



# On the occurrence of relict populations of *Pytho abieticola* J. R. Sahlberg, 1875 in Switzerland (Coleoptera, Pythidae)

Yannick Chittaro<sup>1</sup>, Andreas Sanchez<sup>1</sup>, Alexander Szallies<sup>2</sup>, Martin M. Gossner<sup>3,4</sup>, Thibault Lachat<sup>3,5</sup>

- 1 info fauna, Avenue de Bellevaux 51, CH-2000 Neuchâtel, Switzerland
- 2 ZHAW Zürcher Hochschule für Angewandte Wissenschaften, Wädenswil, IUNR, Grüenthalstrasse 14, CH-8820 Wädenswil, Switzerland
- 3 Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
- 4 Department of Environmental Systems Science, Institute of Terrestrial Eco-systems, ETH Zurich, Universitätstrasse 16, CH-8006 Zürich, Switzerland
- 5 School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, CH-3052 Zollikofen, Switzerland

https://zoobank.org/5013AEC9-A199-4B40-92D2-909F7F8E5CC6

Corresponding author: Yannick Chittaro (yannick.chittaro@infofauna.ch)

Academic editor: C. Bouget ♦ Received 13 December 2022 ♦ Accepted 7 February 2023 ♦ Published 8 March 2023

## **Abstract**

Several adults and larvae of *Pytho abieticola* were discovered in 2021 and 2022 at three different localities in two regions of Switzerland, the Jura mountains and the Swiss National Park in the Eastern Alps. This very rare saproxylic beetle has not been detected in Switzerland so far. Considered a relict of primeval forests, it is in strong decline or has already disappeared from large areas of Central Europe. The isolated Swiss populations are the westernmost in its distributional range. Information on the ecology and distribution of *P. abieticola* in Switzerland and Europe is provided and criteria to distinguish *P. abieticola* from the congeneric and syntopic *P. depressus* are defined.

# Key Words

log, conifer, subcortical, deadwood, faunistics, new record, distribution

# Introduction

Within the family Pythidae, the genus *Pytho* Latreille, 1796 includes ten species, six of which are found in the Palaearctic region (Háva and Zahradník 2021). All species of the genus are saproxylic, with larvae and adults living under the bark of dead conifers (Pollock 1991). Three of them occur in Europe: *Pytho depressus* (Linnaeus, 1767), which is fairly widespread, and the rare *P. abieticola* J. R. Sahlberg, 1875 and *P. kolwensis* C. R. Sahlberg, 1833, which mainly occur in Fennoscandia and Russia (Pollock 2008, 2020). In Central Europe, *P. abieticola* is only represented by very isolated populations. Its sharp decline, relict distribution, and specific ecological requirements justify its presence on the list of primeval forest relict species of Central Europe in category 1, which includes species restricted to a few remnants of natural forests (Eckelt et al. 2017).

In Switzerland, only *P. depressus* was known until now (Chittaro and Sanchez 2016). However, in 2021 and 2022, several specimens of *P. abieticola* were found at different localities. These first Swiss data are presented here and the situation of the species in Europe is discussed. Furthermore, information on its ecology and identification criteria are provided.

# Materials and methods

In 2021 and 2022, the authors carried out different independent inventories of saproxylic beetles at three localities in Switzerland (the precise locations of these sensitive sites are not provided here, but the data have been deposited in the national database info fauna, www.infofauna.ch).

#### Ponts-de-Martel Valley

This site is located in the Ponts-de-Martel Valley in the canton of Neuchâtel, in the heart of the Jura mountains. It is a peat bog of national importance, located about 1000 m above sea level. Scattered stands of birch (Betula pendula Roth, B. pubescens Ehrh., B. nana L.) are present (Fig. 1A) but the site also includes denser forest areas consisting largely of Swiss mountain pine (Pinus mugo uncinata (DC.) Domin), and spruce (Picea abies (L.) H. Karst.) (Fig. 1B). These coniferous forests have existed for a long time: they were already marked on the first edition of the Siegfried National Map published in 1886 (Federal Office of Topography swisstopo; Journey through time – Topographic maps) and possibly also on the Dufour map of 1849 (but the symbolism used at that time was not always clear).

Between April and September 2022, ten "Polytrap" flight interception traps (Brustel 2012) were placed in different forest associations (according to Richard 1961), in particular in *Pino mugo-sphagnetum* (climax forest association of the peat bogs) and in *Sphagno-piceetum betuletosum* (sphagnum-rich waterlogged spruce forests, typical of undisturbed peat bog belts).

# Saignelégier region

This site is located in the region of Saignelégier in the canton of Jura, about 40 km from the Ponts-de-Martel Valley. It is also a peat bog of national importance. Situated at about 1000 m a.s.l., its vegetation is identical to that of the first site (Fig. 2) and also shows significant temporal continuity. This site was studied precisely because it was very similar to the first one, which had proved to be of great faunistic interest. Here, research was conducted for only one day in the fall. Larvae and adults in pupal cells of *Pytho* species were searched for under the bark of spruce (Fig. 2) and Swiss mountain pine logs.

