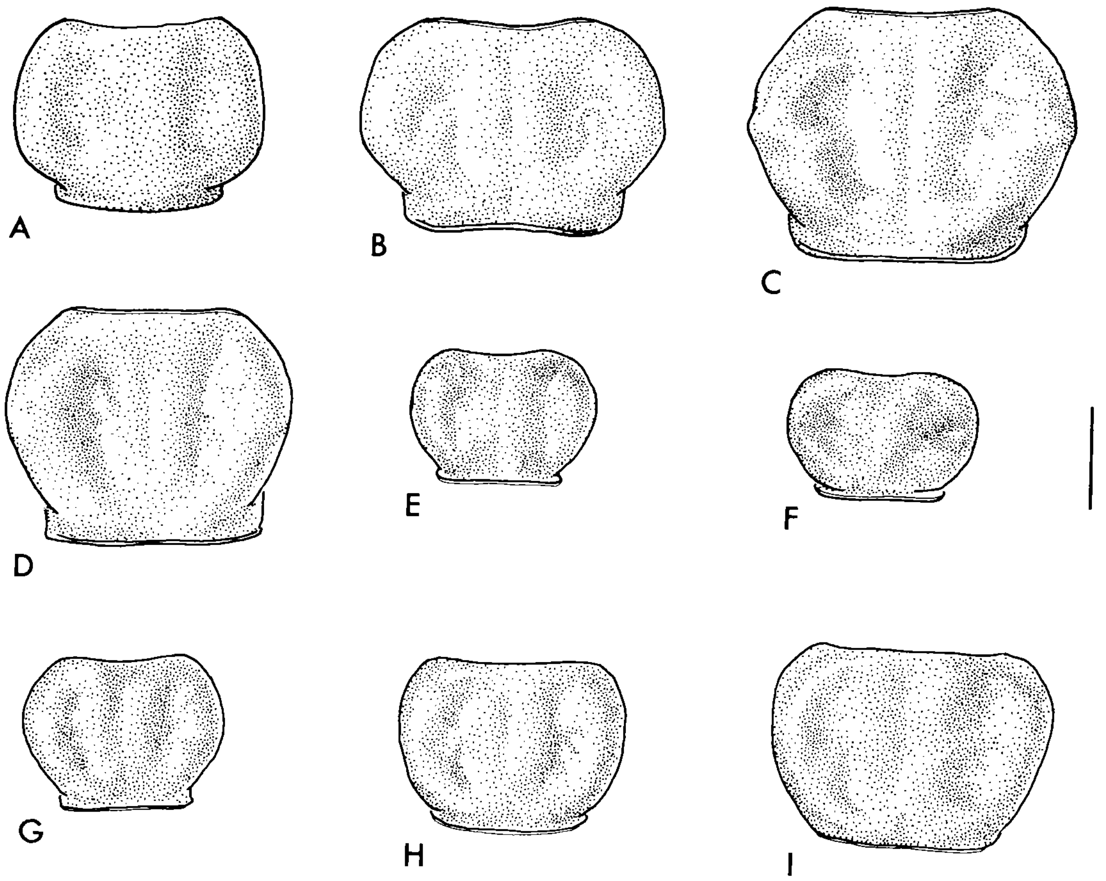


FIG. 2. Pronota of adult stages of species of *Pytho* Latreille: (A) *P. seidlitzi*; (B) *P. strictus*; (C) *P. kolwensis*; (D) *P. nivalis*; (E) *P. niger*; (F) *P. abieticola*; (G) *P. jezoensis*; (H) *P. planus*; (I) *P. depressus* [scale bar = 1 mm].

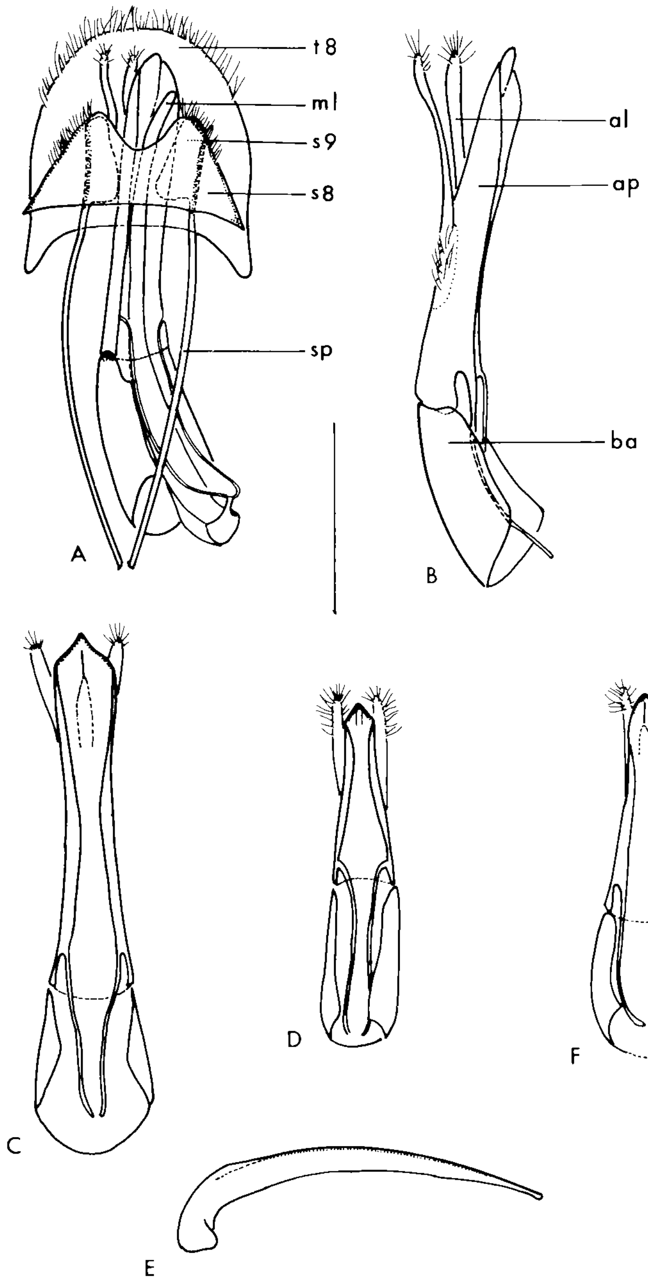


FIG. 3. Male genitalia of selected species of *Pytho* Latreille: (A) *P. seidlitzi*, ventral view of eighth and ninth sternite, eighth tergite, and aedeagus; (B) *P. seidlitzi*, lateral view of aedeagus, median lobe removed; (C) *P. seidlitzi*, ventral view of aedeagus, median lobe removed; (D) *P. planus*, 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; ml = median lobe; sp = spiculum; s8 = eighth sternite; s9 = ninth sternite; t8 = eighth tergite.

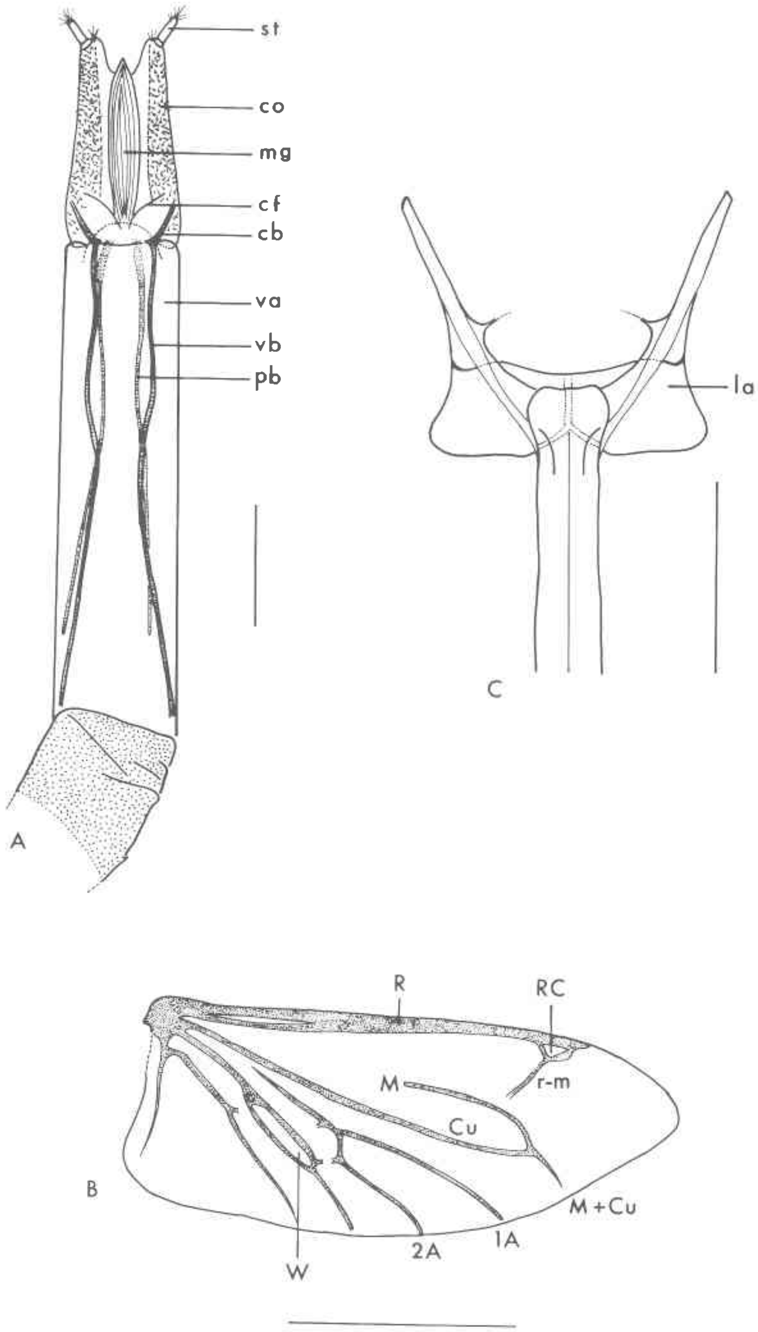


FIG. 4. Female ovipositor, hind wing, and metendosternite of selected species of *Pytho* Latreille: (A) *P. niger*, ventral view of female ovipositor, also showing baculi from dorsal surface [terms from Wheeler (1986)] [scale bar = 0.5 mm]; (B) *P. niger*, venation of right hind wing [scale bar = 5 mm]; (C) *P. seidlitzi*, 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.

