

Příloha I

Wappler, T., Dlussky, G.M., Engel, M.S. Prokop, J., **Knor, S.** 2013. A new trap-jaw ant species of the genus *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) from the Early Miocene (Burdigalian) of the Czech Republic. **Paläontologische Zeitschrift** 88, 495–502. [IF 1.10]

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Paläontologische Zeitschrift
Scientific Contributions to
Palaeontology

ISSN 0031-0220

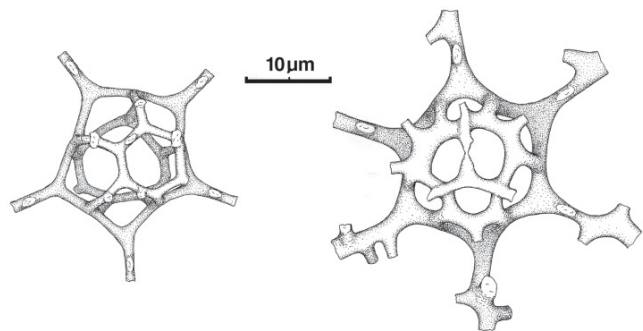
Paläontol Z
DOI 10.1007/s12542-013-0212-2



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Paläontologische Zeitschrift

Scientific Contributions
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A new trap-jaw ant species of the genus *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) from the Early Miocene (Burdigalian) of the Czech Republic

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Received: 10 June 2013 / Accepted: 4 October 2013
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Abstract *Odontomachus paleomyagra* sp. nov. is described from the Early Miocene of the Most Basin (Czech Republic) on the basis of a single-winged female, representing one of the rare reports of fossil Odontomachini. The new species is separated easily from other trap-jaw ant species groups by differences in mandibular morphology (without denticles on the inner side) and distributional occurrence. The evolutionary and biogeographic history of the Odontomachini is briefly discussed.

Keywords Ponerinae · *Odontomachus* · New species · Miocene · Most Basin · Czech Republic · Trap-jaw ants

Kurzfassung Aus dem Unter-Miozän im Most Becken (Nord Böhmen; Tschechische Republik) wird erstmals ein Exemplar der Ameisen-Gattung *Odontomachus* beschrieben und abgebildet. Die neue Art, *Odontomachus paleomyagra* sp. nov., unterscheidet sich von anderen

Angehörigen der Schnappkieferameisen, vor allem durch Unterschiede in der Morphologie der Mandibeln (ohne Zähnnchen an der Innenseite) und ihrer ungewöhnliche biogeographischen Verbreitung. Die evolutionäre und biogeographische Geschichte der Odontomachini wird kurz diskutiert.

Schlüsselwörter Ponerinae · *Odontomachus* · Neue Art · Miozän · Most Becken · Tschechien · Schnappkieferameisen

Introduction

Ants are one of the dominant and more conspicuous groups of animals in terrestrial ecosystems (Hölldobler and Wilson 1990), and their ecological diversity is reflected in both their number of species (>12,750 spp., e.g., Agosti and Johnson 2007) and morphological adaptations. Among the 26 subfamilies presently recognized among ants, species of the Ponerinae are notable predators, armed with powerful mandibles and a well-developed sting (Hölldobler and Wilson 1990). The mandibles contain some of the most important diagnostic characters for ponerine taxonomy and provide a wealth of insights into ecological niches and foraging modes, as reflected in their extreme diversity of mandibular forms and associated structures. Most distinctive are the trap-jaw ants of the genus *Odontomachus* Latreille, easily recognized by their elongate mandibles, which are capable of opening more than 180° and, when a trigger seta is tripped, snap closed rapidly. This powerful, snapping mechanism is used during prey capture, disabling fast or dangerous victims, or in defense, including providing the force for escape jumps, nest construction, and manipulation of larvae and pupae (e.g., Gronenberg 1995;

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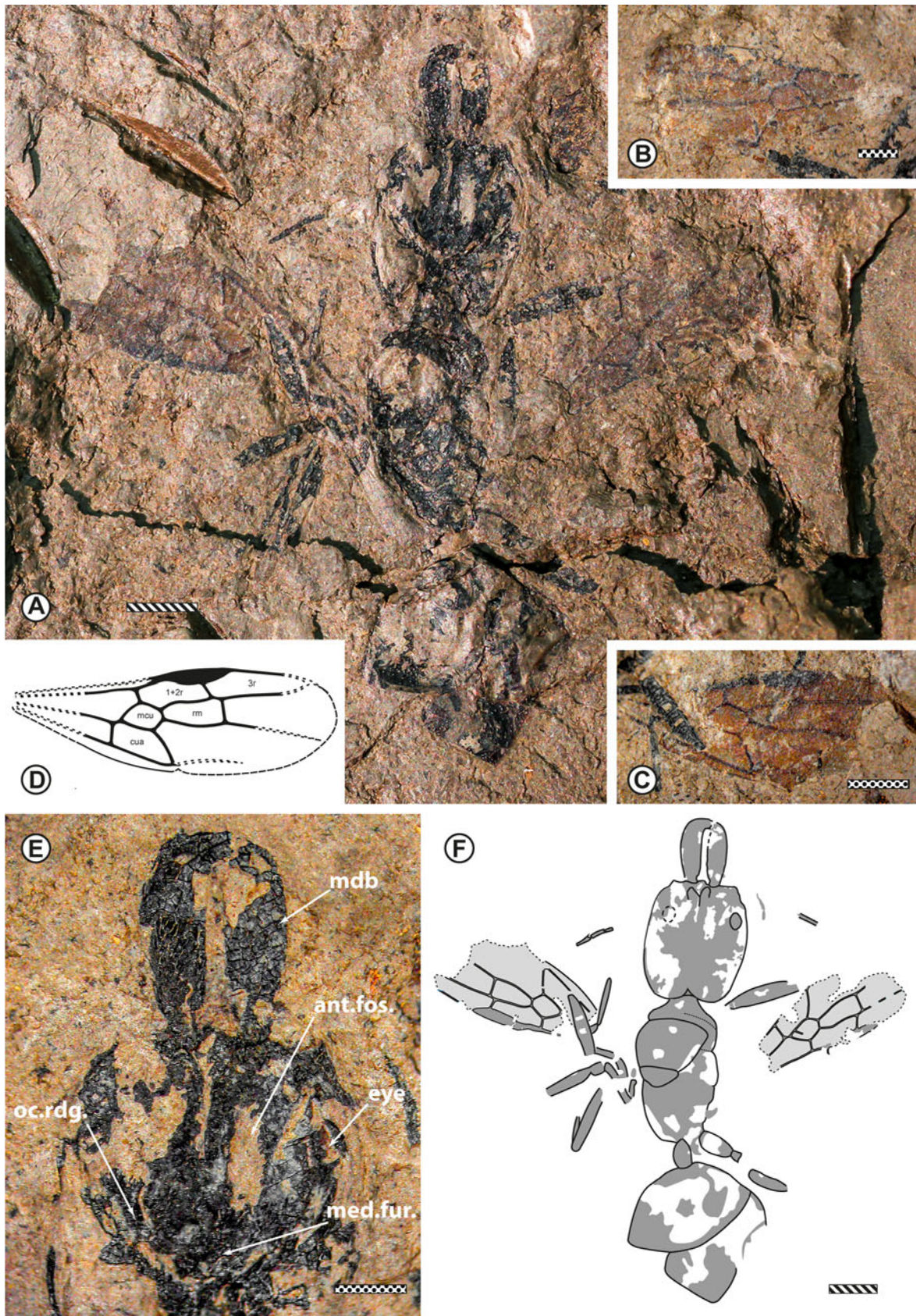


