Abstracts of the Immature Beetles Meeting 2017
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The Seventh Immature Beetles Meeting was held in Prague on October 5–6, 2017. Just like as two years ago, it took place at the Faculty of Science of the Charles University in Prague and was organized in cooperation with the Department of Entomology of the National Museum and the Crop Research Institute in Prague. In total, 63 participants from Europe, South America, Asia and New Zealand attended the meeting (see the list of participants and the group photo in Fig. 1). The attendance has increased since the first meeting took place in 2006. More than 40% of the participants attended the meeting for the first time, and we were again pleased to host not only the established scientists in beetle systematics but also many students. Eighteen oral lectures and one poster were presented, covering a wide spectrum of topics concerning nearly all major clades of beetles (Adephaga, Hydrophiloidea, Staphylinoidea, Scarabaeoidea, Byrrhoidae, Buprestoidea, Elateroidea, Chrysomeloidea and Curculionoidea). The contributions embraced many interesting topics such as unusual adaptation of immature beetles in environments like caves and bromeliad plants, DNA barcoding and its role in ecological and faunistic monitoring, as well as biographic memories of the life and work of the great immature-beetle pioneer, Fritz Isidore van Emden. After the presentations were finished, an optional visit to the Coleoptera collection of the National Museum took place, and was enjoyed by the colleagues who joined. As it became a tradition for the Immature Beetles Meeting, the discussion about beetle topics continued in a traditional Czech pub on both evenings.

We hope that the meeting again fulfilled its main goal – to bring together people with an interest in the immature stages of Coleoptera, and to help specialists to establish and maintain contacts and cooperation with colleagues across countries and generations.

In keeping with the spirit of providing a platform for coleopterists interested in the immature stages, the organizing team of the Immature Beetles Meeting is presenting a new web page. Besides helping to promote the meeting itself, it is intended to be a virtual meeting point for specialists worldwide where their profiles including their publications lists will be available, together with other news regarding the world of beetle larvae. This page is already live at this address: http://www.immaturebeetles.eu/.
The next meeting is planned for autumn 2019 and will be held at the Charles University in Prague again. On behalf of the organizers, we would like to thank again all participants who attended the meeting, shared their research and most importantly contributed to enjoyable and friendly atmosphere. We think it was a success for all of us, and we hope to see new and old faces again in 2019!

The Organizers of the Immature Beetles Meeting

Acknowledgements

We thank all colleagues and students who supported the organization of the Immature Beetles Meeting 2017 by giving an oral presentation or presenting a poster. Furthermore, we are indebted to the students who took care of the refreshments and drinks and help to run the meeting smoothly, as well as to the senior team, who give us all information and advice gained from the previous years of the IBM, namely Martin Fikáček, Jiří Skuhrovec and Petr Šípek.

Pavel Munclinger (Head of the Department of Zoology, Charles University) kindly supported our initiative to organize the meeting financially and provided the space where the meeting took place. The National Museum in Prague and the Crop Research Institute supported IBM 2017 as well. The meeting was organized as a part of research activities of the organizers and partial support by the grant SVV 260 434/2017 (from the Charles University) to MS, EAV, DV and the grant of the Ministry of Culture of the Czech Republic (DKRVO 2017/14) to DV.

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The abstracts should be cited as follows:


The text of the abstracts is published in the original version as received from the authors.
Fig. 1. Participants of the Immature Beetles Meeting 2017 during the second day (Prague, 6th October 2017).
ORAL PRESENTATIONS

Recollections on the Life and Work of a great immature-beetle pioneer, Fritz Isidore van Emden (1898–1958)

by his son Prof. H. F. VAN EMDEN
presented on his behalf by Maxwell V. L. BARCLAY \(^1\) & Beulah GARNER \(^1\)

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Fritz Isidore van Emden (1898-1958) was a leading figure in the development of the study of immature beetles, with a suite of important publications, taxonomic, morphological and methodological. His extensive larval collection is now at the Natural History Museum, London. His son, the leading horticultural entomologist Helmut F. van Emden, offered to share his recollections of his father and his work. Regrettably, because of a medical operation Professor van Emden was unable to travel to Prague, so he asked Max Barclay and Beulah Garner of the Natural History Museum, London, to read his text out on his behalf. Beulah Garner and Max Barclay are completing a handbook for the identification of the British beetle larvae, based on F. I. van Emden’s collection. They gave a presentation where they discussed the collections of the Natural History Museum with particular reference to that of F. I. van Emden, and progress on the production of the larval handbook, before reading out H. F. van Emden’s recollections, which are reproduced in full below.

Reminiscences on my father, Fritz van Emden

My father, Fritz Isidore van Emden, was born in Amsterdam on 3rd October 1898. His father was a textile merchant, but the business became bankrupt two years later in 1890. The family then had to move to Germany and set in business again, since in the Netherlands it was illegal for a bankrupt to start a new business. As he grew up, my father noticed that insects were eating his father’s stock, and this was how his interest in entomology began. Indeed, one of his first publications was a monograph on the insect pests of stored textiles and carpets.