#### Swiss National Park

The third record site is the Swiss National Park in the eastern Alps of Switzerland, a high-altitude region near the borders with Austria and Italy. The Swiss National Park is a strict nature reserve left to its own natural development (no habitat management since 1914 (Parolini 2012)). One third of its 170 km² area is forested (Baur and Scheurer 2014). The higher elevations and southern slopes are dominated by Swiss mountain pine, interspersed with Arolla pine (*Pinus cembra* L.), while in the lower and northern exposed parts spruce, Scots pine (*Pinus sylvestris* L.) and European larch (*Larix decidua* Mill.) are the main forest-forming trees.

Sampling sites investigated with "Polytrap" flight interception traps were established in various regions of

the national park in 2021 and 2022, e.g. at Plan Praspöl (1650 m a.s.l., Fig. 3, from May to August 2021) and in various mountain spruce sites such as Stabelchod (1900 m a.s.l., from May to August 2021 and 2022). Several days each year were also spent actively searching for individuals to supplement the list of species obtained by trapping.

# Results

A total of 29 adults and several dozen larvae of *Pytho abieticola* (Figs 5, 7) were found in 2021 and 2022 at the three sampled localities. The species is new to the Swiss fauna.

# Ponts-de-Martel Valley

SWITZERLAND • 3  $\circlearrowleft$ , Neuchâtel, Ponts-de-Martel Valley, 1000 m a.s.l, 29 Apr.–23 May 2022 (2  $\circlearrowleft$ ) and 23 May–22 Jun. 2022 (1  $\circlearrowleft$ ), Chittaro Y. leg., flight interception traps, Chittaro Y. coll.

These specimens were intercepted at three trap sites about 50 m apart in the *Sphagno-piceetum betuletosum* forest association. The traps were placed near trunks of cut Swiss mountain pine and spruce that had been felled in previous years (to limit public access to this site) and placed on the ground. The traps were hung directly on spruce trees, including one on a dead standing tree.

Further searches in the summer and autumn in the immediate vicinity of the traps where adults had been captured revealed several dozen larvae as well as about ten adults of the congeneric *P. depressus* in pupal cells under the bark of pine and spruce logs on the ground, but no other pre-imaginal stages (larvae and pupae) or adults of *P. abieticola* were found.

#### Saignelégier region

SWITZERLAND • 1  $\circlearrowleft$ , 1  $\circlearrowleft$ , Jura, Saignelégier region, 970 m a.s.l., 20 Oct. 2022, Sanchez A. and Chittaro Y. leg. and coll., under decayed bark of a spruce trunk.

Both specimens were found in a small spruce forest at the edge of a peat bog (Sphagno-piceetum betuletosum forest association). They were in pupal cells under the bark of a spruce trunk of about 30 cm diameter, cut in previous years along a forest path and partially lying above the ground, supported by its branches. The bark was missing for about one half of the length of the trunk (Figs 2, 4). The remaining bark could be easily detached by hand. Eight specimens of P. depressus were also found under the same bark (Fig. 4), as well as several specimens of Ips typographus (Linnaeus, 1758) (Curculionidae), Rhagium inquisitor (Linnaeus, 1758) (Cerambycidae) and Rhizophagus dispar (Paykull, 1800) (Monotomidae).



**Figure 1.** General views of the study site of the Ponts-de-Martel Valley. **A.** Deciduous forest clusters, mainly composed of birch; **B.** Denser forest areas composed of Swiss mountain pine and spruce. (Photos: A. Sanchez).



Figure 2. General view of the study site in the region of Saignelégier. (Photo: A. Sanchez).

# Swiss National Park.

SWITZERLAND, Grisons, Swiss National Park • 8  $\circlearrowleft$ , 6  $\circlearrowleft$ , Plan Praspöl, 1680 m a.s.l., 2–23 Jun. 2021, WSL leg., flight interception traps • 1  $\circlearrowleft$ , 1  $\hookrightarrow$ , Stabelchod, 1900 m a.s.l., 28 May–17 Jun. 2021 (1  $\circlearrowleft$ ), 17 Jun.–7 Jul. 2021 (1  $\hookrightarrow$ ), Abenis AG leg., flight interception traps • 1  $\circlearrowleft$ , 1  $\hookrightarrow$ , several larvae, Laj dad Ova Spin, southeastern

end, 1670 m a.s.l., 18 May 2022, Szallies A. leg., under decayed bark of Swiss mountain pine • 5 ♂, 1 ♀, several larvae, Plan Praspöl, slope towards Laj dad Ova Spin, 1670 m a.s.l., 12 Oct. 2022, Szallies A. leg., under decayed bark of three different spruce trees of about 25 cm diameter. Voucher specimen will be deposited in the collections of A. Szallies, the Bündner Naturmuseum Chur and the Naturhistorisches Museum Basel.