Fig. 1 *Odontomachus paleomyagra* sp. nov. ZD0136 (Bílina Mine Enterprises coll.) from the Early Miocene (Burdigalian), Most Formation, Clayey Superseam Horizon. **a** Gyne, holotype, **b** left forewing, **c** right forewing, **d** Wing reconstruction and nomenclature of venation; cells: *1+2r*, *rm*, *mcu*, *cua*. **e** Detail of the head and pair of large, straight mandibles. *mdb* mandible, *ant.fos.* antennal fossa, *eye* eye, *med.fur.* median furrow, *oc.rdg.* ocular ridge. **f** Habitus drawing of the gyne holotype. Scale bars back slashed 1 mm, dotted 500 μ m

Patek et al. 2006; Spagna et al. 2008). These snapping mandibles make the 69 species of *Odontomachus* among the most specialized of all ponerine ants. Interestingly, such a remarkable specialization is mirrored in the fossil record (LaPolla et al. 2013), as various species in the extinct tribe Haidomyrmecini possess scythe-like mandibles, which appear to have served a similar snapping trap function (Dlussky 1996; Perrichot et al. 2008; Barden and Grimaldi 2012; McKellar et al. 2013). Haidomyrmecines are, however, not related to the Odontomachini and instead are tentatively placed within a different subfamily, the Sphecomyrminae (Perrichot et al. 2008). More importantly, the morphology of their mandibles is distinctively different from that in species of *Odontomachus* (Barden and Grimaldi 2012; McKellar et al. 2013), clearly indicating an independent evolution of snapping trap jaws among the lower ants. Trap jaws are also found independently elsewhere among modern ants, such as *Acanthognathus* Mayr in the Myrmicinae, but those of *Odontomachus* boast the greatest speed of any animal (Patek et al. 2006).

The 69 modern species of *Odontomachus* are widely distributed in tropical regions, with the greatest concentration of species in the Asian and New World tropics (Brown 1976, 1977; Fisher and Smith 2008; Sorger and Zettel 2011; Bolton 2013). Only a few species extend into temperate regions (reviewed in Brown 1976). To date, only two species of *Odontomachus* have been described as fossils, both from the amber mines of the Dominican Republic—*Odontomachus pseudobauri* De Andrade and *Odontomachus spinifer* De Andrade (1994). Species vary considerably in their ecology, including nesting substrates and types of prey, as well as varying morphologically, covering a range of body sizes and mandible lengths (Feitosa et al. 2012). Foraging strategies mainly consist of active hunting for live prey (flies, moths and other ants), gathering of plant and/or insect exudates, and fleshy fruits and seeds (summarized in Schmidt 2011).

Herein, we provide the first description of this peculiar genus of ants from the Early Miocene coal seam deposits of the Most Basin, the third fossil for *Odontomachus* and the first as a compression. Hitherto the composition of this fauna included more than 300 specimens comprising 31 families in 11 insect orders (e.g., Prokop 2003; Kvaček et al. 2004; Fikáček et al. 2008). Ants are the most abundant insect group in the assemblage, comprising nearly

40 % of the recorded specimens, but are mainly represented by isolated wings and disarticulated body structures (personal observation J. Prokop). In addition, we provide some brief comments on the possible affinities of this species relative to species groups within *Odontomachus*.

Materials and methods

The fossil examined in the present work was gathered from the collection of Zdeněk Dvořák deposited in the Bílina Mine Enterprises in Bílina (inventory number prefixed by ZD). The specimen was observed dry and under ethyl-alcohol with an Olympus SZX9 stereomicroscope. All measurements were made using an ocular micrometer and are given in millimeters; anatomical structures were measured as preserved. Line drawings were aided by a camera lucida. All photographs were taken using a Canon EOS 550D digital camera coupled to a MP-E 65-mm macro lens. Morphological terminology used in the descriptions generally follows that employed by Brown (1976); wing vein and cell nomenclature follows Dlussky (2009). The age and stratigraphy of the Bílina Mine coal seam has been summarized briefly in Knor et al. (2013).

Systematic palaeontology

Formicidae Latreille, 1809.

Ponerinae Lepeletier de Saint-Fargeau, 1835.

Odontomachini Emery, 1911.

Odontomachus Latreille, 1804.

Odontomachus Latreille, 1804: 179 (as genus).

Pedetes Bernstein, 1861: 7. Type-species: *Pedetes macrorhynchus* Bernstein, 1861: 8; by monotypy. Dalla Torre, 1893: 51 (*Pedetes* as junior synonym of *Odontomachus*).

Champsomyrmex Emery, 1892: 558. Type-species: *Odontomachus coquereli* Roger, 1861: 30; by monotypy. Brown, 1973: 179 (*Champsomyrmex* as provisional junior synonym of *Odontomachus*).