His interest in entomology flourished with time. Although his PhD at Dresden University was on the care of young by the aquatic crustacean Asellus aquaticus, it was as an entomologist that he later found employment at the famous Zwinger Museum in Dresden. He built up an extensive personal collection of carabid beetles, and became increasingly aware of how little literature was available for the identification of their larvae. He began collecting beetle larvae in general, and these were to become his dominating entomological love for the rest of his life.

The advent of the Nazis cost him his position at the Zwinger. His mother was a Jewess, and for this reason he was debarred from German Civil Service employment.

By now he was married with two young sons, and had to look for employment elsewhere. He was offered a post at the Museum in Budapest, and had more or less decided to move the family to Hungary when Gilbert Arrow, a coleopterist at the Natural History Museum who had been most impressed with my father’s reputation, persuaded him to consider London instead and secured a grant to fund his travel and other expenses. My father always said that it was the English steamed puddings that were the deciding factor, but in any event he decided to go
to London. So in 1936 my mother had to arrange the move of the family to England. I doubt if I would be alive to write this account today had we moved to Budapest!

Then came a major hiccup. The Keeper of Entomology pointed out to Arrow that Museum rules forbade employment of a specialist in a taxon where he had a private collection. Father would have to hand in his carabid collection (I’m not sure they knew about the larvae). My father refused, and by now we had burnt our boats in Germany. The solution agreed by the Museum and father was that he should transfer to the Commonwealth Institute for Entomology staff on the Diptera floor at the Museum. And so my father began from scratch with the taxonomy of tachinid flies, and developed a productive and internationally respected career in a totally unfamiliar taxon. Of course colleagues from overseas would expect to be able to talk with him about beetle larvae when they visited the Museum, and this was not regarded as a problem. Father was quite a polyglot. Fluent in English, German and French, he could hold his own also in Dutch, Italian, Spanish and even the artificial international language Esperanto. On one occasion a Romanian visitor defeated even my father’s linguistic abilities until they realised they had both learnt classical Greek at school. That was probably the last time classical Greek was used as a living language, and to discuss beetle larvae at that!

Tachinidae were therefore his day job, but his life’s ambition was to contribute to beetle larva taxonomy by working at home evenings and weekends. Thus, after the family supper most days, he would retire to his fully equipped study and extensive library to pursue his entomological passion. The larvae were kept in alcohol in glass tubes of the minimum necessary diameter for the species, and with a paper disc bearing a reference number in Indian ink rammed into the curved end of the tube. The open end of the tube was stoppered with cotton wool, and the tube kept inverted in a jar with a bed of cotton wool soaked in alcohol and with alcohol kept topped up to a centimetre or so above the cotton wool bed. The jar was divided into four sections by a plastic cross. Thus on locating the right jar and section, my father could locate any specimens he wished to work on by locating the correct number disc at the tube end with a magnifying glass.

The jars were kept in the dark in a Victorian cupboard brought from Germany, and the strength of its construction was proven by the fact that the collection survived three occasions during the war when the house was badly damaged during bombing raids.

Father would always work with music from a radio beside him, totally involved with his larvae. His taste in music was rather limited and could be described as “light classical” and he was completely unaware that his hand would reach out and change the radio station should his brain subliminally hear the words “conducted by the composer”.

His technique in working out keys was to prepare a table with the species to be included as the rows, and a large number of empty columns. He would then look for any characters which varied between species, allocate a column to this character and then fill in the column with + or – against each species. Whenever possible, he would check every instar, and this often involved breeding from adults. He invented very simple rearing ‘cages’ with plaster of Paris walls and glass lids. These cages could be stood in water-filled trays to keep humidity within them high, and the house was full of such trays. Of course, he also used this system for breeding larvae he had collected to adult; it was a point of principle that he could be certain of the identity of his larvae when so few keys were available. When he had enough specimens he would boil the exoskeleton of one in potash, dissect it into parts, and mount these in Canada
balsam. He found the detail he could see on these slides with a monocular microscope very valuable. He illustrated the characters in his keys with many small drawings – in those days done with a fine pen and Indian ink on thick shiny card called “Bristol board”. I remember him teaching me how to draw a tapering seta with a stroke of the pen nib.

I remember how dismissive he was of keys which used comparative words like “larger” or “more rounded”, since usually they would be used to try to identify a specimen without a comparison being available. He felt characters had to stand on their own, so he would, for example, replace “longer” with a measurement on the same specimen, e.g. “at least half the length of the tibiotarsus”. He also avoided reference to structures which would change in shape with time. For example, the then main key to the soil-dwelling elaterids in the genus Agriotes was based on the “sharpness” of the mandible. As this changed from “sharp” after every moult to “blunt” by the end of each instar, an Agriotes larva of any species would be identified as three different species in the course of each instar.

Our holidays were day trips by rail to the countryside in the county of Surrey with a picnic, particularly to locations were particular beetles and their larvae might be found. An especial favourite was a valley at Box Hill with ant mounds on the slopes, in which my father hoped to find larvae of the pselaphid iniquiline Claviger. The adults were not uncommon, but finding the larvae became somewhat of an obsession. We collected ants with brood and their queen as well as adult Claviger, and moved them into a soil-less plaster of Paris nest. The earth with ant queen, workers and brood would be spread out before the damp plaster nest and a desk lamp lowered over the earth to dry it out. Each time we did this my brother and I would count the number of ants entering the nest per minute and watch how “the word got around” and this number escalated dramatically. I can remember my mother being furious that we were so absorbed that we continued counting instead of coming to the supper table. I tried the same thing with a student field course I ran in North Wales for the Zoology Department at Reading – do you know, we again found it hard to prise the students away when supper was ready!