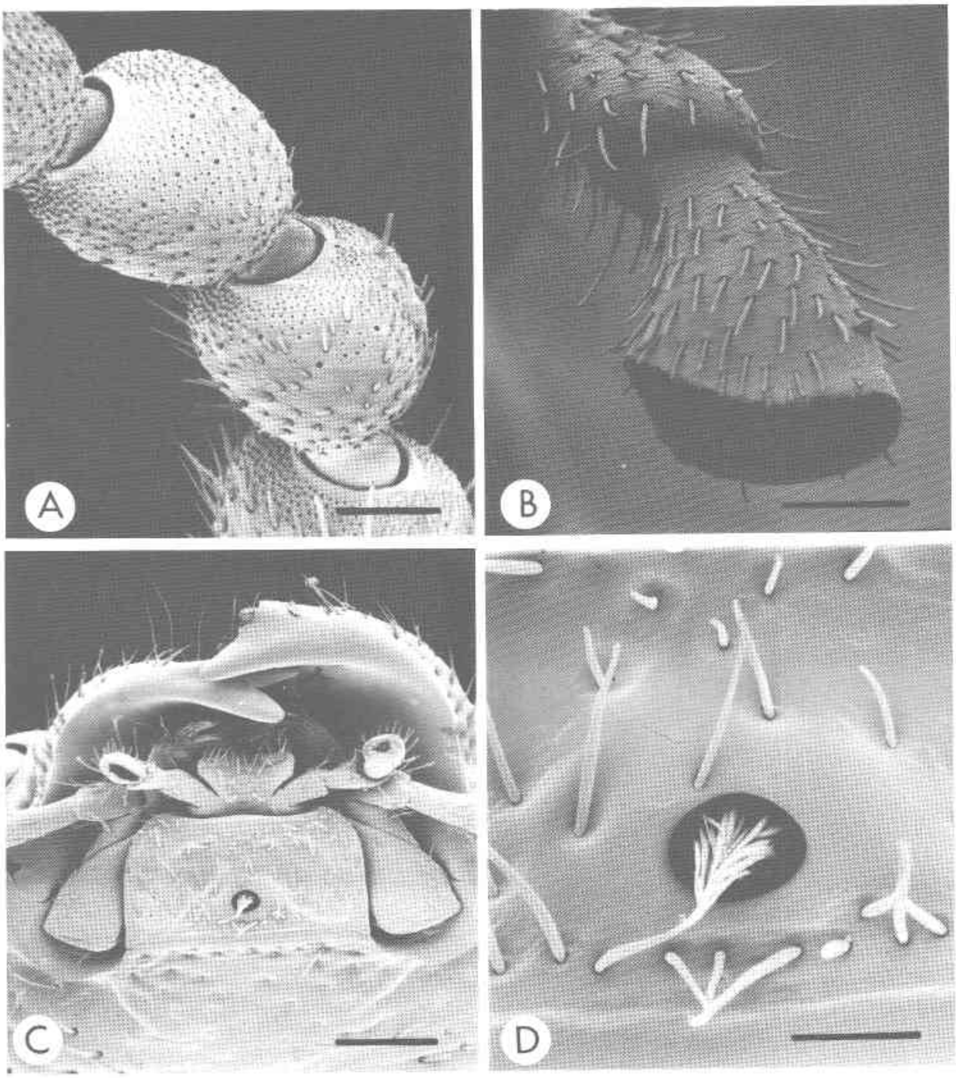


FIG. 5. Scanning electron micrographs of head structures of selected adult stages of *Pytho* Latreille: (A) *P. seidlitzi*, detail of sensilla on apices of antennomeres 8–10 [sensilla have been dislodged during cleaning of the specimen] [scale bar = 0.1 mm]; (B) *P. planus*, apical maxillomere [scale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

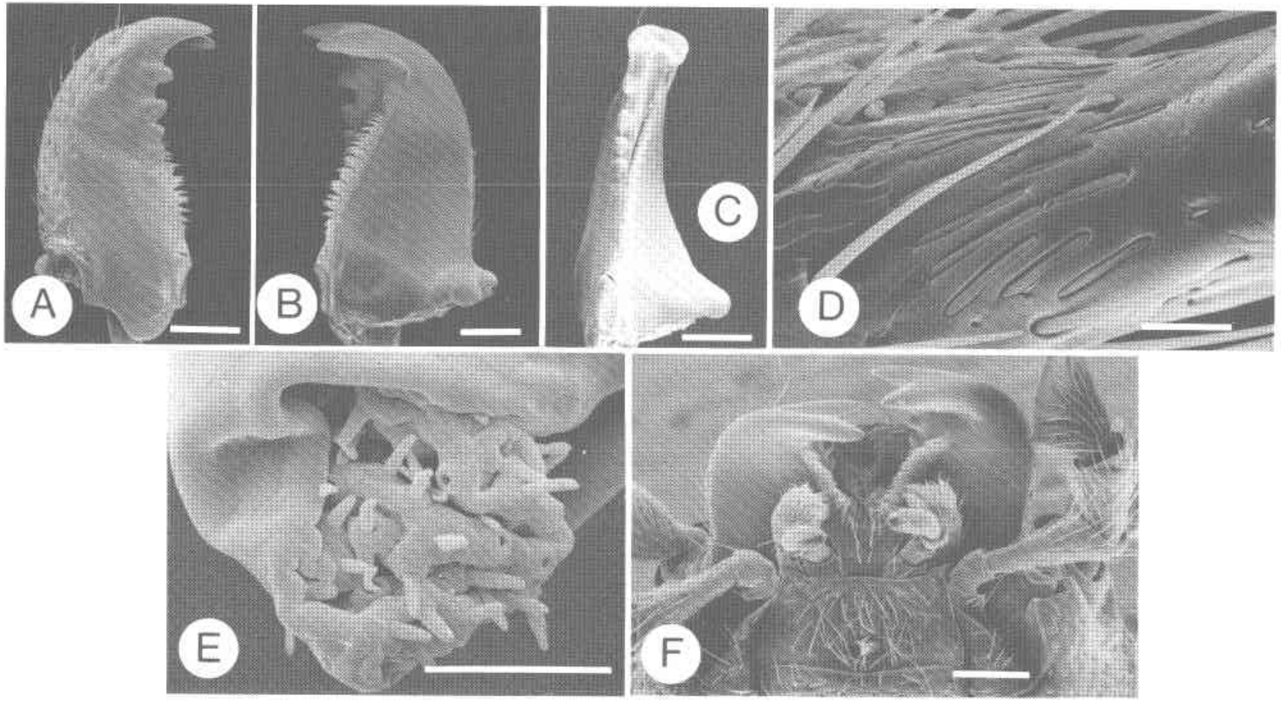


FIG. 6. Scanning electron micrographs of mouthparts of adult *Pytho* Latreille: (A) *P. niger*, left mandible, dorsal view; (B) ditto, ventral view; (C) ditto, occlusal view; (D) *P. seidlitzi*, digitiform sensillae on anterolateral region of apical maxillary palpomere; (E) *P. seidlitzi*, detail of sensillae in apical concavity of apical maxillary palpomere; (F) *P. seidlitzi*, mouthparts, ventral view [scale bar = 0.2 mm, except for D and E, scale bar = 0.02 mm].

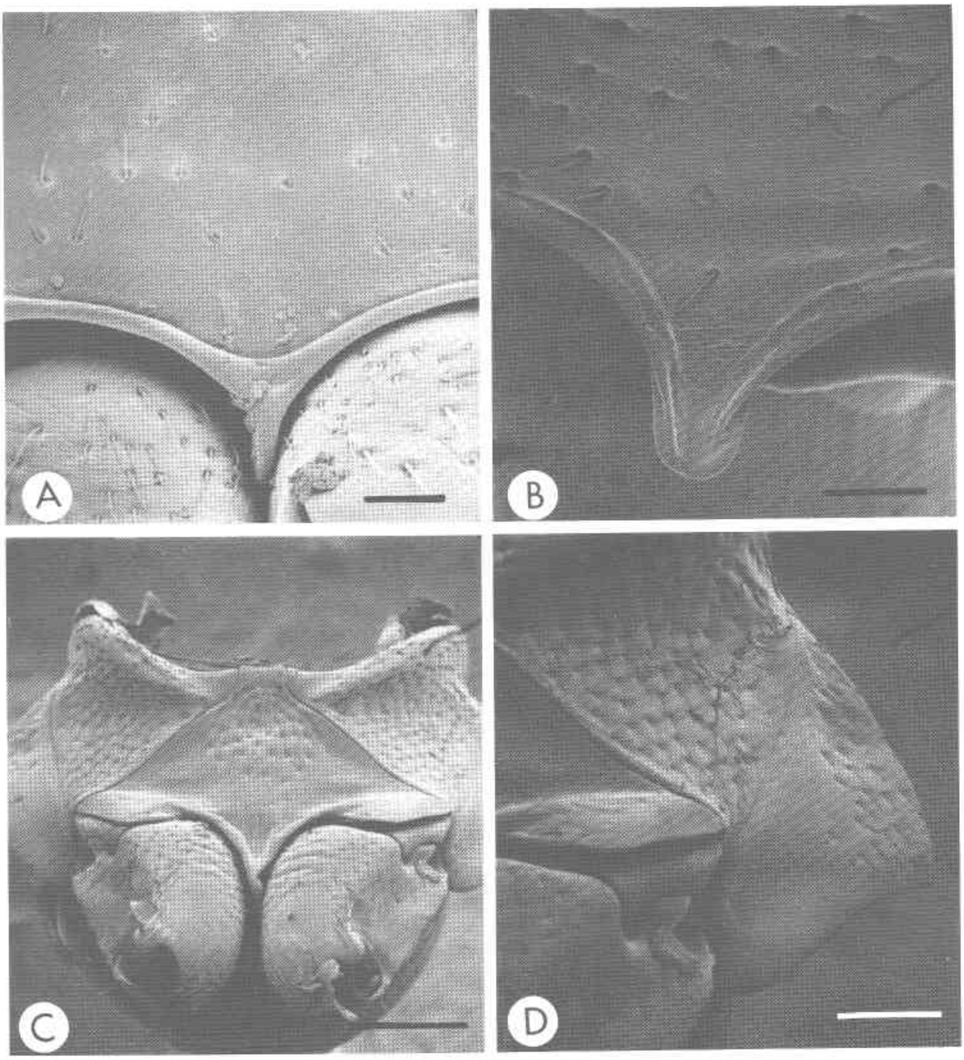


FIG. 7. Scanning electron micrographs of structures on the pro- and mesothorax of selected adult stages of *Pytho* Latreille: (A) *P. niger*, ventral view of prosternal process [scale bar = 0.1 mm]; (B) *P. seidlitzi*, ventral view of prosternal process [scale bar = 0.1 mm]; (C)*P. seidlitzi*, mesosternum [scale bar = 0.4 mm]; (D) *P. seidlitzi*, detail of mesepisternum and mesepimeron [scale bar = 0.2 mm].