Thempsomyrmex Forel, 1893: 163 (incorrect subsequent spelling of *Champsomyrmex*).

Myrtoteras Matsumura, 1912: 191. Type-species: *Myrtoteras kuroiwae* Matsumura, 1912: 192 (junior synonym of *Odontomachus monticola* Emery, 1892). Brown, 1973: 182 (*Myrtoteras* as provisional junior synonym of *Odontomachus*).

Type species: *Formica haematoda* Linnaeus, 1758: 582, by monotypy.

Comments: Based on the following combination of features, the present fossil can be assigned to the trap-jaw ant genus *Odontomachus* (Ponerinae: Odontomachini):

(characters of gyne Ponerinae) waist consisting of one segment (petiole) narrowly attached to first gastral (III abdominal) segment; gaster with constriction between first and second segments; forewing crossvein *cu-a* meeting *M+Cu* near cell *mcu* proximal to section *1M* at distance less than *cu-a* length; (characters of *Odontomachus*) mandibles linear, their bases situated rather close together;

nuchal carina (separating dorsal and posterior surfaces of head) converging in a V at midline.

Odontomachus paleomyagra sp. nov.

Figs. 1, 2

Derivatio nominis: From the Greek *paleomyagra*, ancient mouse-trap (treated as a noun in apposition).



Fig. 2 Reconstruction of the trap-jaw ant *Odontomachus paleomyagra* sp. nov. These predatory insects are noted for their unusual mandibles that are held open at 180° and snap shut on a hair trigger

Holotype: Gyne; specimen No. ZD0136; deposited in the collections of the Bílina Mine Enterprises, Bílina, Czech Republic.

Type locality: Bílina mine near Bílina, Czech Republic. Age and layer: Early Miocene (Burdigalian), Most Formation, Clayey Superseam Horizon, Holešice Member (No. 30).

Measurements (in mm): Mesosoma length 3.3, head length 2.5, head width 2.0, mandible length 1.4, mandible width 0.4, maximum compound eye diameter 0.26, mesoscutum length 1.0, mesoscutellum length 0.4.

Diagnosis. New species is noteworthy for combination of following characters: mandibles comparatively short, straight, without denticles on inner surface; head rather wide and only slightly narrower across vertex than across compound eyes; petiole without dorsal spine.

Description. Gyne. Imprint length 10.5 mm; putative total body length about 12 mm. Head 1.2 times longer than wide, with feebly concave sides, rounded occipital corners, and concave occipital margin; head width across compound eyes 1.06 times as wide as across vertex; anterior part of head with fine striations; anterior margin of clypeus with small rounded lobe; compound eyes oval, weakly convex, strongly shifted anteriorly, such that gena is nearly 1.5 times as long as maximum compound eye diameter; mandibular bases situated close together, mandibles linear, straight, nearly 0.5 times as long as head, and 3.3 times longer than wide; inner (masticatory) border of mandible without teeth or denticles; mandibular apex evidently consisting of three teeth (as in all known *Odontomachus*; however only two teeth are visible on imprint), one rounded and other with truncate tip. Mesosoma rather elongate; mesoscutum slightly wider than long, flat, not overhanging pronotum; mesoscutellum transverse; propodeum angulate in profile. Petiole with narrowly rounded top, without dorsal spine. Forewing with closed cells *I*+2*r*, *rm*, *mcu*, *cua*, and perhaps 3*r*; section *IM* 1.9 times longer than *IRS*; cell *I*+2*r* nearly 3 times longer than wide; section *I*+2*r* S-shaped; cell *rm* pentagonal, 2.2 times longer than wide; crossvein *r-rs* sloping apically and meeting *RS* somewhat basal to junction with *rs-m*, as a result *rs-m* and *r-rs* do not appear as single crossvein; cell *mcu* pentagonal; meeting of crossvein *cu-a* and *M+Cu* proximal to *IM* and *ICu* fork, separated from it by more than 3 times width of vein.

Comments: De Andrade (1994) described two fossil species of *Odontomachus* from Miocene amber of the Dominican Republic: *O. spinifer* and *O. pseudobauri* (Table 1). These species belong to the Neotropical *haematodus* species group as defined by Brown (1976) and

Table 1 Diversity of Miocene ants of the subtribe Odontomachiti

Subtribe Odontomachiti [§]	References
Genus <i>Odontomachus</i> Latreille	
<i>Odontomachus pseudobauri</i> de Andrade [DA]	de Andrade (1994)
<i>Odontomachus spinifer</i> de Andrade [DA]	de Andrade (1994)
<i>Odontomachus paleomyagra</i> sp. nov. [BM]	This study
Genus <i>Anochetus</i> Mayr	
<i>Anochetus corayi</i> Baroni Urbani [DA]	Baroni Urbani (1980)
<i>Anochetus brevidentatus</i> MacKay [DA]	MacKay (1991)
<i>Anochetus ambiguus</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus conisquamis</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus dubius</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus extinctus</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus intermedius</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus lucidus</i> de Andrade [DA]	de Andrade (1994)

[§] Comprising ponerine ants with trap-jaws sensu Brown's (1976, 1978) classification of the "subtribe Odontomachiti"

DA Dominican amber (23–19 Ma); The age and origin of Dominican amber is reviewed by Iturralde-Vinent and MacPhee (1996) and Grimaldi and Engel (2005)

BM Bílina mine (~20 Ma)

today include the large majority of New World species in the genus. Taxa of the *haematodus* species group differ from *O. paleomyagra* by the form of the head and longer mandibles with numerous denticles on the inner (masticatory) margins. The construction of the mandibles of the new species is most similar to *O. assiniensis* Emery, 1892, which today occurs in SE Africa, and the Oriental *rixosus* species group, including *O. rixosus* Smith, 1857, *O. monticola* and *O. latidens* Mayr, 1867, mainly occurring today in SE Asia, Sumatra, Borneo and Java (Brown 1976). However, these species have a more elongate head: (1.3–1.5 times longer than wide). The head width across the compound eyes is 1.08–1.16x as wide as across the vertex within the *rixosus* species group, 1.07–1.11x in *O. assiniensis*, whereas this is only 1.06x in *O. paleomyagra*.