Anyway, back to Claviger. In spite of repeated trips to Box Hill and setting up new plaster nests, there was no luck in getting the beetles to breed. My father re-designed the nest to enable the nest to accommodate root aphids on grasses in case the adult Claviger needed honeydew – still no luck. After many such attempts my father wondered whether perhaps the larvae lived elsewhere, and for reasons I cannot recall homed in on the flower buds of hawthorn bushes. He even obtained a licence for a colleague to shoot a few blue tits Cyanistes caeruleus so that he could look for the larvae in their guts, but again drew a blank.

As his 60th birthday drew ever nearer, father was really looking forward to retirement and the opportunity to work full time on his larvae with the aim of producing a Royal Entomological Society Handbook for British beetle larvae, but tragically he died from a brain tumour on 2nd September 1958, just a month before his due retirement date. He had of course hoped that one of his sons would carry on his work. My older brother, however, decided to concentrate on languages and finished up as a specialist in medieval French literature. Indeed eventually he applied for and was appointed to the Chair in French Studies at Reading University, where I was already long established. I was more interested in sciences, and took a degree in Zoology and Applied Entomology at Imperial College, London. My undergraduate research project was indeed a key to beetle larvae in the genus Elater [Ampedus in the contemporary concept]
(Elateridae), stimulated by my father finding the first couplet of the existing Victorian key unsatisfactory. It read “larva yellowish-brown” with the contrast “larva brownish-yellow”. At this time I still had an open mind about my future entomological career. However, a surprising observation on aphids during my PhD at Imperial College took my research career in a completely different direction, and I was drawn to the nutritional physiology of aphids and how this determined whether predators had any impact on aphid populations. Soon after I secured my first permanent position, at The University of Reading, I did publish a key to the larvae of tortoise beetles, but was roundly told off by my Head of Department and instructed not to waste any more time on taxonomy, a discipline that in his opinion was only suitable for those “not intelligent enough to do experiments”.

After my father’s death, I moved his collection of larvae to Reading, and at least kept it in good condition by checking it regularly and topping up the alcohol when necessary.

I was therefore glad when, in the early 1970s, the Museum asked me whether they could have the larva collection, to enable a new appointee to produce the Handbook that my father had hoped to complete in the retirement that never happened.

Unfortunately, after only a short time, the young entomologist concerned had to resign through illhealth. Although a more senior colleague then did quite a lot of work, by the start of the 1990s the project had been kicked into the long grass. I was told it took the form of a brown paper parcel which hadn’t been opened for years. I regularly pestered four Heads of Entomology at the Museum in succession, all of whom said “leave it to me” without achieving any progress. I more or less gave up on ever seeing the promised Handbook, even when a few years ago I heard that a new generation of coleopterists at the Museum had picked up the project. The good news is that the Handbook is completed and expected to be published by the Royal Entomological Society in time for a copy to be presented to me, hopefully at the 2018 Verrall Supper. This is a dinner for entomologists held in London every year on the first Wednesday in March. I am really most grateful that Beulah Garner and Max Barclay at the Museum were prepared to add the completion of this Handbook to their already heavy workload, and that my father, through his collection, has made a major contribution to the Handbook that he was unable to complete himself.

Helmut van Emden
The University of Reading

**Bromeliads as beetle birthscentres in Brasil with remarkable news on Chelonariidae immatures**

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Bromeliads is a magnificent group of plants representing a monophyletic family, the Bromeliaceae. The bromeliad lineage arose around 100 Mya, but the strongest species radiation shall have occurred from 12 to 20 Mya. Unless by a unique species from Africa, the whole family is endemic from the American Continent, and it is represented by more than 3,000
species (PAHM-SILVA et al. 2016). Bromeliads stands as a truly micro-ecosystem with an inordinate variety of designs and places where they grow on, resulting on distinct ways of retaining water and leaf litter, and accordingly, to the interaction with their associated fauna and flora (PICADO 1913, RICHARDSON 1999).