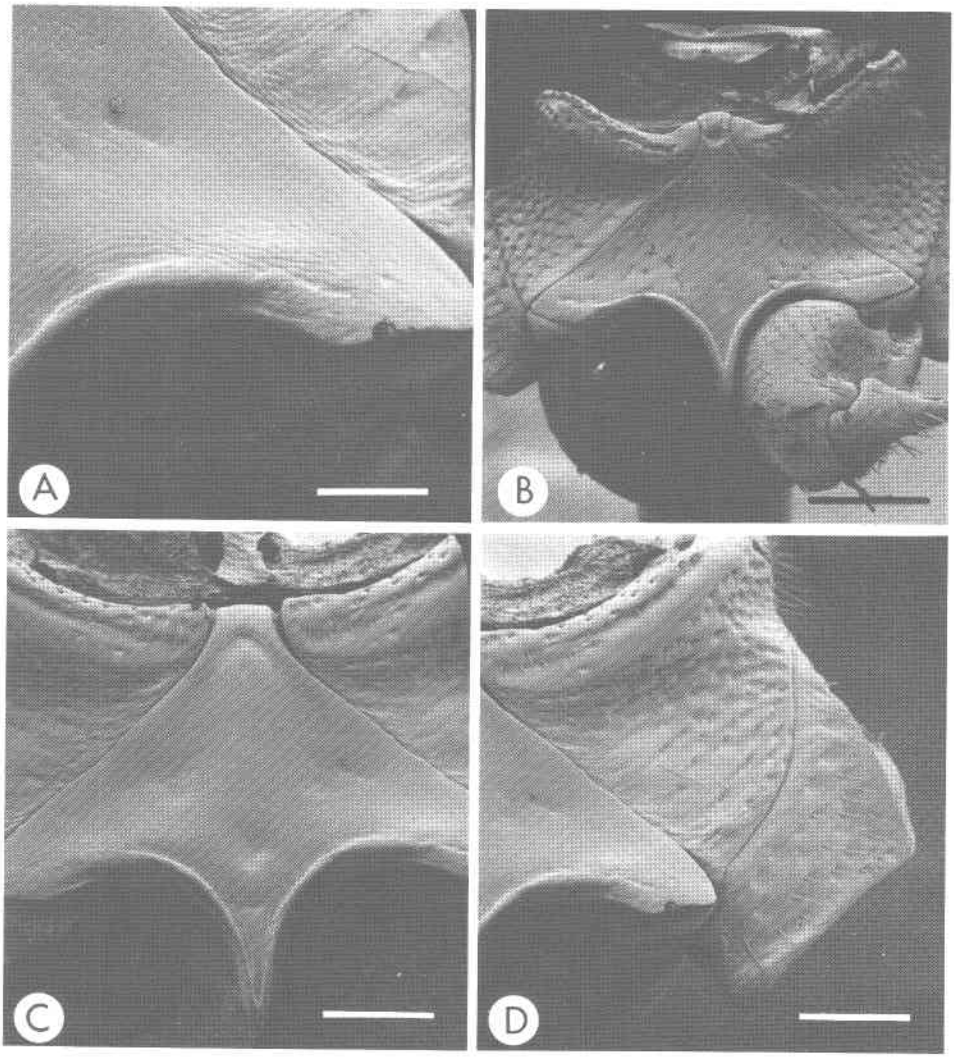


FIG. 8. Scanning electron micrographs of the mesothorax of selected adult stages of *Pytho* Latreille: (A) *P. abieticola*, lateral region of mesosternum [scale bar = 0.1 mm]; (B) *P. niger*, mesosternum [scale bar = 0.4 mm]; (C) *P. abieticola*, mesosternum [scale bar = 0.2 mm]; (D) *P. abieticola*, detail of mesepisternum and mesepimeron [scale bar = 0.2 mm].

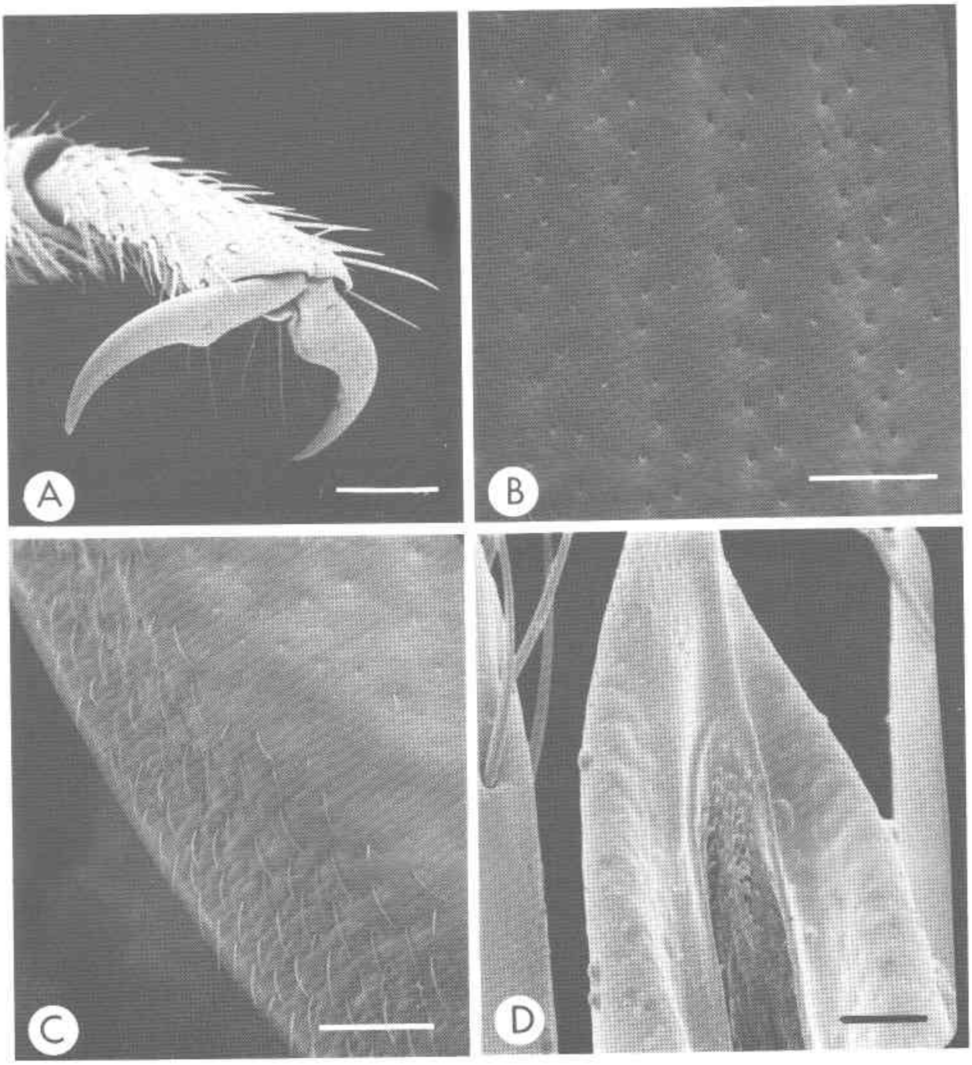


FIG. 9. Scanning electron micrographs of the tarsus, elytron, and aedeagus of selected adult stages of *Pytho* Latreille: (A) *P. niger*, female, oblique lateral view of apical tarsomere [scale bar = 0.1 mm]; (B) *P. seidlitzi*, detail of elytral disc [scale bar = 0.2 mm]; (C) *P. planus*, posterolateral margin of left elytron [scale bar = 0.2 mm]; (D) *P. planus*, male, detail of apicoventral region of apicale [scale bar = 0.05 mm].

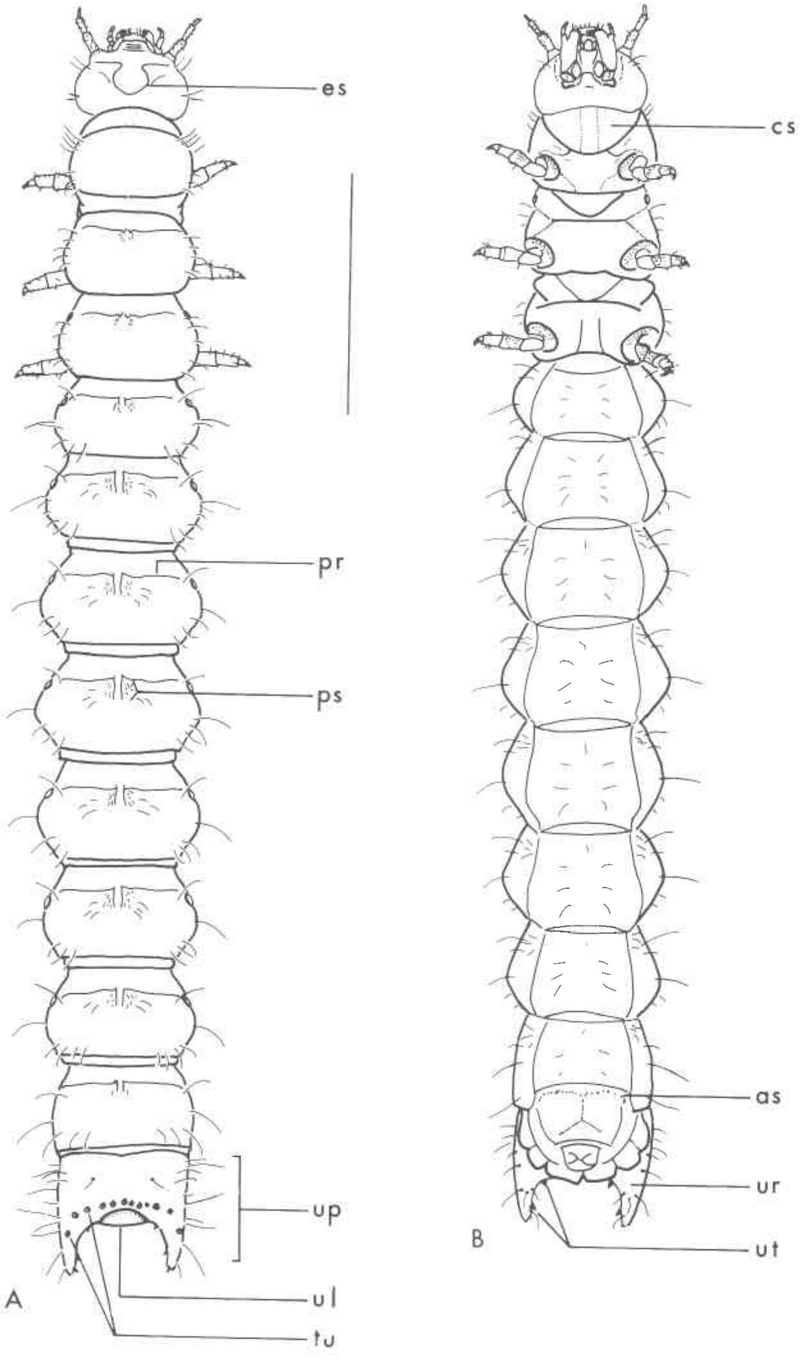


FIG. 10. *Pytho planus*, habitus of larval stage: (A) dorsal habitus; (B) ventral habitus [scale bar = 5 mm]. as = row of asperities; cs = cervicosternum; es = epicranial suture; pr = parabasal ridge; ps = parabasal setae; tu = urogomphal tubercles; ul = urogomphal lip; up = urogomphal plate; ur = urogomphus; ut = urogomphal teeth.