Discussion

The subtribe Odontomachiti sensu Brown (1976, 1978) today consists of only the closely related genera *Odontomachus* Latreille and *Anochetus* Mayr. These genera are known only from a handful of fossils from Dominican amber and dating no older than the Early Miocene (summarized in Table 1), but these records and their surprisingly modern character (rather than belonging to stem-group Odontomachiti) serve to demonstrate that this clade is considerably older. Indeed, Ponerinae as a whole extends well into the Mesozoic (e.g., Grimaldi et al. 1997; Engel

and Grimaldi 2005; Grimaldi and Engel 2005; LaPolla et al. 2013) and has experienced a rich history of continuous diversification throughout the Tertiary (e.g., Dlussky and Wedmann 2012; LaPolla et al. 2013). This impressive diversification resulted in a collection of taxa so divergent from one another that some have at times been placed in distinctive tribes (Ouellette et al. 2006; Fisher and Smith 2008; Santos et al. 2010). More recent phylogenetic studies support the sister group relationship between *Odontomachus* and *Anochetus*, and suggest that they may be subdivided into some rare taxa that are present in the Palaearctic Region versus putatively ‘old’ lineages that ‘are predominantly tropical or straddle the temperate-tropical transition zone of East Asia’ (Ouellette et al. 2006; Fisher and Smith 2008; Santos et al. 2010). Certainly, the biogeographic history of this clade is complicated, and, unfortunately, the few fossil records shed relatively little light on the matter, particularly given that the fossils are all well placed within their respective monophyletic genera and, as noted above, emphasize that they are considerably older than the Miocene (Fig. 3). One possible scenario is that the *Odontomachus* group is at least as old as the Paleocene–Eocene with stem members of each genus spreading from Asia into the various parts of the world. These various tropical elements would eventually have become isolated and continued to speciate in those regions after the Eocene–Oligocene transition when considerable climatic cooling and drying took place, whereas the plant assemblage of the lower

Miocene Bílina locality indicates rather moderate to sub-tropical climatic conditions (Kvaček 1998). Such a scenario would account for the modern distribution of the species as well as the few known fossils, but requires considerable testing against future palaeontological discoveries and phylogenetic analyses. Certainly fossils can provide some of the most critical data for illuminating historical biogeographic patterns. For instance, the discovery in northern deposits of otherwise ‘austral’ lineages has greatly revised our interpretations of the evolution of many plant and animals clades, especially among insects (e.g., Grimaldi and Engel 2005). Accordingly, fossils such as *O. paleomyagra* have the potential, when ultimately included in cladistic studies, to transform our understanding of historical patterns.

The present fossil, along with those in amber, also demonstrates the antiquity and relative evolutionary stability of the unique mandibular morphology of these trap-jaw ants. While there are subtle differences in the mandibles among the numerous species groups of *Odontomachus*, the overall groundplan of the odontomachine trap jaw is relatively conserved. This effective prey-capture mechanism as well as its suitability for constructing and manipulating nest elements has apparently persisted for ~20 million years, and likely much longer. It would be interesting to look for morphological or morphometric proxies permitting an estimation of the force and speed potentially produced in the fossil species. This would allow

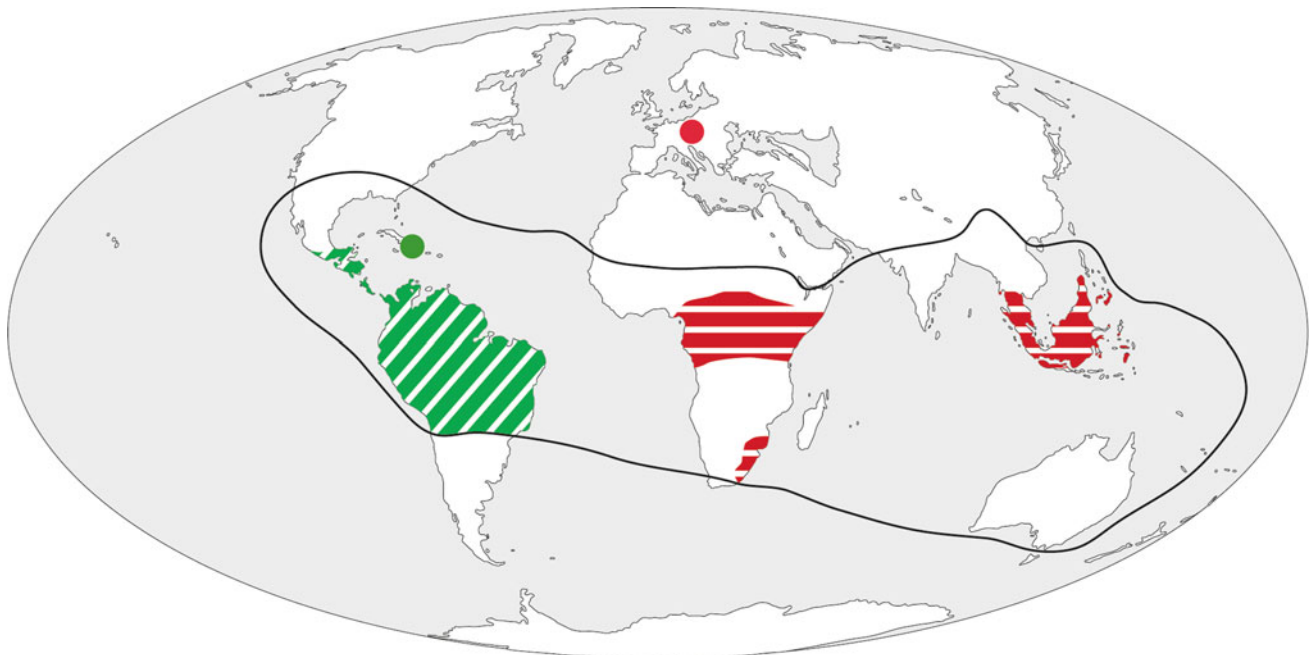


Fig. 3 Present-day distribution of the genus *Odontomachus*. The shaded areas represent the distribution of recent species closely related to the known fossils, both corresponding in color (green dot

amber specimens, red dot compression specimen). Palaeogeographic reconstruction for the Miocene Epoch based on the plate model presented in Blakey (2011)

a quick estimation of these values for all of the living species and, when placed in a phylogenetic framework, would result in a reconstruction of mandibular force evolution across this clade. Perhaps the considerable power produced by the mandibles of *O. bauri* (Patek et al. 2006; Spagna et al. 2008) is shared across additional species of *Odontomachus* and even ancient in origin, a fascinating area for investigation. Eventual discovery of the origins of the genus group temporally and biogeographically will permit placing the common ancestor of odontomachines in its original ecological context and could shed light on those factors resulting in the spectacular evolutionary novelty of their prominent mandibles. Such hypotheses will only be successfully tested and resolved by continued palaeontological work among the ants.