Within this context, it is not surprising that several species of distinct niches of beetle larvae live in bromeliads in Brazil, and thus, bromeliads stands as actually birthcentres of those species. Few are phytophagous beetles of the families Chrysomelidae, Curculionidae, Dryophthoridae and Scarabaeidae. The chrysomelid larvae of Calliaspis umbonata Hincks, 1956 and Calliaspis cinnabarina Boheman, 1950 (Cassidinae: Imatidiini) have the body plan similar to the known larvae of Cephaloleia (GARCIA-ROBLED0 et al. 2010). Although leaf-scrapers, they feed on tough mature leaves and do not seriously damage the leaves (ALBERTONI 2017). On the other hand, Cephaloleia sp. scraps the youngest leaves from the rosette centre, causing considerable damage to them, but usually not leading to leaf senescence (Albertoni, unpub. data). In addition, the larva of Spaethiella intricata (Boheman, 1850) (Cassidinae: Hemisphaerotini) are leaf-scrapers, and depending on the number of larvae on the same leaf, they can significantly damage it (Albertoni & Leocádio, in preparation). Larvae of Acentroptera basilica Thomson, 1956 and A. cf. tesselata Baly, 1958 (Cassidinae: Sceloenoplini) were leaf miners and shall be responsible for senescence of few leaves. They feed inside the leaf, between the two most external leaf tissue layers, and can go out from one leaf into another to keep feeding. Pupation also occurred within leaf layers. However, although larvae of only two species are known, they bear significant morphological differences for such a close related species (ALBERTONI & CASARI 2017).

The representative of Dryophthoridae, Paradiaphorus crenatus (Gyllenhal, 1838) are stalk borer of several bromeliad species, including pineapple (Ananas comosus L. Merr.) of which can cause damage of economic relevance on plantations (ALBERTONI et al. 2016). A Curculionidae larvae found several times inside the inflorescence stem of Vriesea frimburtensis Mez in Florianópolis city, Santa Catarina state, must likely belong to Cholus parcus Fahraeus, 1844 (Albertoni, unpubl. data). It feeds on the content present inside the inflorescence stem (Albertoni, unpubl. data). There is yet, the larva of the odd Scarabaeidae Platypheileurus felscheanus Ohaus, 1910 (Dynastinae: Oryctini). When young it feeds on the litter that accumulates in the rosette, but in the last or penultimate instar it migrates to the rosette centre and feeds on living tissue, the stalk and the proximal part of leaves. Predator larvae are those of the family Elateridae, Platycrepidius bicinctus Candêze, 1859 and Platycrepidius dewynteri Chassain, 2009; they are dorsoventrally flattened well-fitting among the leaves of the rosette, and are candidate to be restricted bromeliad-living larvae (ROSA et al. 2015, COSTA et al. 1988). Lachnodacnum luederwaldti Orchymont, 1937 is a bromeliad-inhabiting Hydrophilidae, whose larvae are predators and were observed feeding on dipteran larvae (CLARKSON et al. 2014, ALBERTONI et al. 2016). It is also expected that predator larva of Dytiscidae, Copelatus bimaculatus (RESENDE & VANIN 1991) lives in the water accumulated within the rosette. The immatures of the family Chelonariidae, Chelornarium cf. basale Méquignon, 1934 and Ptilodactylidae, Ptilodactyla sp. are saprophagous leaving on the leaf litter inside bromeliad rosette and feeding on decaying plant material as leaves and tiny twigs of the leaf litter (ALBERTONI et al. 2016).

Something slightly peculiar of C. cf. basale larvae is that in their natural habitat, larvae are
mostly strongly impregnated with dirt and as a result, their general body aspect is strongly deceptive with the medium it is inserted. Their whole body integument is dark brown with isolated setae besides tufts of setae on each of the thoracic and abdominal segment. The head is relatively small comparing to body width. Few other specific characteristics as several types of the setae design are still present (Spangler 1980, Costa et al. 1988, Albertoni, unpubl. data.). However, first instar larvae of C. cf. basale were around two millimetres long, with no dirt at all impregnated on the integument and except by few isolated setae distributed through body segments, the integument is smooth. Besides, their head is at the same size or wider than body width and their overall appearance. Few species of Scirtes sp. (Scirtidae), inhabit bromeliads during the larval and pupal stage. Often they are the most abundant insect inside the rosette (Picado 1913, Richardson 1999, Albertoni et al. 2016). Presumably, they feed on plant debris in decaying advanced stage and on fungus. Important to notice that several of those immatures, not only the decomposer, but most of them contribute to plant nutrition by releasing soluble nutrients into the rosette. Furthermore, in respect to species lifestyle among their own life stages, most species display distinct habits as larva and as adult.


### Description of mature larva and pupa of Conotrachelus dimidiatus: the adversary of the delicious Psidium guajava

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The representatives of *Conotrachelus* are distributed naturally exclusively only in North, Central and South America. In Mexico, around 86 *Conotrachelus* species are known, and three of them are known as pests on guava *Psidium guajava* L. (Myrtaceae). Guava is a native fruit of America and has been cultivated for more than a century in Mexico, primarily in Aguascalientes, where it is very important for the economy as fresh fruit for national consume or export and as raw material for the manufacture of jellies, marmalades, liquors and candies. The damage to the fruits attacked by *C. psidii* and *C. dimidiatus* can reach 100% and 60%, respectively. Despite *Conotrachelus* species being known as very important pests, knowledge about the group is incomplete. In the light of the poor knowledge of adults, it is not surprising that the morphology of immature stages is almost unknown, despite the larval stage of the insect is the most harmful and identification is important for the management of the plague and biological control.