Figure 3. General view of the study site in Plan Praspöl. (Photo: B. Wermelinger).



**Figure 4. A.** Spruce trunk in the Saignelégier region where adults of *P. abieticola* and *P. depressus* were found under the bark; **B.** A close-up to show the appearance under the bark. (Photos: A. Sanchez).

At Plan Praspöl, the specimens were sampled in 5 of 11 installed polytraps running from May to August 2021. Four of these 5 traps were installed at sites with high amount of lying and standing dead wood (Fig. 3). At Stabelchod, a Swiss mountain pine forest with a southern exposure, no additional specimens were found, despite an intensive active search, and it is likely that the trapped specimens originated in the wetter neighbouring forests.

The four trees with larvae of *P. abieticola* (three spruce and one Swiss mountain pine) were lying horizontally just above ground in a very humid and moist environment on the steep slope to the Spöl stream near Laj dad Ova Spin. The bark was heavily infested with fungi and no other beetle species were present. In the areas above the wet steep Spöl slope, only *P. depressus* was found, which apparently lives in drier habitats with fewer fungi.

#### Discussion

# Diagnosis

Identification keys for adults of *Pytho* species were proposed by Kaszab (1969), Burakowski (1976), Iablokoff-Khnzorian (1985), Pollock (1991) and Háva

and Zahradník (2021). *Pytho abieticola* differs from *P. depressus* on the basis of several characters, the most relevant of which are listed below:

Identification keys of larvae are provided by Burakowski (1976), Iablokoff-Khnzorian (1985) and Pollock (1991). These are modified below to discriminate *P. abieticola* larvae from those of *P. depressus*. Additional criteria were provided by Siitonen J. (pers. comm.).

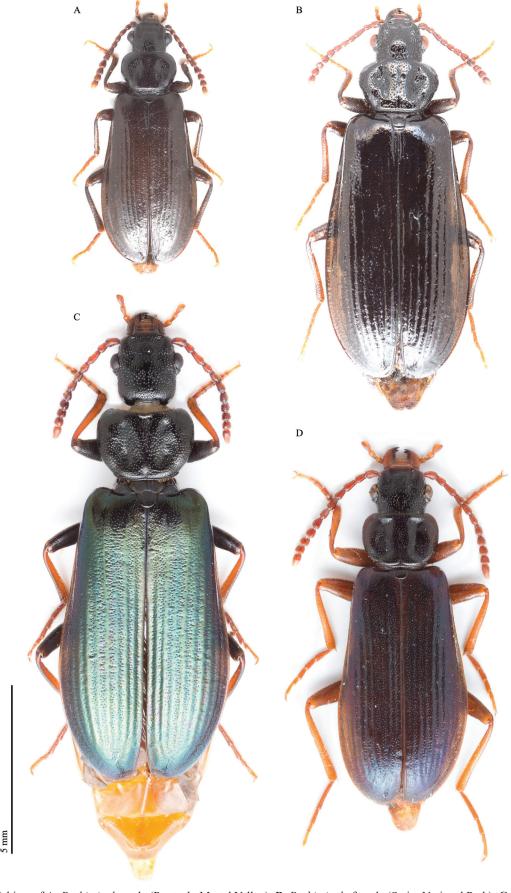
#### Distribution and status

To place our records in a broader geographical context, we sought as much data as possible. Data published on GBIF.org (2022), which are very complete for Fennoscandia and Austria, were used as a basis. Additionally, we searched for further data from various Central European publications. Other data certainly exist in museums or in scattered publications, but the map below (Fig. 8) gives a good overview of the general distribution of P. abieticola in Europe. Although data for the Eastern Palaearctic region is scarce, the species appears to be widespread in Russia, from Karelia (Painter et al. 2007; Laaksonen et al. 2008) to Yakutia (now Republic of Sakha) (Iablokoff-Khnzorian 1985). A few localities were mentioned, for example, in Sergeeva and Stolbov (2020) and Yuferev (1986). Pytho abieticola also occurs in northern China (Painter et al. 2007).

In the Fennoscandinavian countries, the species is widespread in Sweden (SLU Artdatabanken 2022) and Finland (Rassi et al. 2015, and laji.fi), while it is rare in Norway, where its distribution is restricted to the easternmost part near the Swedish border.

In the Baltic States, its presence was recently confirmed in Estonia using flight interception traps in old-growth forests (Roosileht U., pers. comm.; unpublished data). The species is not known in Latvia or Lithuania and its occurrence is considered unlikely (Telnov D., pers. comm.).