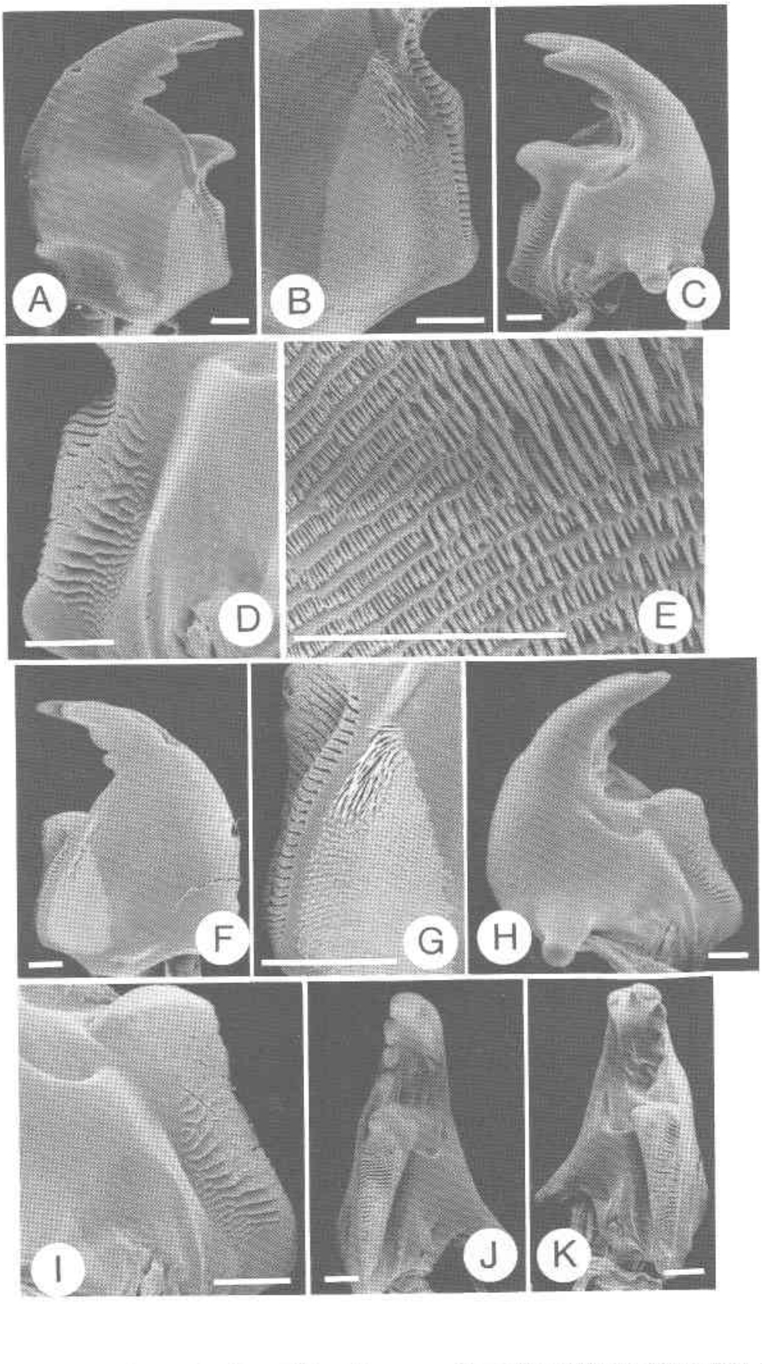


FIG. 11. Scanning electron micrographs of mandibles of larva of *Pytho seidlitzi*: (A) left, dorsal view; (B) left, detail of dorsal molar region; (C) left, ventral view; (D) left, detail of ventral molar region; (E) left, detail of dorsal molar region; (F) right, dorsal view; (G) right, detail of dorsal molar region; (H) right, ventral view; (I) right, detail of ventral molar region; (J) left, occlusal view; (K) right, occlusal view [scale bar = 0.1 mm, except for E, scale bar = 0.05 mm].

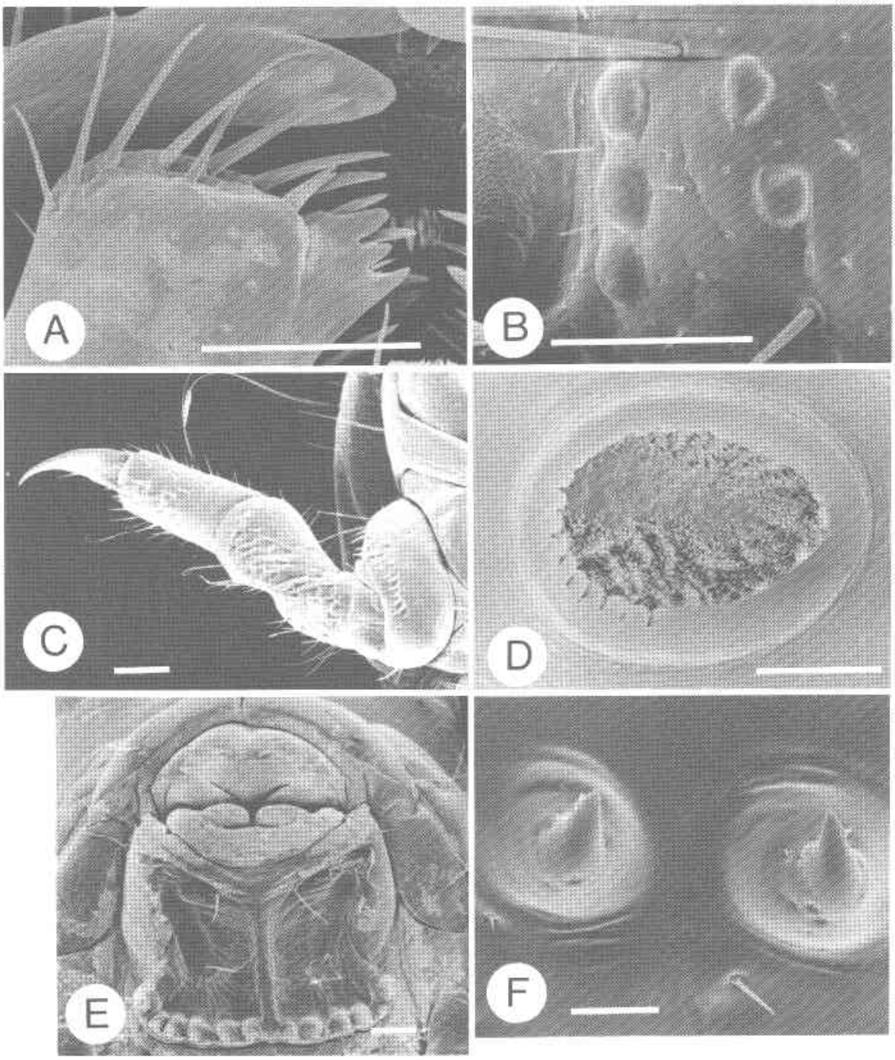


FIG. 12. Scanning electron micrographs of selected features of larva of *Pytho seidlitzi*: (A) distal region of maxillary mala; (B) left stemmata, lateral view; (C) right proleg, ventral view; (D) prothoracic spiracle; (E) abdominal apex, ventral view; (F) detail of urogomphal tubercles [scale bar = 0.2 mm, except for D and F, scale bar = 0.05 mm].