Since the available data of *C. dimidiatus* do not fit with the morphology of known weevils, the present work comprises: a redescriptions of the immature stages of this weevil, a comparison of the chaetotaxy on the larval and also pupal body with other known immature stages of this genus, a key for them, the determination of the number of larval instars via morphometric measurements, and finally details of its life history based on field observations in Mexico. The immatures of the described *Conotrachelus* species are also compared with available data on immatures of several tribes in the subfamily Molytinae. The larvae of genus *Conotrachelus* have a distinct endocranial line of different size and only three setae on frons. The presence of these two distinct characters in larvae of all eight known *Conotrachelus* species is absolutely unique in contrast with other tribes in the subfamily Molytinae.

**The importance of immature traits in Cantharidae systematics (Coleoptera)**

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In spite of the diversity of the family, Cantharidae immatures are poorly known. Brief descriptions and illustrations are currently available for larvae of approximately 40 species, primarily from Europe. These characterizations, however, each tend to focus on different structures, which are described with non-standardized terminology. Published data concerning immature morphology is available for Palearctic species of the subfamilies Cantharinae and Malthininae (c.f. FITTON 1976, KLAUSNITZER 1997) and for Neotropical Chauliognathinae (BIFFI & CASARI 2017). Additional information is also available for particular structures in Silinae larvae (VERHOEFF 1923, GARDNER 1947, FITTON 1976), and for the larval exuviae of an unidentified species of Dysmorphocerinae (CROWSON 1972). Some authors have attempted to assemble these scattered records to help define cantharid subfamilies and genera (e.g. BÖVING
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More recent contributions in Chauliognathinae (Biffi & Casari 2017) and Silinae (Biffi & Casari, in prep.) have corroborated the importance of diagnostic features previously ascribed to these subfamilies, such as the shape of nasale and mandibles, and the number of maxillary palpomeres. In this study, we report immature characters that are pertinent for recognizing closely related species, including variation in the color pattern and chaetotaxy of larvae, as well as the shape of the urogomphi in pupae. When these characters are mapped onto a morphology-based phylogeny of Chauliognathinae (Biffi, unpublished), they are recovered as putative synapomorphies defining various lineages up to species groups. This endeavor emphasizes the importance of detailed and standardized descriptions and illustrations of immatures as a major source of relevant information for both reconstructing phylogenetic hypotheses and characterizing lineages of catharid beetles at multiple taxonomic levels.


Contraction of life cycle in cave beetles

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Beetles represent more than 30% of the species in the animal kingdom and are sharing with the other holometabolous insects a peculiar life cycle including a larva radically differing from the adult in terms of ecology and morphology and a complete metamorphosis. Presence of larval stages is arguably considered as an evolutionary key innovation fuelling lineages diversification. However, in few cases, alternative strategies emerged; this is the case of some lineages of Coleoptera that colonize the subterranean environment. There are some species where larval life is so strongly abbreviated that the hatched, non-feeding larva pupates immediately without moulting. Such strategy is known in the two groups of beetles that successfully diversified in subterranean environment, Leiodidae Leptodirini and Carabidae Trechini, in which it is associated with a reduction in the number of ovarioles. The comprehensive phylogenies available for these two groups in the Pyrenean area (France, Spain) allow to understand the origin of these remarkable convergent strategies.
Usual and unusual ways of breathing in hydrophiloid larvae (Coleoptera: Hydrophiloidea): are textbooks wrong?

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Larvae of the hydrophiloid family Hydrophilidae are adapted to the aquatic life style in many aspects, including the modification of the tracheal system. The tracheal system is supposed to be metapneustic, i.e. with only the spiracles on abdominal segment VIII open and situated in the closable spiracular atrium; the remaining spiracles are supposed to be reduced, closed and hence non-functional. The same is supposed for the families Spercheidae and Hydrochidae which also have the spiracular atrium at the end of the abdomen. In contrast, the spiracular system of remaining three families (Helophoridae, Epimetopidae and Georissidae) is considered as peripneustic, i.e. with one pair of thoracic and eight pairs of abdominal functional spiracles. The hydrophilid genus *Berosus* is mentioned as the only exception from this situation: its larvae are apneustic, i.e. have totally closed spiracular system, the spiracular atrium is absent (reduced) and gas exchange is possible through long abdominal tracheal gills.

Larvae of the hydrophilid genus *Tritonus* (Hydrophilidae: Hydrophilinae: Laccobiini) living in hygropetric habitats in Madagascar and the Seychelles differ from the ‘textbook’ metapneustic situation expected for the family: the first instar larvae have most (i.e. one pair of thoracic and seven pairs of abdominal) spiracles placed on the top of short tubes, and the examination by SEM and light microscopy revealed that these spiracles are normally developed, biforous, and probably functional. The spiracles of second and third instar larvae are also biforous, situated on low tubercles. The spiracular atrium is normally developed in all three instars. We considered this situation as a special adaptation to the life in a thin film of water, with the tubes in the first instar larva possibly working as snorkels. To our surprise, the same modification (biforous spiracles on short tubes) was found in the related terrestrial genus *Tormus*, and the quick examination of few other aquatic genera (*Hydrobius, Oocyculus*) revealed that their spiracles are biforous, with well-developed tracheal tube and hence likely to be functional as well. This indicates that larvae of the Hydrophilidae may be in fact peripneustic, i.e. with all spiracles functional, and the last pair enlarged and situated in the spiracular atrium (for details see Fikáček et al. 2017).