In Central Europe, the species has a relict distribution in isolated populations, often occurring in mountains (Iablokoff-Khnzorian 1985). In Poland, Kubisz et al. (2014) give a few localities and state that it is a rare species with a scattered distribution, a situation identical to that in the Czech Republic (Horion 1956; Heyrovský 1960; Streček 1988; Vávra and Stanovský 2013; Horák 2017). In Slovakia, the only known record is mentioned by Švec (1984). In Austria, only a few old records are known (Reitter 1892; Franz 1974), the last from 1909. In Germany, the only known record dates to 1959 ("Kreuzlinger Forst bei München von M. Hüther" in Horion 1960). However, this observation is considered doubtful, as it is not supported by a specimen in the Hüther collection in the Zoologische Staatssammlung München (Hendrich L., pers. comm.). Furthermore, it purportedly comes from an unsuitable forest site where the congeneric species *P. depressus* occurs (Bussler H. and Fuchs H., pers. comm.).



**Figure 5.** Habitus of **A.** *P. abieticola* male (Ponts-de-Martel Valley); **B.** *P. abieticola* female (Swiss National Park); **C.** *P. depressus* female (Ponts-de-Martel Valley); **D.** *P. depressus* male (Ponts-de-Martel Valley). (Photos: A. Sanchez).



**Figure 6.** Male genitalia in ventral view of **A.** *P.abieticola* and **B.** *P.depressus*. Last segment of maxillary palpi of **C.** *P.abieticola* and **D.** *P.depressus*. (Photos: A. Szallies and A. Sanchez)

The discovery of *P. abieticola* in Switzerland significantly extends the limit of its range westward (Fig. 8). The Swiss records are also among the few recent (post-2000) known from Central Europe.

## **Ecology**

While the ecological requirements of the at least partially sympatric species *P. kolwensis* are relatively well known (see e.g. Burakowski 1962; Siitonen and Saaristo 2000), those of *P. abieticola* are still incomplete and some information in the literature is even contradictory.

Pytho abieticola is associated with spruce forests, often in primeval forest areas (Burakowski et al. 1987; Horák 2017), and usually inhabits swampy sites (Saalas 1917, 1923). According to Saalas (1917, 1923) and Pollock (1991), P. abieticola is exclusively a spruceassociated beetle, but data on Pinus and Abies are also reported (Koch 1989), although the accuracy of these data is unknown. With its flattened and flexible body perfectly adapted to subcortical life (Burakowski 1976), the larva develops under the bark of fallen trees of medium or small size (7-18 cm diameter according to Saalas 1923 and Burakowski et al. 1987, 6-25 cm according to Saalas 1917), that are freshly dead (within the last few years). According to Pollock (1991), the logs used by the different Pytho species are probably only suitable for 4–10 years. Pytho abieticola often lives in older and drier trees than the other two European Pytho species, although all three species are sometimes found on the same tree (Siitonen J., pers. comm.). Fallen trees favourable to P. abieticola lie horizontally (Saalas 1917) and ideally are not in direct contact with the ground (Saalas 1923; Burakowski et al. 1987; Siitonen J., pers. comm.). This happens, for example, when trees are broken or uprooted by the wind (Burakowski 1976) and are then supported by their branches. Saalas (1923) stated that he was not aware of any findings of the species on standing dead trees, which is generally also true for other *Pytho* species (Pollock 1991). Favourable logs are not in dense forest but in semi-shaded or open places (Siitonen J., pers. comm). Generally, the dry bark has already partially loosened and is easily detached in pieces (Siitonen J., pers. comm).

Like other species of the genus, P. abieticola, according to Saalas (1923), uses trees previously colonised by bark beetles (Curculionidae, Scolytinae), especially Pityogenes chalcographus (Linnaeus, 1760), Polygraphus spp. and Hylastes spp. The larvae likely feed principally on the decaying cambial-phloem layer that remains after the other insects have left the layer. Although some literature sources (e.g. Koch 1989) classify P. abieticola as zoophagous, it is indeed more likely that its larvae feed primarily on decaying wood and fungi, as has been shown for P. depressus (Andersen and Nilssen 1978; Smith and Sears 1982; Watt 1987; Pollock 1991; Vázquez 1993). However, they are probably also opportunistic and cases of cannibalism between P. abieticola larvae have been reported (Sahlberg 1875; Saalas 1923). They can easily be reared following the recommendations of Andersen and Nilssen (1978) and Pollock (1988).

Larval development probably takes several years (at least three, according to Burakowski et al. 1987), and larvae of various size can be found throughout the year (Saalas 1923). Pupation takes place between the second half of July and the first half of September (Burakowski et al. 1987). The pupal stage lasts about two weeks (Sahlberg 1875). The adults overwinter in pupal cells under bark. They are most easily found during this period, before emerging in spring, primarily in April and May.