Acknowledgments We thank Ryan C. McKellar for his constructive comments on the manuscript. Our special thanks go to Zdeněk Dvořák (Bílina Mine) for assistance and access to the Bílina Mine enterprise collection and Dorothea Kranz for the reconstruction. The research received support from grants of the German Science Foundation WA 1492/3-1; 4-1; 6-1 (to T.W.) and the grant agency of the Czech Republic No. 205/09/J019 (to J.P.). G.M.D. was most recently funded by the Russian Foundation for Basic Research, project no. 11-04-00421. S.K. acknowledges the support of his doctoral study by the Charles University Grant Agency (GAUK) (No. 287911/2011/B-Bio/PiF) and SVV project (Integrative Animal Biology) No. SVV-2013-267-201.

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Příloha II

Censier, F., Chavalle, S., **Knor, S.**, De Proft, M., Bodson, B., Skuhrava, M. 2014. Unusual Occurrence of Cocoons in Population of *Haplodiplosis marginata* (Diptera: Cecidomyiidae) in Belgium. **Journal of Insect Science**, DOI: 10.1093/jisesa/ieu101. [IF 0.921]

RESEARCH

Unusual Occurrence of Cocoons in Population of *Haplodiplosis marginata* (Diptera: Cecidomyiidae) in Belgium

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Subject Editor: Phillippe Usseglio-Polatera

J. Insect Sci. 14(239): 2014; DOI: 10.1093/jisesa/ieu101

ABSTRACT. The saddle gall midge, *Haplodiplosis marginata* (von Roser) (Diptera: Cecidomyiidae), is a phytophagous species that develops in saddle-shaped galls on stems of wheat *Triticum vulgare*, barley *Hordeum sativum*, rye *Secale cereale*, and some other species of Poaceae. Only one generation develops per year. Full-grown larvae leave galls and drop onto the soil where they remain up to the springtime of the following year. Larvae do not usually spin cocoons. However, formation of cocoons by larvae was observed in populations developing in western Europe: in England in 1954, in the Netherlands in the 1960s, and in Belgium in 2011. On the basis of our analysis, a part of the larval population forms cocoons as protection against unfavorable weather conditions, especially drought.

Key Words: salivary gland, life cycle, development, Europe

The cocoon is a case produced by some animals during the larval stage. The cocoon may protect larva or pupa or eggs. It is known that some butterflies (Lepidoptera), lower flies (Diptera: Nematocera), and worms (Hirudinea and Oligochaeta) form cocoons. Some spiders (Araneae) also spin a fibrous mass, to cover their eggs. Larvae (caterpillars) of the domesticated silkworm *Bombyx mori* (Lepidoptera: Bombycidae) form cocoons, the fiber of which is used to weave silk.

In Diptera, cocoons protect larvae or pupae against the attack of predators or parasitoids and under changes in climatic conditions. It is constructed by the previous larval instar. The cocoon may also include soil particles, small stones, particles of leaves, or may only be made of silk. The formation of cocoons is frequent in Chironomidae, Keratoplatidae, Mycetophilidae, and Cecidomyiidae. This phenomenon has been described in detail by Darvas and Fónagy (2000).

Larvae of the gall midge family (Cecidomyiidae) use various strategies and adaptations to survive unfavorable environmental conditions (Skuhravý et al. 1996). One of them is creating or spinning cocoons during their life cycle. They use the secretion of salivary glands to create the cocoon. During this period, the salivary glands change and gradually reduce in size (Skuhravý 2007). Considerable variation occurs in cocoon making. In nature, this variation may be a response to the environment (Gagné 1989).

The saddle gall midge, *Haplodiplosis marginata* (von Roser, 1840), is a polyphagous species belonging to the family Cecidomyiidae that develops on various cereals (wheat *Triticum vulgare*, barley *Hordeum sativum*, and rye *Secale cereale*) and grasses (mainly on *Argopyron repens*). It is a minor pest in cereals in northern Europe, but a major pest in central Europe (Skuhravý et al. 1993, Skuhrová 2000). *H. marginata* mainly affects wheat and barley. Larvae cause saddle-shaped galls on the stems covered by the leaf sheaths. The full-grown larvae are 2.5–4-mm in length and rose red. They have a strongly sclerotized organ called “sternal spatula” on the ventral side of the prothoracic segment.

Only one generation of *H. marginata* develops per year. The life cycle starts in springtime. Adults generally emerge in May and at the beginning of June, sometimes the flight of adults may be prolonged up to the end of June. After mating, the females lay eggs on the leaves of

cereals. The life of an individual is very short, lasting 1–4 d. Larvae hatch from the eggs and move to the stem where they feed under the leaf sheaths and cause saddle-shaped galls. A single larva develops in each gall. There are usually two or three galls per stem but during outbreaks up to 60 larvae develop on one stem. The larvae quickly develop in galls from June to mid-July. The full-grown larvae leave galls and drop onto the soil where they spend the majority of their life from July to April of the following year. Most larvae hibernate at depth of 10–20 cm, and some larvae were found as deep as 40 cm. In the springtime, the larvae move up from deeper layers to the surface of the soil where they pupate. Pupation lasts 14–25 d and then adults emerge (Skuhravá 2000, Skuhrová and Skuhrový 2013).

Forming a cocoon during the life cycle of *H. marginata* has not been previously described in detail. Only Barnes (1956) mentioned that pupation of *H. marginata* takes place in a cocoon in the springtime not long before the emergence of the midges. One larva in a cocoon and eight larvae without cocoons were observed in soil samples at Harpenden (Hertfordshire, England) in the springtime of the year 1954.