Long spiracular gills on abdominal segments are present in four clades of the Hydrophiloidea: the genus *Berosus* (Hydrophilidae: Berosini) (e.g., Minoshima & Hayashi 2015), the
New Caledonian endemic subgenus *Laccobius* (*Yateberosus*) (Hydrophilidae: Laccobiini) (FIKÁČEK et al., in prep.), some species of the genus *Epimetopus* (Epimetopidae) (FIKÁČEK et al. 2011) and in the larva of *Helophorus* (*Lihelophorus*) *lamicola* (Helophoridae) (ANGUS et al. 2016). In all these taxa except of *Lihelophorus*, the tracheal system seems to be closed (i.e. all spiracles are reduced, non-functional, and the spiracular atrium is absent). In *Lihelophorus*, the tracheal gills are present in parallel to the open tracheal system (with branchial tracheal tubes connecting as a side branch of spiracular tracheal tubes). In all four groups, the presence of tracheal gills seems to go in parallel with the modification of mouthparts: at least the left epistomal lobe is large, mandibles are modified, asymmetrical, in all genera except *Helophorus* with dorsal groove on the left mandible. Similar head morphology is also known in the Australian endemic *Hybogralius* with reduced spiracular atrium but no tracheal gills (Hydrophilidae: Hydrobiusini), in *Hemiosus* with poorly developed spiracular atrium (Hydrophilidae: Berosini), and in *Laccobius* (except *Yateberosus*) and *Oocyclus* with well-developed spiracular atrium (Hydrophilidae: Laccobiini). Mapping of these characters on the phylogenetic tree of the Hydrophilidae reveals that the modification of head morphology always predates the modification of the tracheal system. It probably allows for underwater processing of prey (which is normally not possible in larval Hydrophiloidea due to preoral digestion) and probably opens the evolutionary space for further adaptations for benthic life style, including those of the tracheal system.


**Morphology of immature stages of *Otiorhynchus smrezynski* and *O. coecus***

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Due to previous incomplete descriptions the mature larva and pupa of *Otiorhynchus* (*Otiorhynchus*) *coecus* Germar, 1824 and *Otiorhynchus* (*Proremus*) rotundus Marseul, 1872 (syn. *O. smrezynskii* Cmoluch, 1968) are re-described and illustrated. Biological data obtained from breeding and field-collecting are compared. Diagnoses of the larval and pupal morphology and upgraded keys for selected *Otiorhynchus* species are given. In addition, diagnostic
characters of larvae and pupae of the subfamily Entiminae were studied due to their usability in taxonomic studies, and a key to selected tribes is provided.

Up to now we described or re-described the immature stages of larvae and/or pupae of 18 species from 12 subgenera. Our data show that – despite high variety in morphological structures – a good characterisation of a typical *Otiorhynchus* larva and pupa is still possible allowing the differentiation from any other Entiminae.

This large genus with high biodiversity in mountain areas and a few noxious species of lower altitudes is also characterised by different patterns of development as well.

**A few new facts about larvae of *Leiodes (Leiodes) cinnamomea* (Leiodidae, Leiodini)**

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*Leiodes cinnamomea* (Panzer, 1793) is a member of worldwide family Leiodidae, which includes over 4,000 species. It belongs to Leiodinae, one of two the most diversive subfamilies. However, immature stages in the subfamily are described mostly for Agathidiini and a few Scotocryptini. Among 429 known species of Leiodini, only larvae of *L. cinnamomea* were described till now, except short note by Lyszkowski about *Leiodes rufipennis*.

*L. cinnamomea* is a well-known European truffle beetle, mainly feeding on *Tuber melanosporum* and *T. aestivum*. Although the species is the pest of the most economically valuable fungi, its biology is not well studied and immature stages were described by Arzone in seventies of the last century. Her studies had rather ecological character and many morphological aspects were not described. New morphological data on this subterranean fungi beetle are provided, with some observation on its biology.

The two characters never seen in the leiodid larvae are: tubercules on the dorsal side of cranium and large, blunt-ended, strongly sclerotized spines on the mid line of dorsal abdominal segment IX. These two characters may be connected with stridulation behavior of arching up the abdomen over the head as was suggested by Lyszkowski.

**DNA barcoding of Coleoptera larvae: its impact for ecological-faunistic monitoring studies on the example of woodlands south of Münster (Germany)**

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Saproxylic Coleoptera – species dependent on deadwood – are an often applied group in biological monitoring projects to evaluate the ecological conditions of forest ecosystems. However, beetle’s larvae were not considered within those projects due to the lack of experts
and the difficulty of their identification. Here, a first monitoring study using beetle larvae as well as imagos was realized. During one vegetation period in 2015, 40 sifting samples from deadwood structures, which also comprised beetle’s larvae aside from imagos, were taken in eight different forest sites near Münster (Germany). The sites represented a utilization gradient, including two commercial forests, two wilderness development forests, and four nature reserves. Adult specimens of these samples were identified in a separate previous study based on morphology. For the determination of the larvae, DNA barcoding (CO-I) was used. The main objective of the present study was to figure out whether larvae can be recorded on a large scale, if they can be barcoded and identified successfully, and whether the inclusion of larval data may improve ecological and taxonomic (find scientifically undescribed larvae) results of field surveys.