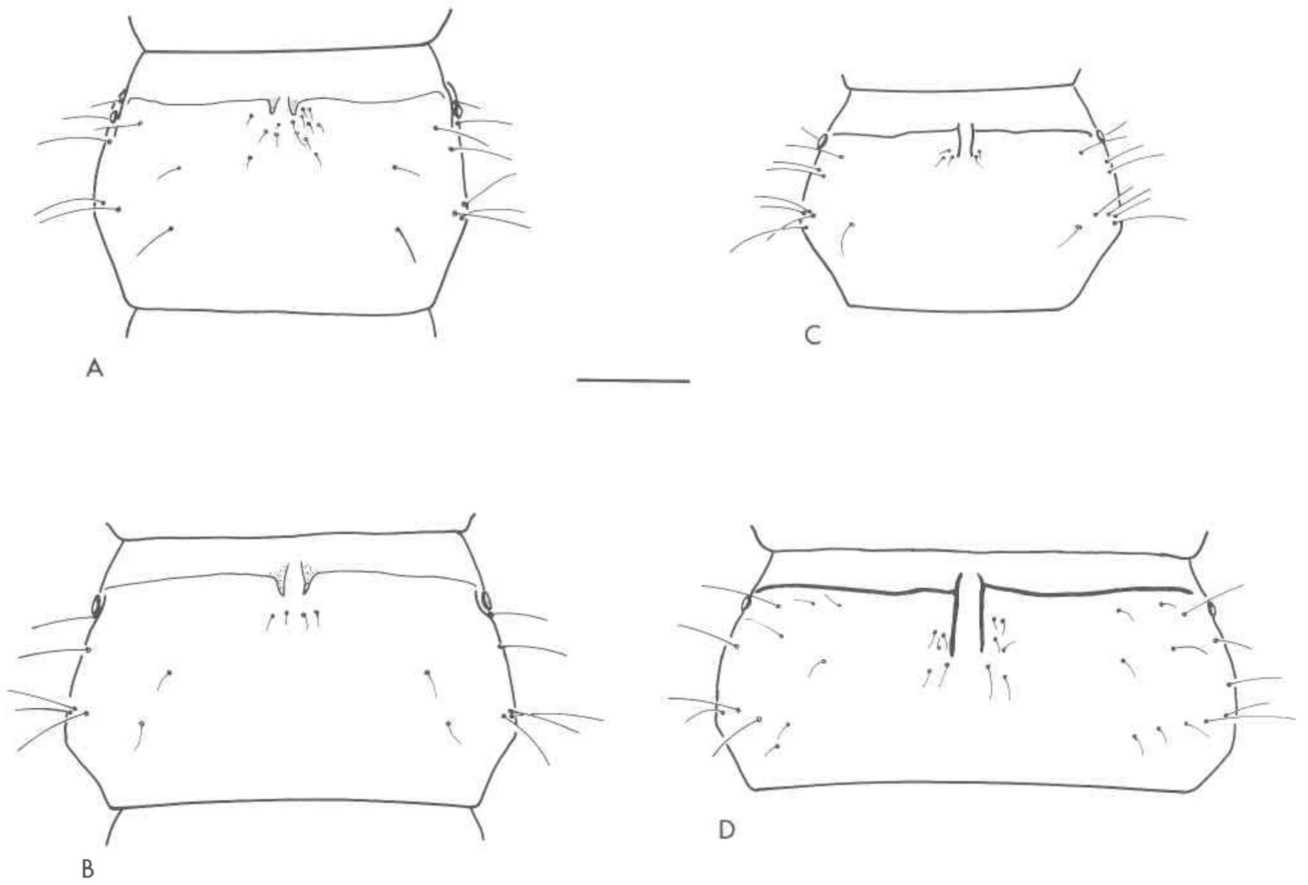


FIG. 13. Third abdominal tergites of representative larval stages of the species-groups of *Pytho* Latreille: (A) *P. seidlitzi* group (*P. seidlitzi*); (B) *P. kolwensis* group (*P. strictus*); (C) *P. niger* group (*P. abieticola*); (D) *P. depressus* group (*P. depressus*) [scale bar = 1 mm].

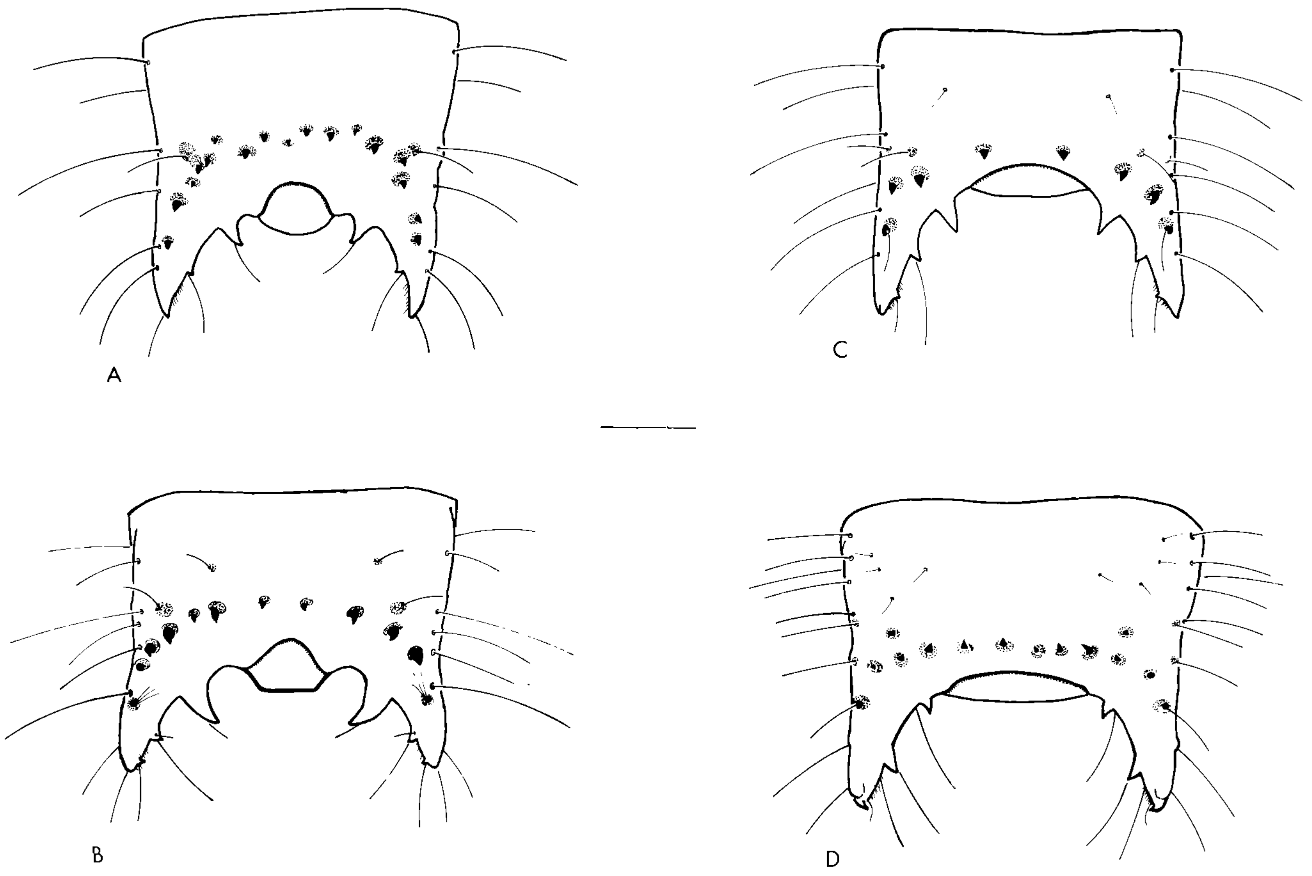


FIG. 14. Urogomphal plates of representative larval stages of the species-groups of *Pytho* Latreille: (A) *P. seidlitzi* group (*P. seidlitzi*); (B) *P. kolwensis* group (*P. kolwensis*); (C) *P. niger* group (*P. niger*); (D) *P. depressus* group (*P. planus*) [scale bar = 1 mm].

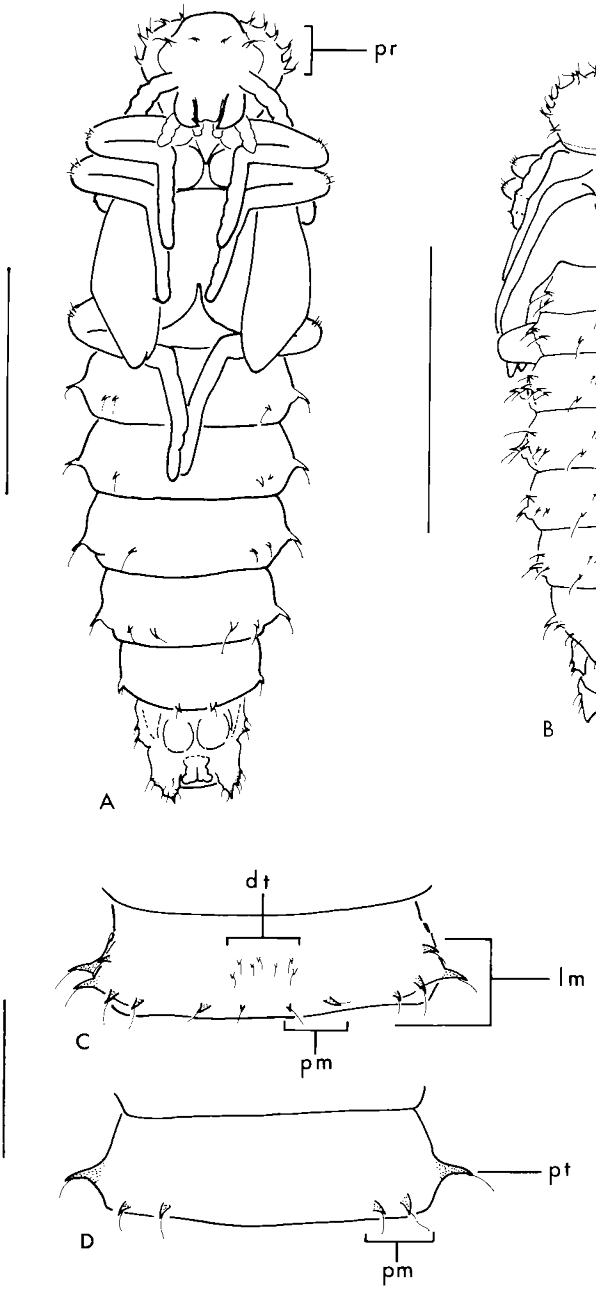


FIG. 15. Dorsal and ventral habitus, and detail of third abdominal tergite and sternite of the pupa of selected species of *Pytho* Latreille: (A) *P. planus*, ventral habitus [scale bar = 5 mm]; (B) *P. abieticola*, dorsal habitus [scale bar = 5 mm]; (C) *P. seidlitzi*, detail of tubercle arrangement on third abdominal tergite (right pleural tubercle has been omitted to show arrangement of lateral marginal tubercles); (D) *P. seidlitzi*, detail of tubercle arrangement on third abdominal sternite [scale bar = 1 mm]. dt = discal tubercles; lm = lateral marginal tubercles; pm = posterior marginal tubercles; pr = pronotal tubercles; pt = pleural tubercle.