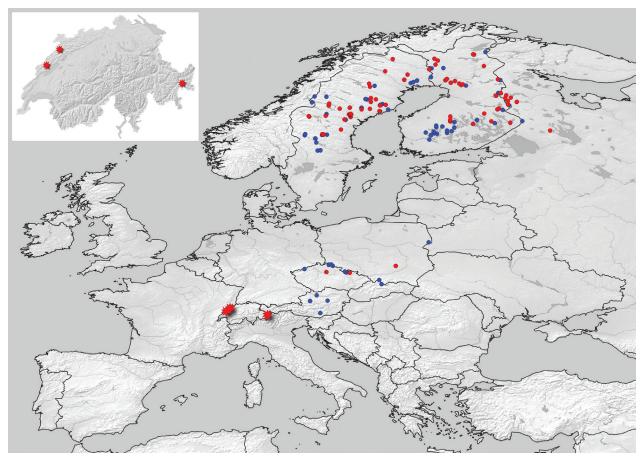
**Figure 7.** Larvae of **A.** *P. abieticola* (from Swiss National Park) and **B.** *P. depressus* (from Ponts-de-Martel Valley). Dorsal view (**C**, **D**) and lateral view (**E**, **F**) of tergite 9 of the same larvae. (Photos: A. Sanchez).

Our catches fit well into this general framework, as our sites in the Jura mountains were in spruce forests bordering peat bogs. The specimens were found in relatively open forest areas where some logs had been mechanically felled in previous years and were lying above the ground. In the Swiss National Park, most of the specimens were also found in particularly humid environments, especially on the steep slope to the Spöl stream. All larvae were found on trees lying horizontally just above the ground. Although most of our subcortical findings of larvae and adults of P. abieticola were made on spruce, as reported in the literature, we were also able to confirm the use of Swiss mountain pine as a host species, at least occasionally. In our three Swiss localities, we could also find the more widespread P. depressus in more or less close proximity to P. abieticola (in the Saignelégier region, they were even found on the same log). Both species are thus sympatric in the study area, a coexistence that has already been reported, e.g. in the primeval forest of Białowieża (Kubisz et al. 2014).

#### Status and threats

Pytho abieticola is in severe decline in Fennoscandia and even more so in Central Europe. With the exception of Finland, where it is only considered 'Near Threatened NT' (Malmberg et al. 2019), it is thus threatened (or regionally extinct) in all European countries where it occurs (respectively occured). It is considered 'Vulnerable VU' in Sweden (SLU Artdatabanken 2020), 'Endangered EN' in Poland (Pawłowski et al. 2002), 'Critically Endangered CR' in the Czech Republic (Horák 2017) and in Norway (Ødegaard et al. 2021), and 'Regionally Extinct RE' in Austria (Jäch et al. 1994) and in Germany (Schmidl et al. 2021), even though its occurrence in Germany is questionable. While it was not possible to find information on its threat status in Russia, the species is not mentioned in the Slovakian Red List (Holecová and Franc 2001). At the global scale, the species is considered 'Least concern LC' by Pettersson et al. (2010), probably assuming that its situation is better in Western Russia, where a large part of *P. abieticola* populations certainly occur. This assumption seems to be confirmed by the results obtained by Laaksonen et al. (2008), who showed that Karelian forests in Russia, where forest management was very limited until recently, were better preserved (and less fragmented), and therefore harboured more populations of P. abieticola (and even more of P. kolwensis) than forests in neighbouring Finland. However, the global status of *P. abieticola* is under revision and the species will certainly be classified as threatened in the next European Red List (Dodelin B., pers. comm.).

Degradation and destruction of natural forests through intensive logging and the resulting fragmentation of habitat represent the greatest threat to the species. Like all other species of the genus, *P. abieticola* occurs only in old-growth forest areas and requires continuous spatial and temporal availability of large amounts of dead wood, which qualifies it as a typical "Primeval forest relict" species (Eckelt et al. 2017). In the case of *P. abieticola*,



**Figure 8.** Distribution of *Pytho abieticola* in Europe, with a close-up of Switzerland (in blue: observations before 2000; in red: observations since 2000). Swiss localities are indicated by stars. The species is also widespread in Russia and reaches northern China, but data are scarce. (Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com).

the required resources are very specific: small to medium-sized spruce logs, with already partially loosened dry bark, that are elevated off the ground in semi-shaded or open spaces. Moreover, they quickly (after only a few years) become unsuitable for the species, for example when the bark becomes too loose, or the trunks reach a more advanced stage of decay. Thus, these resources must be regularly "renewed" and constantly available. Since the species can also colonise trees felled mechanically, effective measures to promote *P. abieticola* can simply be established even if favourable dead wood (i.e. naturally fallen) is lacking. Following our observations, cantonal authorities and site managers should take local measures to ensure the conservation of this species.

# Conclusion

The knowledge on the distribution of *P. abieticola* has improved since Horion (1960), who mentioned only four records in Central Europe. However, its situation remains extremely critical, as only very few populations remain (Fig. 8). The discovery of new populations of this patrimonial species, wherever they may be located, is therefore very encouraging from a conservation point of view.