Altogether 129 species were found as larva (313 as imago) within all sifting samples. Four larva species (eight specimens) could not be identified to species level because reference sequences were missing. 51 (41 %) of the species recorded as larva were not collected as imago within all sifting samples. Moreover, nearly 30 % of the identified larvae are unknown to science and are in need of detailed morphological description. The inclusion of larvae increased the expected species richness. Furthermore, the addition of larval records generated a more precise differentiation between the study sites in respect of saproxylic species richness, because of undiscovered and rare specialized species, which were not recorded as imago. As another result, it has become apparent that the nature reserve sites were clearly more species rich than the remaining sites. The results indicate that barcoding of larvae provides useful taxonomic and ecological insights, but the economic effort might not justify its application in monitoring projects yet. Further reduction of sequencing costs and methodological progress will make the sequencing and inclusion of larvae in monitoring projects worthwhile and highly useful.

Larval morphology of Goliathini (Coleoptera: Cetoniinae) and its contribution towards the understanding of the group’s evolution

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Currently there are almost 4000 described species of rose chafers (Scarabaeidae: Cetoniinae) but larvae of less than 200 species are described. In this work we studied larval morphology of 86 species belonging to 58 genera with focus on the tribe Goliathini. The larvae of 21 genera were studied for the first time. 77 morphological characters on head, mouth parts, legs and thoracal and abdominal segments were studied. This resulted into large matrix of morphological characters, which were further tested in separate phylogenetical analyses. A checklist of studied characters and their states and also large databasis of photographs of the characters are also amongst the results of the thesis. Five independent datasets were
tested, three were based singly on morphology, one on molecular sequences and one on a combined dataset. The phylogenetic analysis was made by three methods, maximum parsimony, maximum likelihood and Bayesian interference. Eleven different phylogenetic trees were obtained as a result, based on which we tried to reconstruct the relationships between the inner groups of Cetoniinae with focus on relationship of subtribes of tribe Goliathini. Monophyly of the tribe Goliathini as well as some other groups could not be confirmed, as well as the alleged basal position of the genus *Xiphoscelis*, which is here investigated for the first time. It remains clear that the group is in desperate need of re-definition of its internal classification, but prior to that a comprehensive study including the morphological and up to date molecular approaches is needed.

The current state of knowledge of the larvae of Drilini
(Elateridae: Agrypninae)

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Drilini is a small tribe of the click-beetle subfamily Agrypninae. Due to their malacoderm appearance they had been long classified in their own family, Drilidae, within Cantharoidea. Males are soft-bodied and capable of flight, whereas neotenic females undergo incomplete metamorphosis and remain larva-like and wingless throughout their lives. Drilini currently contains about 130 species classified in eight genera. *Drilus* Olivier, 1790 and *Malacogaster* Bassi, 1834 occur mainly in the Mediterranean, *Selasia* Laporte, 1836 is distributed in the Ethiopian, Palaearctic and Oriental realms, and remaining genera are known only from tropical Africa.

There is very little information available on the immature stages of Drilini. Larvae are known only for eight *Drilus* species, *Malacogaster passerinii* Bassi, 1834, and *Selasia unicolor* (Guérin-Méneville, 1829). The vast majority of morphological studies and ecological observations are based on *Drilus concolor*, *D. flavescens* (both distributed in most of Europe) and *D. mauritanicus* (Spain, Morocco). All known Drilini larvae are predators of terrestrial snails. The European and Mediterranean species prey on representatives of Clausiliidae, Helicidae, Hygromiidae and Subulinidae, whereas the African lineages were found mainly in the shells of Achatinidae. The larval development takes usually two or three years and proceeds through hypermetamorphosis. During winter the active larva develops into a resting stage called pseudopupa. There is no conclusive data on the number of instars for each species but they probably differ among different lineages. Drilini larvae are morphologically relatively uniform and the only known reliable diagnostic characters are the body coloration, color pattern on the dorsal surface, and the shape of urogomphi. Since the data on the immature stages of Drilini are very scarce I take this opportunity to encourage colleagues to pay attention to these snail predators and help us to understand their diversity, ecology and behavior.
Riffles and mosses: systematics and larvae of New Zealand *Hydora* (Coleoptera: Elmidae)

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*Hydora* Broun (Larainae) is the sole genus of the riffle beetle family present in New Zealand, containing 7 described spp. Preliminary sorting of specimens and two years of intensive field work indicate that there may be as many as 15 species, but the adult material has not been thoroughly dissected and exact geographic data are lacking to adequately determine if morpho-taxa or valid species are range-restricted or widespread. The species can be classified into three ecological groups: one group with fully aquatic larvae and adults living in riffles, one with fully aquatic larvae and riparian adults, and a third group that is riparian with larvae that are associated with mosses. Phylogenetic data for the family indicates that the two subfamilies of elmids are not monophyletic, and the presence of riparian and benthic species in the single genus *Hydora* suggests that the behavioral dichotomy between the “riparian” Larainae and “fully aquatic” Elminae may be arbitrary.