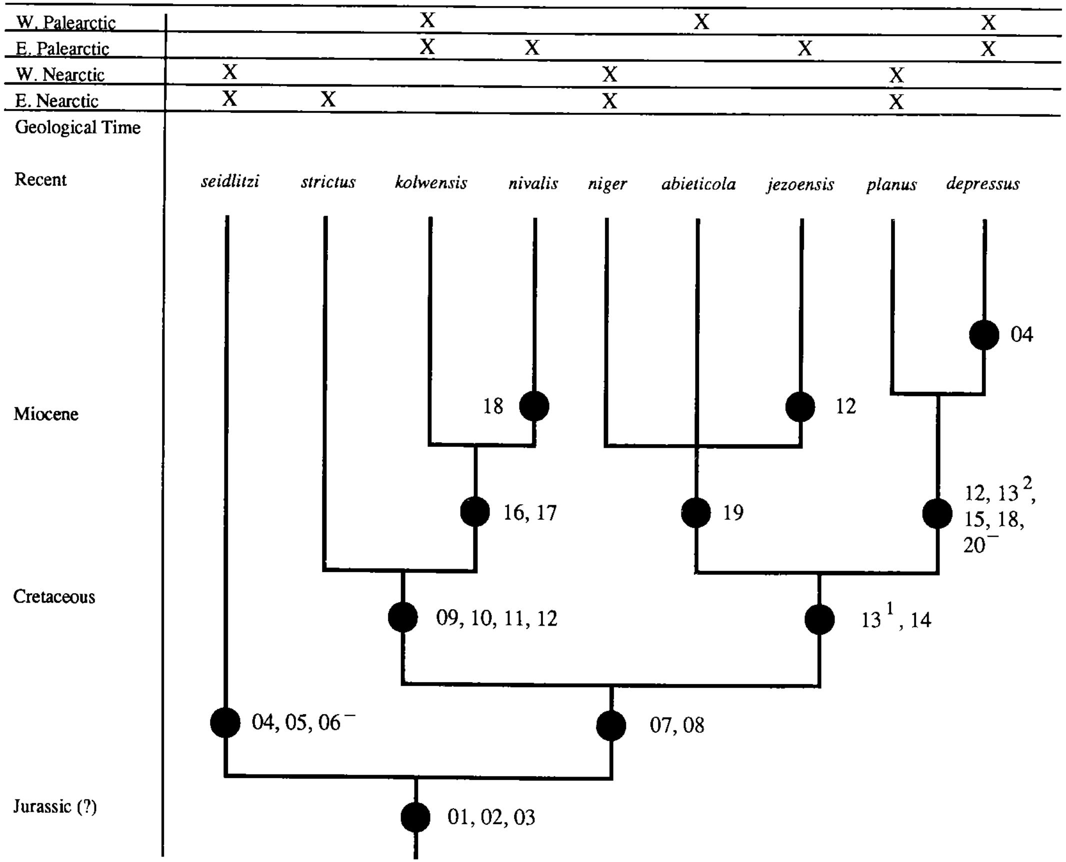
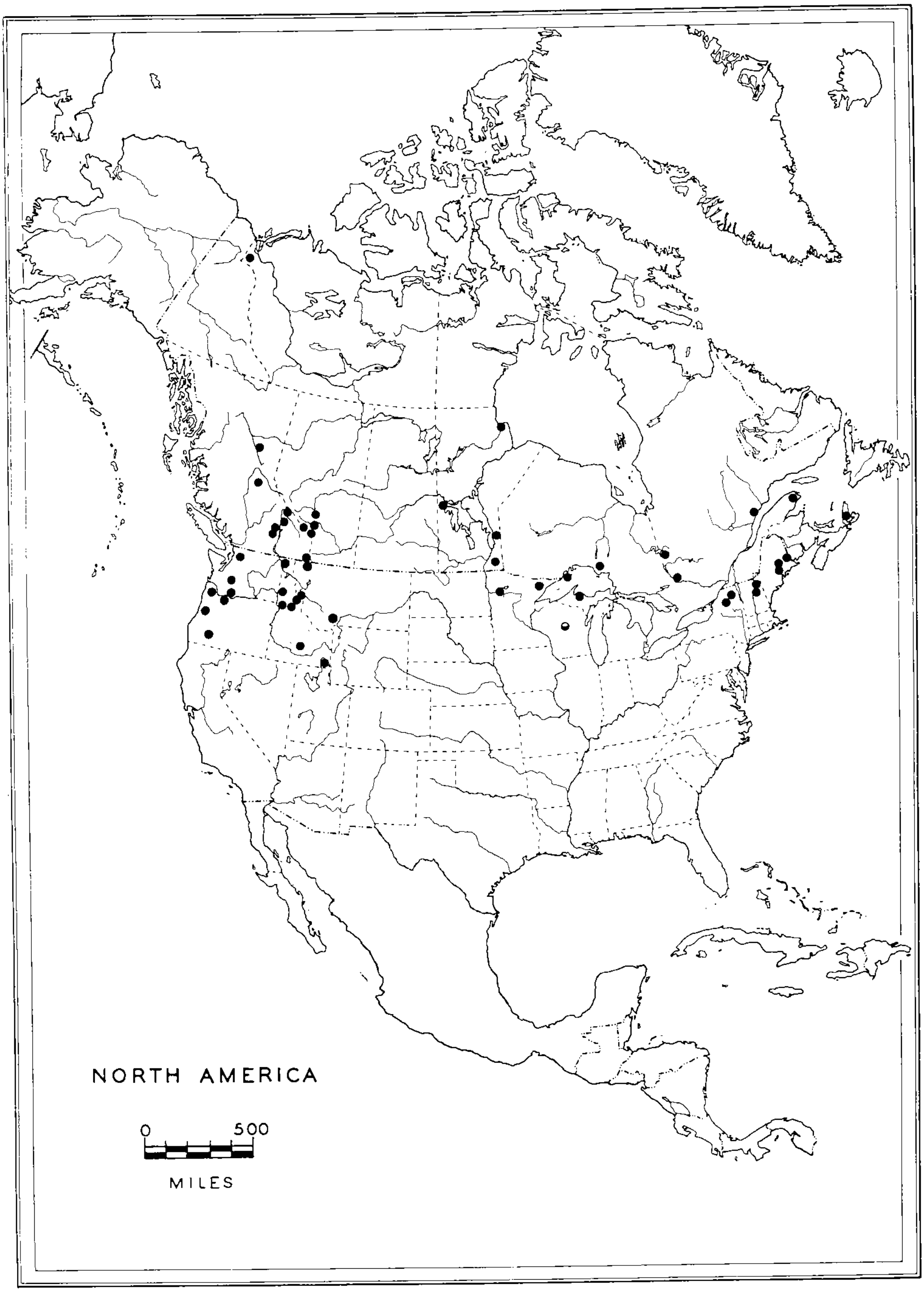
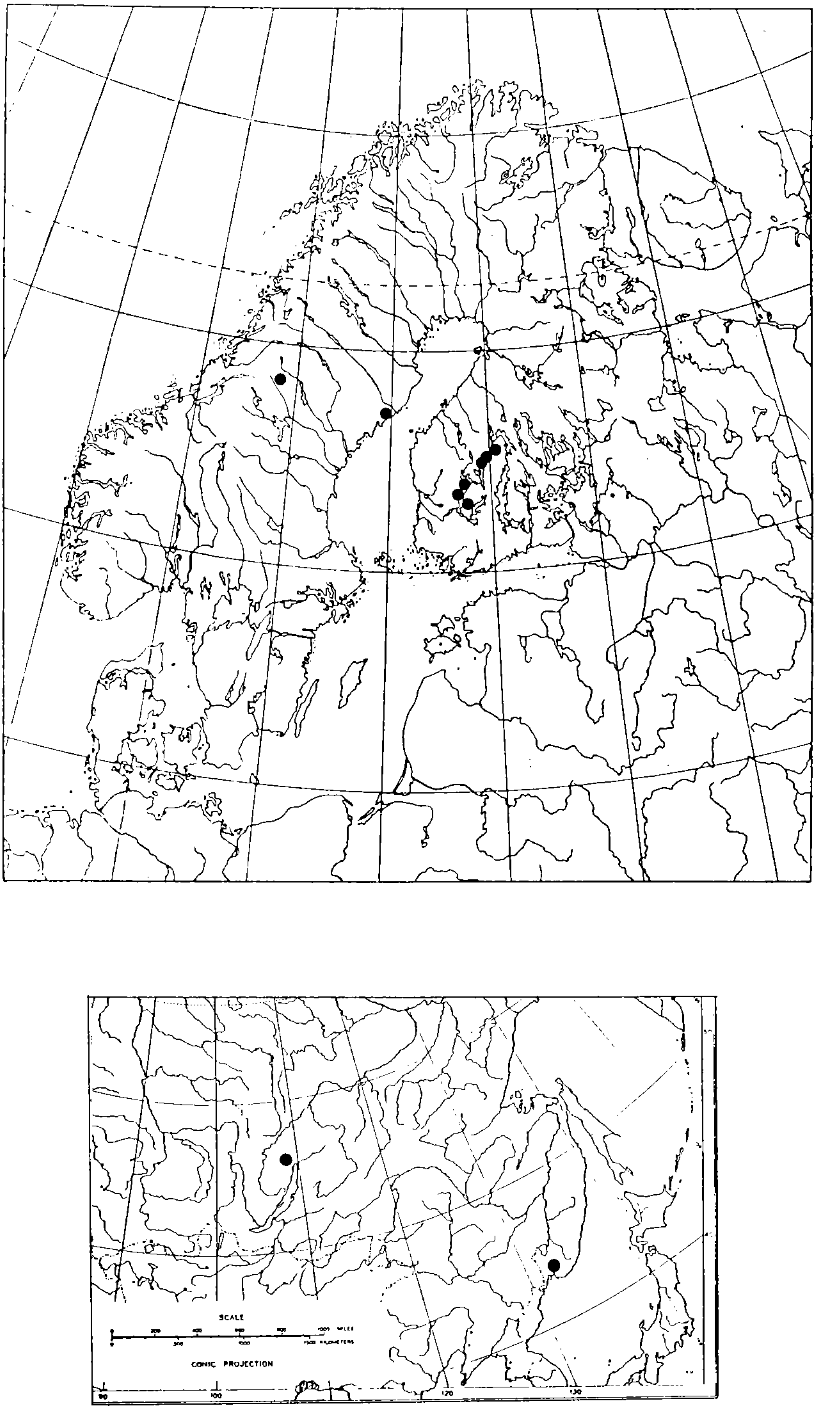


FIG. 16. Cladogram depicting the reconstructed phylogeny of species of the genus *Pytho* Latreille, with associated chorological data and geological time scale. Character states are listed in Tables 3 and 4.