Surveys in other old-growth coniferous forests, especially at the edges of open peat bogs, should be carried out and may reveal further populations of *P. abieticola*. Swiss localities in the Jura mountains, within 10 km of the French border, indicate a very probable occurence in that country, particularly in peat bogs of the Jura. An occurrence in northern Italy also seems likely, as the Swiss national park borders Italy.

# Acknowledgements

We would like to thank the Service de la Faune, des Forêts et de la Nature of the canton of Neuchâtel, and particularly Sébastien Tschanz, for financing the inventory of the Pontsde-Martel Valley, as well as the sponsors of the research carried out in the Swiss National Park (ANU, AWN, FOEN, the Bündner Naturmuseum Chur and the Parrotia foundation). We also thank the regional authorities (Canton of Neuchâtel and of Jura, Swiss National Park) for the attribution of collection permits. We are grateful to Carl-Michael Andersson, Pablo Hebeisen, Beat Wermelinger, Nicolas Roth and Romain Angeleri for their support of the field work in the National Park and we would like to thank Abenis AG, and particularly Romano Costa, Remo Wild,

and Barbara Huber for the good collaboration. Our thanks to Hervé Brustel, Heinz Bussler, Benoît Dodelin, Andreas Eckelt, Herbert Fuchs, Nicolas Gouix, Lars Hendrich, Erwin Holzer, Uwe Hornig, Ondřej Konvička, Frank Lange, Uno Roosileht, Juha Siitonen, and Dmitry Telnov for sharing their information on the species and European localities. Thanks to Michel Sartori for providing us with the photographic equipment, and to Christian Monnerat and Laurent Juillerat for various advice. Finally, we are grateful to Jessica Litman for checking and improving the English, and to Hervé Brustel and Darren Pollock for their valuable comments on the manuscript.

# References

- Andersen J, Nilssen AC (1978) The food selection of *Pytho depressus* L. (Coleoptera, Pythidae). Norwegian Journal of Entomology 25: 225–226.
- Baur B, Scheurer T [Eds] (2014) Wissen schaffen: 100 Jahre Forschung im Schweizerischen Nationalpark. Nationalpark Forschung in der Schweiz 100/I. Haupt Verlag, Bern, 384 pp.
- Brustel H (2012) Polytrap 2010: new "soft design" window flight trap for saproxylic beetles. In: Jurc M (Ed.) Saproxylic beetles in Europe: monitoring, biology and conservation. Ljubljana, Slovenian Forestry Institute, Silva Slovenica 137: 91–92.
- Burakowski B (1962) Obserwacje biologiczno-morfologiczne nad Pytho kolwensis C. Sahlb. (Coleoptera, Pythidae) w Polsce. Fragmenta Faunistica 10: 173–204. https://doi.org/10.3161/001593 01FF1962.10.12.173
- Burakowski B (1976) Coleoptera: Pythidae-Lagriidae-Alleculidae. Zeszyt 88, Rozmiazgowate-Pythidae. In: Mikolajczyk W (Ed.) Klucze do oznaczania owadów Polski. Wrocławska Drukarnia Naukowa, Warsaw, 3–18.
- Burakowski B, Mroczkowski M, Stefańska J (1987) Chrząszcze Coleoptera. Cucujoidea, część 3. Katalog Fauny Polski 23(14): 309.
- Chittaro Y, Sanchez A (2016) Liste commentée des Tenebrionoidea (Coleoptera) de Suisse. Partie 1: Aderidae, Anthicidae, (Boridae), Melandryidae, Meloidae, Mycetophagidae, Mycteridae, Prostomidae, Pyrochroidae, Pythidae, Ripiphoridae, Salpingidae, Tenebrionidae, Tetratomidae, Zopheridae. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 89: 183–235.
- Eckelt A, Müller J, Bense U, Brustel H, Bussler H, Chittaro Y, Cizek L, Frei A, Holzer E, Kadej M, Kahlen M, Köhler F, Möller G, Mühle H, Sanchez A, Schaffrath U, Schmidl J, Smolis A, Szallies A, Németh T, Wurst C, Thorn S, Christensen RHB, Seibold S (2017) "Primeval forest relict beetles" of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation 22: 15–28. https://doi.org/10.1007/s10841-017-0028-6
- Franz H (1974) Die Nordost-Alpen im Spiegel ihrer Landtierwelt, Band IV. Universitätsverlag Wagner, Innsbruck-München, 707 pp.
- GBIF.org (10 August 2022) GBIF Occurrence Download. https://doi. org/10.15468/dl.6wuhvj
- Háva J, Zahradník P (2021) A contribution to the knowledge of the genus *Pytho* Latreille, 1796 (Coleoptera: Pythidae) from China, with the description of *Pytho sichuanicus* sp. n. Acta Zoologica Bulgarica 73(1): 27–30.