The unusual formation of very thin cocoons in the population of *H. marginata* was observed in the Netherlands in the 1960s by Nijveldt and Hulshoff (1968). They explained this phenomenon as a layer produced by larvae, by their own slime, to protect themselves against severe drought, when the climatic conditions were very unfavorable. They mentioned that such coverings are rarely observed by researchers because they can be quickly destroyed as they are extracted from the soil samples.

In the Czech Republic, the larvae of *H. marginata* enveloped by cocoons have never been found although many soil samples including about 100 specimens of larvae were taken and examined during outbreaks of this gall midge species from 1971 to 1989 (Skuhravý et al. 1993).

In 2011, *H. marginata* larvae enveloped by thin cocoons were observed in Belgium during investigations in areas where wheat is cropped intensively (Censier et al. 2012).

In this article, we describe the cocoon of *H. marginata*, its shape in color photographs, and its occurrence in Belgium. We try to elucidate

the reasons why a cocoon is formed on the basis of the analysis of environmental conditions and the comparison of occurrence of this phenomenon in other gall midge species.

Materials and Methods

Occurrence of *H. marginata* in the studied areas was evaluated by taking soil samples and counting larvae from soil surface up to a depth of 15 cm. Soil samples were taken from wheat fields in two localities in Belgium: Sauvenière and Meetkerke.

Sauvenière is a village near Gembloux, in the province of Namur, at about 127 km southeast from the North Sea. The geographical coordinates are 50° 34'30" N and 4° 44'28" E, at an altitude of 153 m a.s.l. The field, of a size of 5 acres with a loamy soil, has not been plowed before setting up the trial. A part of the trial was sown on 14 October 2010, and the other on 23 November 2010, using several varieties of wheat.

Meetkerke is a village located in the Belgian polders near Bruges, in the Province of West Flanders. The geographical coordinates are 51° 14'51" N and 3° 08'55" E. The altitude is 1 m a.s.l. The 8-acres field has a clay soil with a high content in organic matter (>10%). It was sown with spring wheat (variety Marin) on 2 February 2011 without prior tillage.

Meteorological data for surveyed sites come from the stations of Gembloux and Jabbeke, which are, respectively, 4 and 8 km away from the fields of Sauvenière and Meetkerke (Meteobelgique 2012).

In the field of Sauvenière, one soil sample was taken in the middle of the field on 22 April 2011. The sampled area was 0.16 m² and 5 cm in depth. The soil sample had been frozen at -17.5°C until the larvae extraction.

Four soil samples were also taken in the middle of the field in Meetkerke on 8 June 2011. Three layers of 0.02 m² and 5 cm deep (0–5, 5–10, and 10–15 cm depth) were taken for each sample. In this case, the larval extraction took place just after sampling.

For the extraction of larvae, each soil sample was placed in a 5-liter bucket filled with water and then kneaded until the full dispersion of soil particles. Water containing soil was poured on three successive sieves with openings of 3 mm, 1 mm, and 500 µm. This operation was repeated until the entire sample was filtered. The larvae were extracted from the sieves with a paintbrush and finally counted.

Regarding the soil samples taken in Meetkerke, the vertical distributions of free larvae and larvae in cocoons were statistically compared by using a chi-square test of independence ($\alpha = 0.05$).

In Prague, a picture of cocoons with larvae of *H. marginata* was taken using the Canon D550 camera with a reverse MP-E 65 mm lens. Cocoons containing larvae of *H. marginata* were mounted on microscope slides to allow their structure description.

Results

In 2011, a total of 1,359 larvae of *H. marginata* were extracted from all the soil samples: 13 larvae in Sauvenière and 1,346 larvae in Meetkerke (Tables 1 and 2). In both study areas, most of the larvae of *H. marginata* were found without cocoon, the usual phenomenon connected with the life cycle of this gall midge species. Only a small

proportion of larvae were enveloped by thin cocoons, a rare phenomenon observed in this species.

The cocoons were ball shaped, globular or spherical formations, about 2 mm in diameter. The larva inside a cocoon is bent or rolled into the shape of a crescent (Fig. 1). One can see the dark-brown-colored sternal spatula situated on the ventral side of the larval prothorax. The cocoon is quite translucent and is formed of a very thin layer, without any structures, and it seems that it is not spun from fibers (as cocoons usually are), but it includes very small particles, small stones, or very small grains of sand.

Larvae of *H. marginata* enveloped by cocoons were observed for the first time in Sauvenière on 22 April 2011. In one soil sample, 13 larvae of *H. marginata* were found. Seven of them were in cocoons. The ratio between larvae enveloped with cocoon (54%) and larvae without cocoon (46%) was ~1:1. In this soil sample, the number of larvae enveloped by a cocoon was high, but the total number of larvae was very low.

The larvae of *H. marginata* enveloped by cocoons were also observed in soil samples taken in Meetkerke on 8 June 2011. In total, 1,346 larvae were found in four soil samples on a depth of 15 cm (Table 1). The majority of them, 1,238 larvae (92%), were without cocoon, and 108 larvae (8%) were enveloped by thin cocoons.

At the beginning of June, the largest number of larvae of *H. marginata* (~48%) occurred in the upper soil layer at the depth of 0–5 cm (Table 2). The number of larvae decreased with increasing depth. In the deep soil layer of 10–15 cm, only 8% of the larval

Table 2. Distribution of larvae of *H. marginata* in different soil depths in Meetkerke (Belgium) on 8 June 2011

Depth of sample	Number of larvae	Free larvae	Larvae in cocoon
0–5 cm	647 (48%)	585 (47%)	62 (57%)
5–10 cm	586 (44%)	550 (44%)	36 (33%)
10–15 cm	113 (8%)	103 (8%)	10 (9%)
Total	1,346	1,238	108