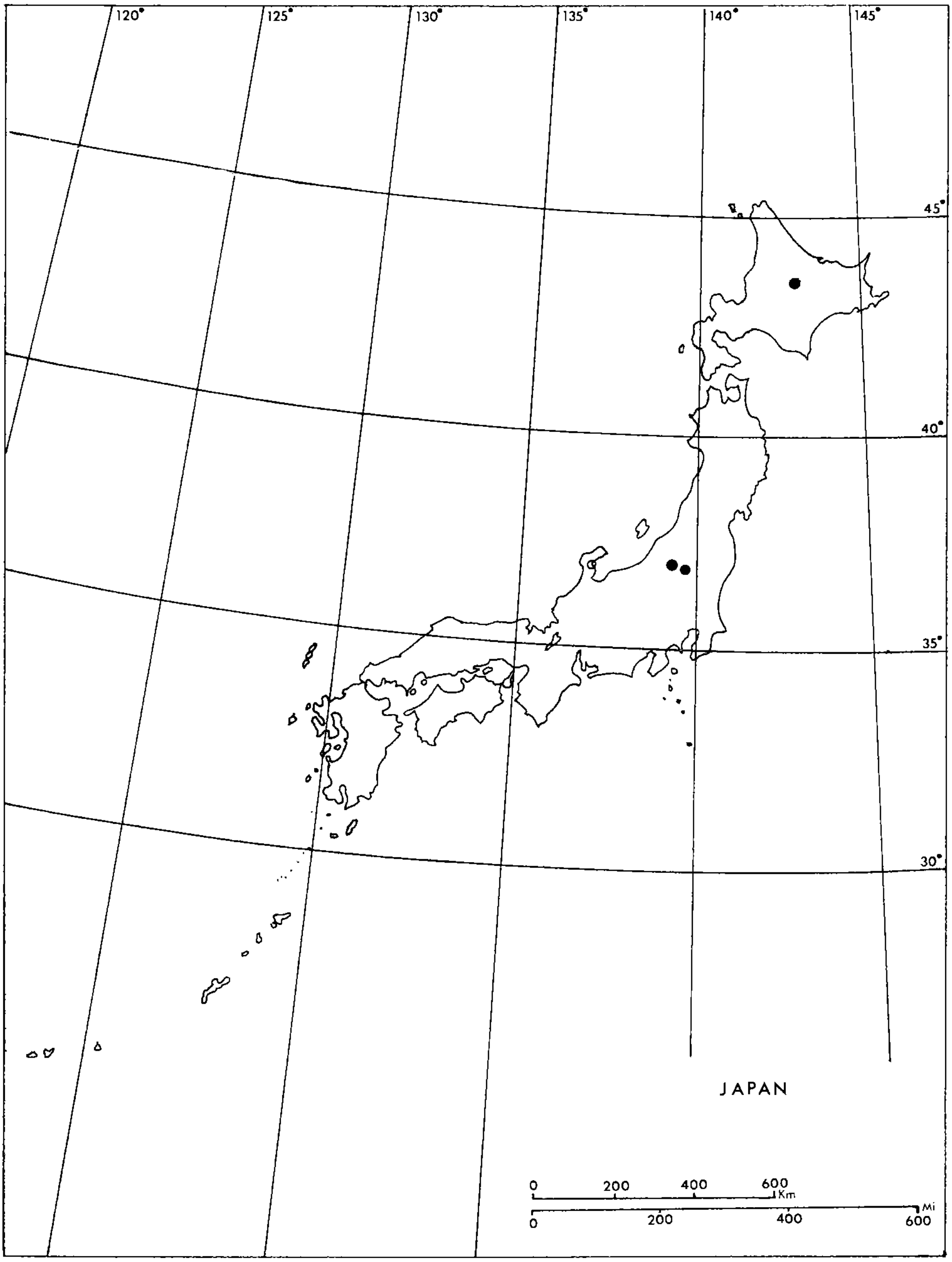


MAP 1. Distribution map derived from examined specimens of *Pytho seidlitzi* Blair. Half-filled circles represent state records only.

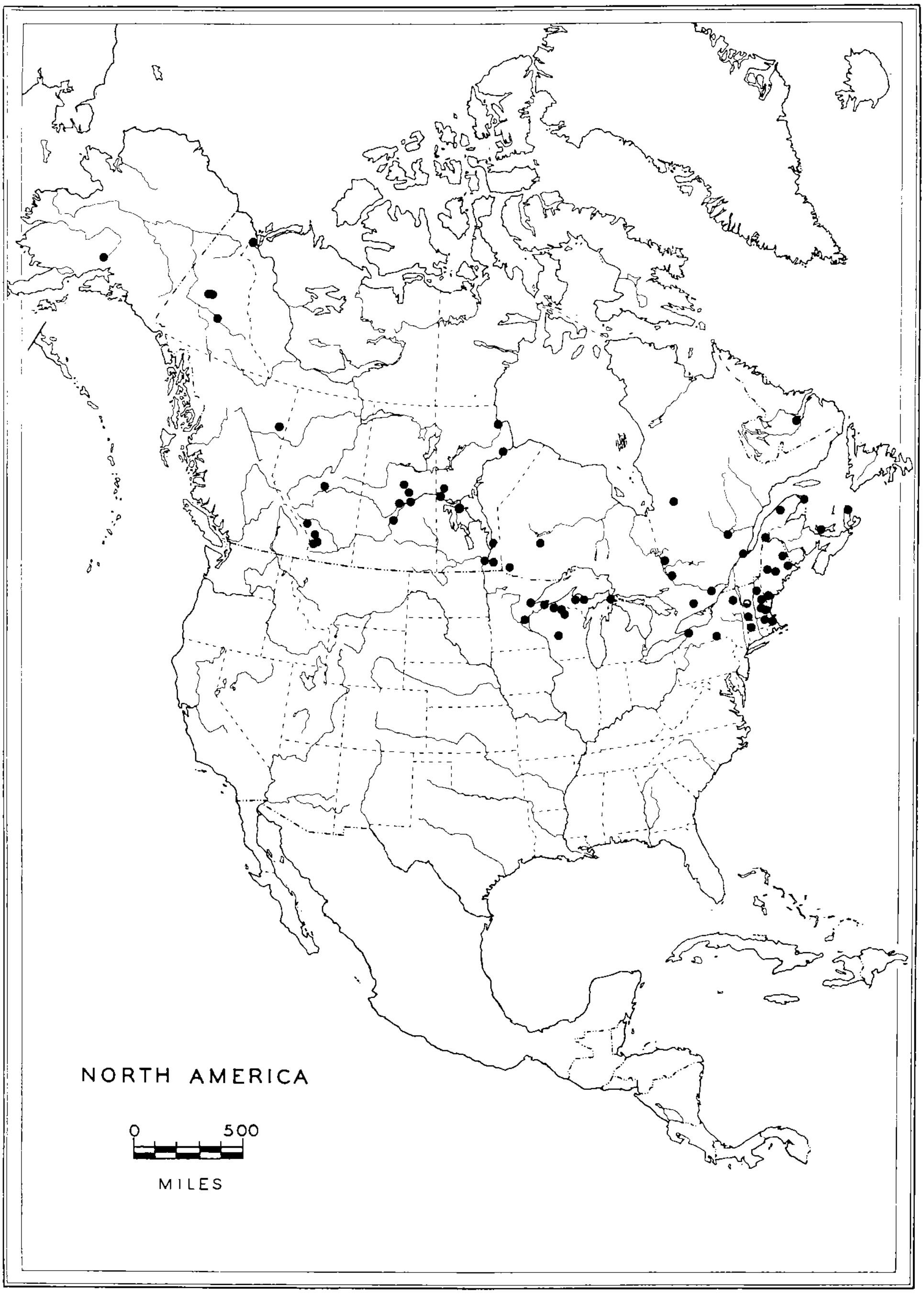
MAP 2. Distribution map derived from examined specimens of *Pytho strictus* LeConte. Half-filled circles represent state records only.



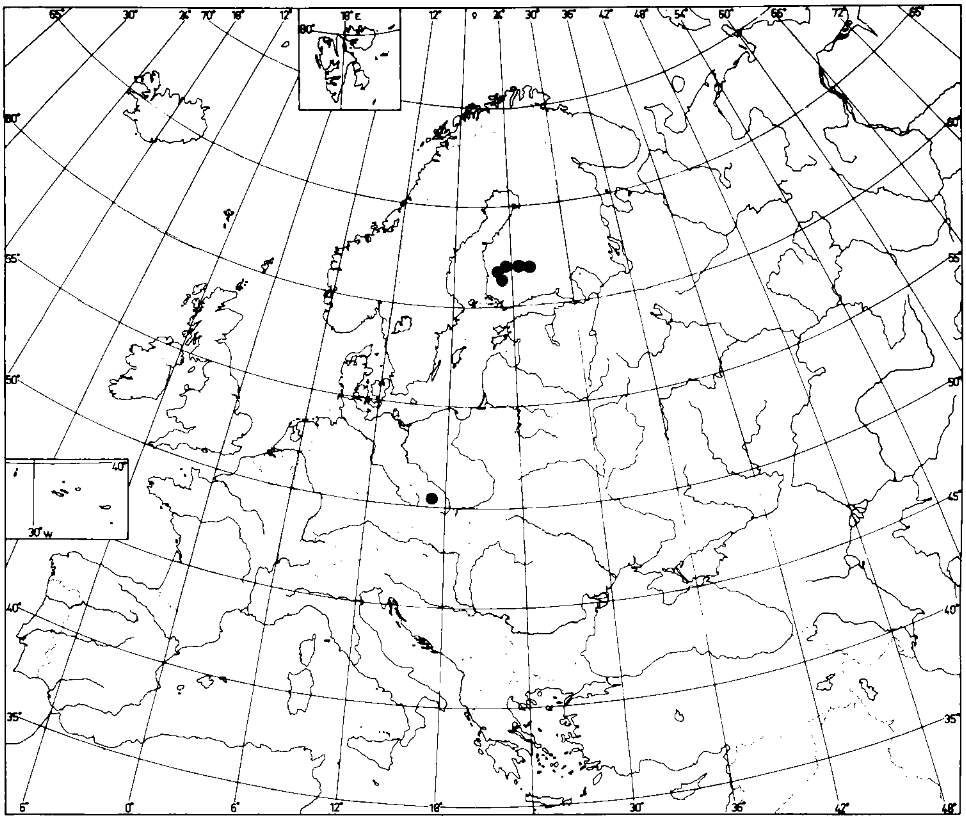
MAP 3. Distribution map derived from examined specimens of *Pytho kolwensis* C. Sahlberg.