- Heyrovský L (1960) K bionomii a zoogeografii druhů rodu *Pytho* F. v Československu (Col., Pythidae). Časopis Slezského muzea v Opavě, Series A, 9: 41–43.
- Holecová M, Franc V (2001) Červený (ekosozoologický) zoznam chrobákov (Coleoptera) Slovenska. In: Baláž D, Marhold K, Urban P (Eds) Červený zoznam rastlín a živočíchov Slovenska. Ochrana Prírody, 20 (Suppl.): 111–128.
- Horák J (2017) Pythidae. In: Hejda R, Farkač J, Chobot K (Eds) Červený seznam ohrožených druhů České republiky. Bezobratlí. Agentury ochrany přírody a krajiny ČR, Praha, 403–404.
- Horion A (1956) Faunistik der mitteleuropäischen Käfer. Band V: Heteromera. Entomologische Arbeiten aus dem Museum G. Frey Tutzing bei München, Sonderband, 1–336.
- Horion A (1960) Koleopterologische Neumeldungen für Deutschland. IV. Reihe. Nachtrag zum "Verzeichnis der mitteleuropäischen Käfer". Mitteilungen der Münchner Entomologischen Gesellschaft 50: 119–162.
- Iablokoff-Khnzorian SM (1985) Les Pythidae paléarctiques. Deutsche Entomologische Zeitschrift 32: 193–229. https://doi.org/10.1002/ mmnd.19850320129
- Jäch MA, Adlbauer K, Barries W, Cate PC, Franz H, Geiser E, Geiser R, Holzschuh C, Kirschenhofer E, Kreissl E, Novak G, Probst J, Reiser P, Schillhammer H, Schmid H, Schödl S, Suppantschitsch W, Zabransky P, Zelenka W (1994) Rote Liste der gefährdeten Käfer Österreichs (Coleoptera). Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie, Band 2: 107–200.
- Kaszab Z (1969) 11. Fam. Pythidae. In: Freude H, Harde KW, Lohse GA (Eds) Die K\u00e4fer Mitteleuropas. Band 8: Teredilia, Heteromera, Lamellicornia. Goecke & Evers, Krefeld, 92–99.
- Koch K (1989) Die K\u00e4fer Mitteleuropas. \u00f6kologie, Band 2. Goecke & Evers, Krefeld, 382 pp.
- Kubisz D, Iwan D, Tykarski P (2014) Tenebrionoidea: Tetratomidae, Melandryidae, Ripiphoridae, Prostomidae, Oedemeridae, Mycteridae, Pythidae, Aderidae, Scraptiidae. Critical checklist, distribution in Poland and meta-analysis. Coleoptera Poloniae 2. University of Warsaw – Faculty of Biology, Natura optima dux Foundation, Warszawa, 470 pp.
- Laaksonen M, Peuhu E, Várkonyi G, Siitonen J (2008) Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests. Oikos 117: 1098–1110. https://doi.org/10.1111/j.0030-1299.2008.16620.x
- Malmberg S, Mannerkoski I, Martikainen P, Clayhills T, Helve E,
  Hyvärinen E, Karjalainen S, Mattila J, Muona J, Rassi P (2019)
  Kovakuoriaiset Beetles. In: Hyvärinen E, Juslén A, Kemppainen E, Uddström A, Liukko UM (Eds) Suomen lajien uhanalaisuus Punainen kirja 2019. The 2019 Red List of Finnish Species.
  Ympäristöministeriö & Suomen ympäristökeskus, 391–425.
- Ødegaard F, Hanssen O, Laugsand AE, Olberg S (2021) Biller: Vurdering av granbarkflatbille *Pytho abieticola* for Norge. Rødlista for arter 2021. Artsdatabanken.
- Painter JN, Siitonen J, Hanski I (2007) Phylogeographical patterns and genetic diversity in three species of Eurasian boreal forest beetles. Biological Journal of the Linnean Society 91(2): 267–279. https://doi.org/10.1111/j.1095-8312.2007.00797.x
- Parolini JD (2012) Vom Kahlschlag zum Naturreservat. Geschichte der Waldnutzung im Gebiet des Schweizerischen Nationalparks. Haupt Verlag, 213 pp.
- Pawłowski J, Kubisz D, Mazur M (2002) Coleoptera. In: Głowaciński Z (Ed.) Red-List of Extinct and Endangered Animals. Instytut Ochrony Przyrody PAN, Kraków, 88–110.