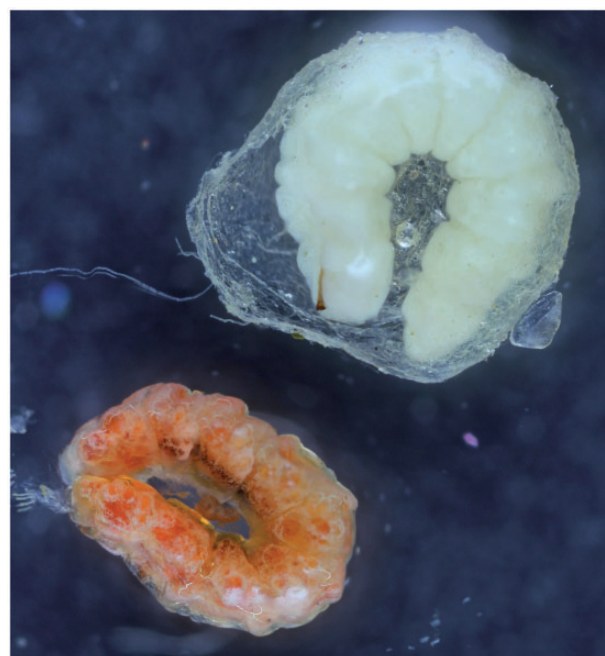


Fig. 1. Two larvae of *H. marginata* enveloped by thin and translucent cocoons. Rose/orange colored larva of future female (below), and white larva of future male with brown colored sternal spatula on the anterior body part (above).

Table 1. Occurrence of larvae of *H. marginata* in soil samples in Meetkerke (Belgium) on 8 June 2011

Sample	Number of larvae	Larvae in cocoon	Percentage of larvae in cocoon
A	57	7	12%
B	559	35	6%
C	517	46	9%
D	213	20	9%
Total	1,346	108	8%

Average proportion of cocoons (A–D): $9.2 \pm 2.5\%$.

population occurred. A high proportion of larvae in the upper soil responded to the state before the emergence of adults. A part of the population of *H. marginata* occurring in deeper soil layers (8%) will probably remain in this layer, they will not move up, and will hibernate there.

In these samples, several larvae in cocoons were found in each soil layer, ranging from 10 to 62 (Table 2). The number of larvae enveloped by cocoons, as well as the number of free larvae, decreased with increasing depth. The Chi-square test did not demonstrate a significant difference between the vertical distributions of larvae in cocoons and free larvae ($\chi^2 = 5.04$; $df = 2$; $P > 0.05$).

Discussion

Larvae of gall midges form cocoons in response to changes in their environment. Depending of the species, creating a cocoon may be a permanent part of the life cycle, or a cocoon is formed only under certain unfavorable environmental conditions. It gives physical protection against bad conditions or natural enemies. The formation of a cocoon is a permanent part of the life cycle of the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin 1857). The larvae spin cocoons to overwinter, but this can only take place under some conditions. This is also the case of *Resseliella dizygomyzae* (Barnes 1933), which larvae hibernate in a cocoon if they are in the soil, while the larvae remaining

in burrows on the rods of *Salix viminalis* hibernate without spinning cocoon (Urban and Skuhravý 1982).

Some gall midges can also adapt their behavior according to altitude. Larvae of *Thecodiplosis brachyntera* (Schwägrichen 1835) spin cocoons in the soil at low altitudes but hibernate at the base of pine needles without creating cocoons in mountains at altitudes over 1,200 m a.s.l. (Skuhravý 1991).

It seems that the formation of thin cocoons by larvae of *H. marginata* is correlated with environmental conditions. Nijveldt and Hulshoff (1968) considered it as a mechanism of resistance to drought. Our observations reported here support this hypothesis. Indeed, in 2011, cocoons including larvae of *H. marginata* were only found during drought conditions, resulting from the combination of higher average monthly temperatures and a lack of rainfall, when compared with the average of the last 10 yr (Fig. 2).

H. marginata occupies a large distribution area in Europe. It occurs in 20 countries (out of 40 countries from which data are available), and it occurs from western Europe (e.g., the southern part of United Kingdom) to eastern Europe (e.g., Romania and Bulgaria), reaching up to the Black Sea. It is a serious pest of cereals mainly in central and eastern Europe: in Germany, Poland, Czech Republic, Slovakia, and Romania (Skuhravý and Skuhravý 2013).