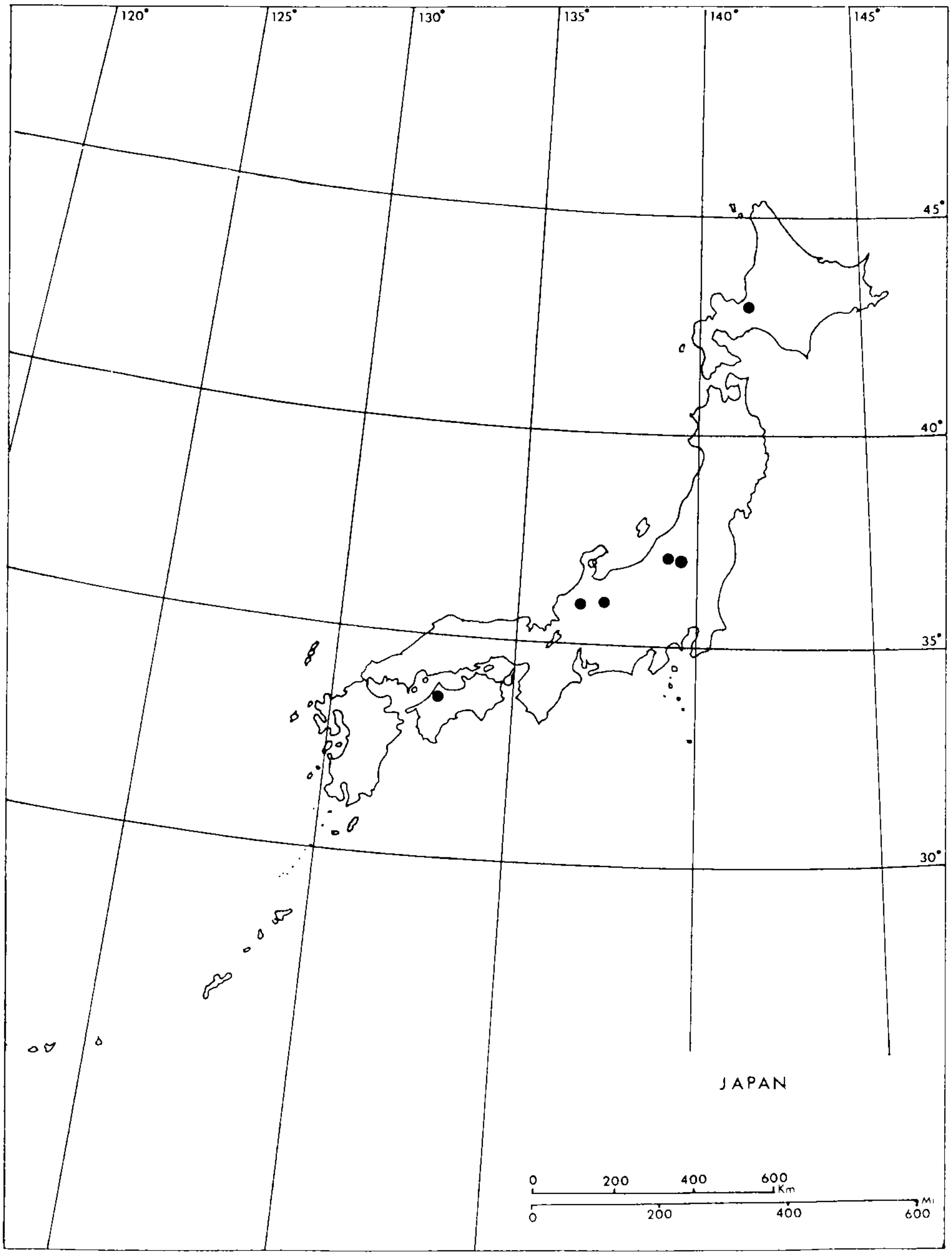
MAP 4. Distribution map derived from examined specimens and literature records of *P. nivalis* Lewis.



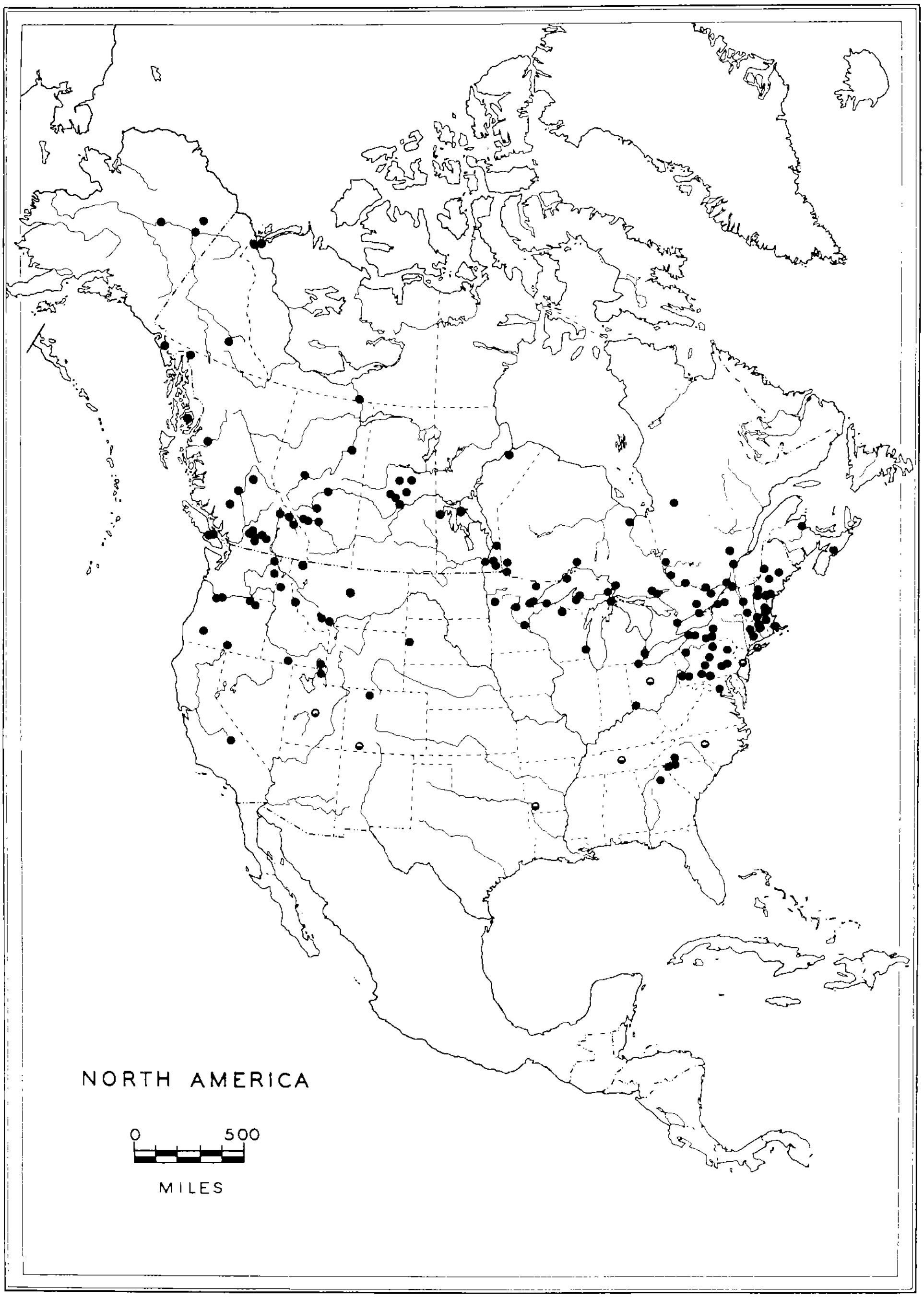
MAP 5. Distribution map derived from examined specimens of *Pytho niger* Kirby. Half-filled circles represent state records only.



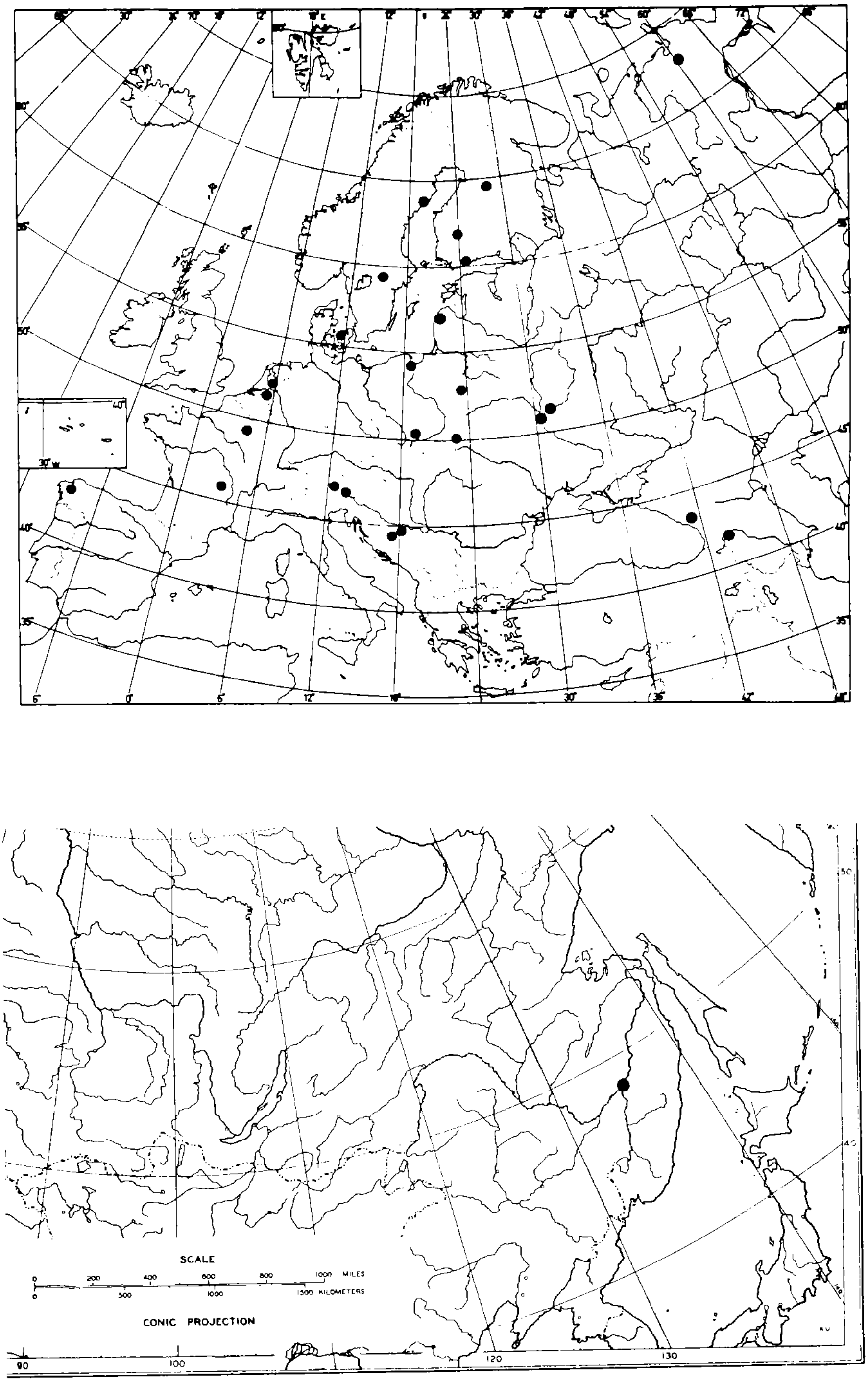
MAP 6. Distribution map derived from examined specimens of *Pytho abieticola* J. Sahlberg.



MAP 7. Distribution map derived from examined specimens and literature records of *P. jezoensis* Kôno.



MAP 8. Distribution map derived from examined specimens of *Pytho planus* (Olivier). Half-filled circles represent state records only.



MAP 9. Distribution map derived from examined specimens of *Pytho depressus* (Linnaeus).