- Pettersson R, Hyvärinen E, Munteanu N, Istrate P, Schlaghamersky J, Schmidl J (2010) Pytho abieticola. The IUCN Red List of Threatened Species 2010: e.T157801A5149331. [Accessed on 16 September 2022]
- Pollock DA (1988) A technique for rearing subcortical Coleoptera larvae. The Coleopterists Bulletin 42: 311–312.
- Pollock DA (1991) Natural history, classification, reconstructed phylogeny and geographic history of *Pytho* Latreille (Coleoptera, Pythidae). Memoirs of the Entomological Society of Canada 154: 1–104. https://doi.org/10.4039/entm123154fv
- Pollock DA (2008) Pythidae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea. Stenstrup: Apollo Books, 413–414.
- Pollock DA (2020) Pythidae. In: Iwan D, Löbl I (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Revised and Updated Second Edition. Tenebrionoidea. Leiden, Boston, E. J. Brill, 564–565.
- Rassi P, Karjalainen S, Clayhills T, Helve E, Hyvärinen E, Laurinharju E, Malmberg S, Mannerkoski I, Martikainen P, Mattila JA, Muona JE, Pentinsaari M, Rutanen I, Salokannel J, Siitonen J, Silfverberg H (2015) Provincial list of Finnish Coleoptera 2015. Sahlbergia 21, Supplement 1.
- Reitter E (1892) Coleopterologische Notizen. XLV. Wiener Entomologische Zeitung 11: 186–188. https://doi.org/10.5962/bhl.part.27706
- Richard JL (1961) Les forêts acidophiles du Jura: étude phytosociologique et écologique. Matériaux pour le levé géobotanique de la Suisse 38, 164 pp.
- Saalas U (1917) Die Fichtenkäfer Finnlands. Studien über die Entwicklungsstadien, Lebensweise, und geographische Verbreitung der an Picea excelsa Link. lebenden Coleopteren nebst einer Larvenbetimmungstabelle. I. Allgemeiner Teil und Spezieller Teil I. Suomalaisen Tiedeakatemian Justantama, Helsinki, 547 pp. https://doi.org/10.5962/bhl.title.38683
- Saalas U (1923) Die Fichtenkäfer Finnlands. II. Studien über die Entwicklungsstadien, Lebensweise, und geographische Verbreitung der an *Picea excelsa* Link. lebenden Coleopteren nebst einer Larvenbetimmungstabelle. Annales Academiae Scientiarum Fennicae A 22, 746 pp.
- Sahlberg J (1875) Ueber die Finnischen Arten der Käfer-Gattung *Pytho* und deren Larven. Deutsche Entomologische Zeitschrift 19(1): 219–224. https://doi.org/10.1002/mmnd.48018750118

- Schmidl J, Bense U, Bussler H, Fuchs H, Lange F, Möller G (2021)
  Rote Liste und Gesamtartenliste der "Teredilia" und Heteromera
  (Coleoptera: Bostrichoidea: Lyctidae, Bostrichidae, Anobiidae,
  Ptinidae; Tenebrionoidea) Deutschlands. In: Ries M, Balzer S, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Matzke-Hajek G (Eds)
  Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band
  5: Wirbellose Tiere (Teil. 3). Münster (Landwirtschaftsverlag). Naturschutz und Biologische Vielfalt 70(5): 165–186.
- Sergeeva EV, Stolbov VA (2020) A review of Tenebrionoid beetle fauna (Coleoptera, Tenebrionoidea) of the Tyumen region. Amurian Zoological Journal 12(2): 224–242. https://doi.org/10.33910/2686-9519-2020-12-2-224-242
- Siitonen J, Saaristo L (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation 94: 211–220. https://doi.org/10.1016/ S0006-3207(99)00174-3
- SLU Artdatabanken (2020) Rödlistade arter i Sverige 2020. SLU, Uppsala, 242 pp.
- SLU Artdatabanken (2022) Pytho abieticola. https://www.artportalen. se/search/map/taxon/101691
- Smith DB, Sears MK (1982) Mandibular structure and feeding habits of three morphologically similar coleopterous larvae: Cucujus clavipes (Cucujidae), Dendroides canadensis (Pyrochroidae) and Pytho depressus (Salpingidae). The Canadian Entomologist 114(2): 173–175. https://doi.org/10.4039/Ent114173-2
- Streček J (1988) Zajímavé nálezy brouků ze skupiny čeledí Heteromera a Clavicornia v ČSSR. Zprávy Československé společnosti entomologické při ČSAV 24 (3–4): 65–66.
- Švec Z (1984) Faunistic records from Czechoslovakia. Pythidae. Acta Entomologica Bohemoslovaca 81: 398.
- Vávra JC, Stanovský J (2013) Brouci (Coleoptera). In: Roháček J, Ševčík J, Vlk R (Eds) Příroda Slezska. Slezské zemské muzeum, Opava, 295–311.
- Vázquez XA (1993) Fauna Iberica. Vol. 5. Coleoptera: Oedemeridae, Pyrochroidae, Pythidae, Mycteridae. Museo Nacional de Ciencias Naturales, Madrid, 181 pp.
- Yuferev GI (1986) Ecological characteristics of terrestrial coleopterofauna of Svecha district of Kirov oblast. Ecology of animals of the Volga and Urals region, 25–32. [in Russian]