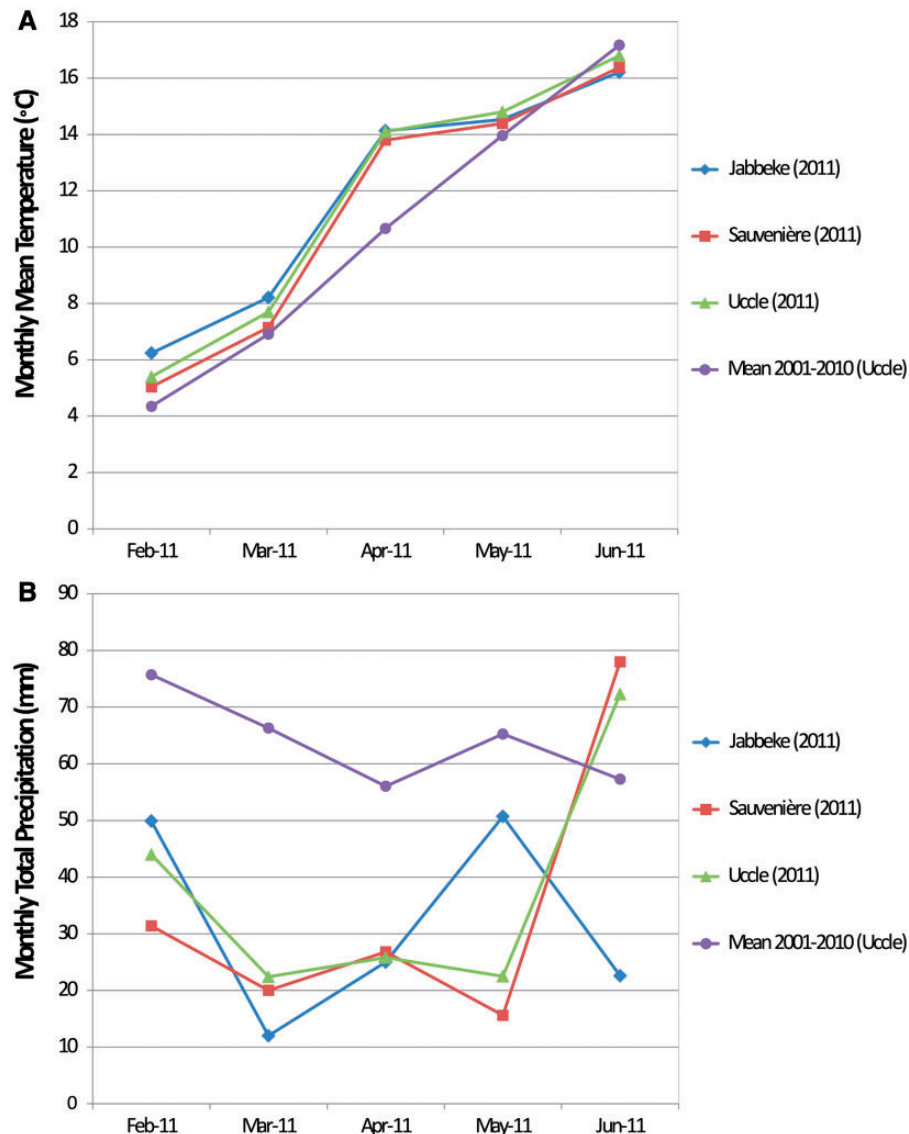


Fig. 2. Monthly mean temperature (A) and monthly total precipitation (B) between February and June 2011 for the two studied sites and for the reference meteorological station in Belgium (Uccle), and monthly means of the last 10 yr for Uccle.

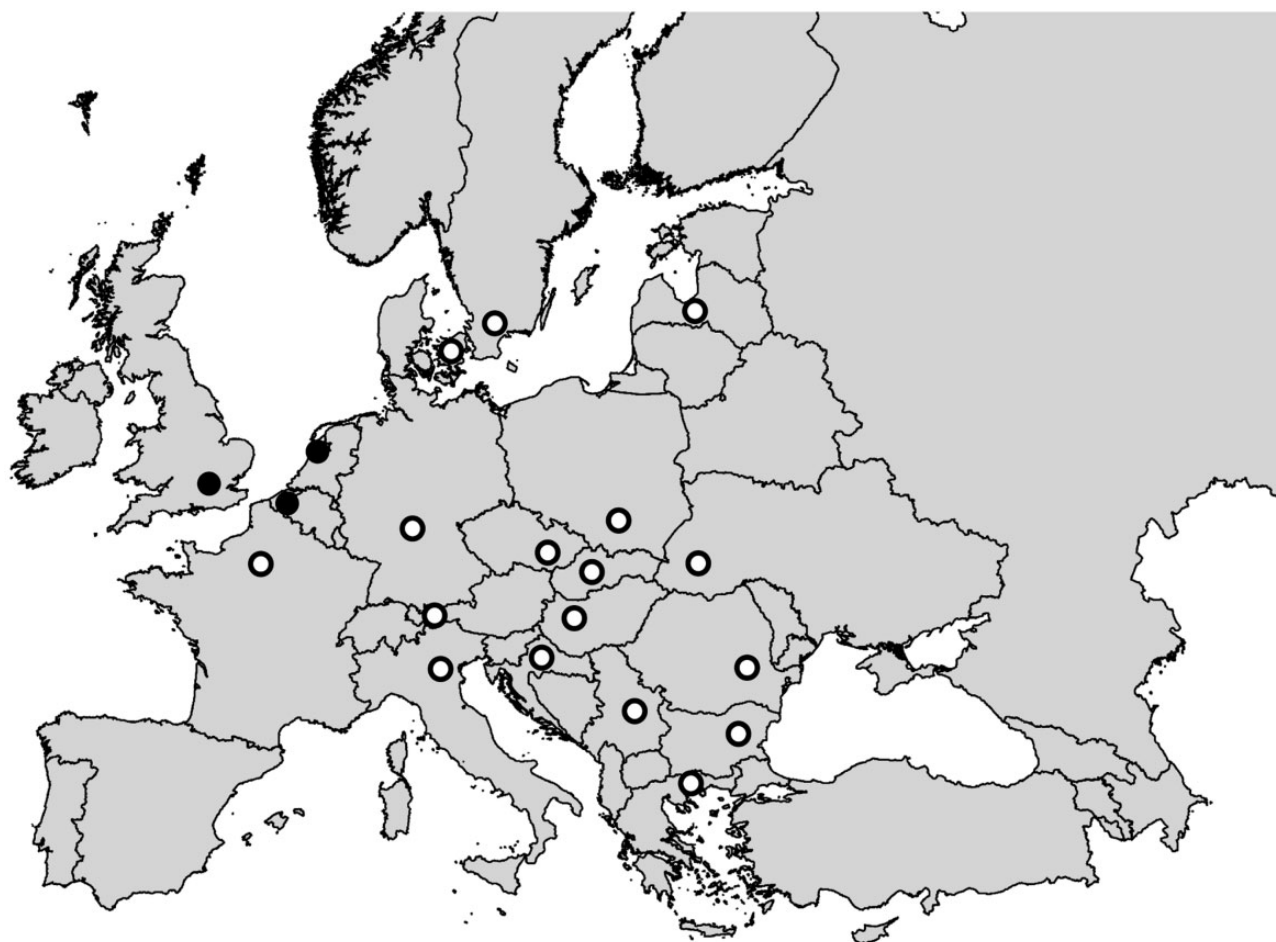


Fig. 3. Occurrence of *H. marginata* in countries of Europe: black circles, population including larvae of both types, with and without cocoons; white circles, population including larvae without cocoons.

It is interesting to notice that the larvae of *H. marginata* enveloped by cocoons were discovered in soil samples only in three countries of western Europe, all situated near the sea: Harpenden (United Kingdom), Arnhem-Nijmegen (the Netherlands), and recently in Belgium (Fig. 3). They have never been found in soil samples collected from countries of continental Europe. The formation of thin cocoons by larvae in the soil might thus be connected with the geographical position of localities and their degree of oceanity-continentiality. Future research should focus on central Europe and the Mediterranean area to validate this hypothesis.

Acknowledgments

F.C. gratefully thanks Jessica Denayer and Alain Mahieu (Plant Protection and Ecotoxicology Unit, CRA-W) for their help in field work. S.C. acknowledges the financial support from the Walloon Region (D GARNE). S.K. acknowledges the support of Charles University Grant Agency (GAUK) (287911/2011/B-Bio/PřF) and SVV project (Integrative Animal Biology) SVV-2013-267 201.

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Received 24 July 2013; accepted 9 January 2014.