Discovery of a new genus and species of Penicillophorinae (Phengodidae) from Southeastern Brazil: description of larva, pupa, neotenic female and male

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Phengodidae (Elateroidea) comprises about 244 species included in three subfamilies, Phengodinae, with 4 genera and 2 subgenera; Mastinocerinae with 25 genera and Penicillophorinae with 5 genera. They occur only in America, from southern Canada to northern Argentina. Male phengodids have soft body with variably reduced elytra and may be or not bioluminescent. Females and larvae are known of three Phengodinae genera and four Mastinocerinae genera; both subfamilies emit yellow to red bioluminescence through dorsolateral lanterns on thorax, abdomen and sometimes on the head. Females are noticeable by having the highest level of paedomorphosis retaining more larval features than any other Elateroidea family. Females are very similar to larvae, of which they can only be distinguished by the lighter coloration or by the presence of an oopore and annular spiracles (biforous in larvae) (COSTA & ZARAGOZA-CABALLERO 2010).
So far the Penicillophorinae comprising six species from Central America and Colombia have been known only by rare male specimens. Its species are characterized by having a head with one or two tentorial pits, without sulci or antennal tubercles; antennae 10 or 11-segmented, serrate or sub-moniliform; 3 or 4-jointed maxillary palps with a securiform apical palpomere; 1-segmented labial palps; pronotum without explanations and wing venation variably reduced. Most of those diagnostic characters assigned to penicillophorines are quite variable among genera and their phylogenetic relationships with Phengodidae, have been questioned. A recent phylogenetic analysis found them closer to Telegeusidae species (ZARAGOZA-CABALLERO 2008, ZARAGOZA-CABALLERO & ZURITA-GARCÍA 2015).

Larvae of a new genus and species of Penicillophorinae have been found in ravine soil at the Municipal Biological Reserve of the “Serra dos Toledos”, Itajubá, Minas Gerais, Brazil. In the laboratory, larvae were kept in small jars with moist soil. One outstanding larval characteristic is the beaked form of its buccal apparatus. The mandibles and labium are very elongated and at first sight, they seem to work together to suck liquid. Although its feeding preferences are unknown to us, we have tried to feed them with termites, roots collected in the same place from where the larvae lived, and with yam and a paste of roots and yam. We were not able to observe if larvae fed by a sucking act. We have collected 15 larvae but only two reached the adult stage, a male and a female, and a third one, which was killed and fixed as pupa. Bioluminescence was not visible at naked eye.

The proposition of a new genus and species presented here based on the male, which differs from other Penicillophorinae genera by the following combination of characters: head with two tentorial pits, two-jointed labial palpi, 4-jointed maxilary palpi, apical maxillary palpomere acuminate, abdominal segments without setose patches, tarsi without spines and wing venation reduced to vestigial RA and CuA₂.

Larvae are very small (5–9.5 mm) cylindrical with thoracic and abdominal tegument weakly sclerotized, cream-white, very short legs and heavily sclerotized head with a unique mouthpiece, with mandibles and labium forming a beak. The wingless female has general body similar to that of the larvae, except by the distinct pronotum, legs with four simple tarsomeres and two simple claws, head sclerotized, with falcate mandibles and 10-jointed and somewhat moniliform antennae. Those larval and female characters are unique among Phengodidae. Although many questions remain unanswered, as the presence of bioluminescence and feeding habits, with this study we aim to improve the knowledge of the Penicillophorinae.


**Larval morphology of *Sandracottus mixtus* (Coleoptera: Dytiscidae) with biological notes and phylogenetic considerations**

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This presentation is aimed to introduce a paper on larval morphology of the genus *Sandracottus* Sharp, 1882, which is in preparation now. Larval morphology of the genus is studied for the first time with emphasis on chaetotaxy and morphometry. The paper will be based on the descriptions of three larval instars of two species. One of them is *Sandracottus mixtus* (Blanchard, 1853), preliminary data on which larval morphology will be presented and discussed in the frame of diagnostics and phylogeny of the tribe Aciliini. Notes on species biology and phenology are provided.

**Larval performance differences between *Aegus chelifer chelifer* stag beetles (Coleoptera: Lucanidae) from urban and forest habitats**

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Stag beetle larvae are considered as saproxylic insects due to their feeding on decaying wood. Larval development is usually restricted by resource available in their habitats. Some stag beetles are found to inhabit urban areas where the quantity and duration of decaying wood are limited from human management. Therefore, it is possible that those urban population stag beetles may possess some traits that assist them to survive under an unfavorable condition. In this study, we conducted an experiment with *Aegus chelifer chelifer* MacLeay, 1819, a tropical stag beetle species which is widely distributed in the main land of Southeast Asia and can be found in both urban and forest habitats. Stag beetles collected from urban and forest habitats of Thailand were bred and reared under the same laboratory condition to compare larval performances between populations. Relative growth rate of the two populations was similar, but feeding period was significantly different (male-urban = 35 days; male-forest = 40 days; female-urban = 30 days; female-forest = 25 days). Maximal larval weight and head capsule width at the third instar were significantly larger in the forest population (males: 6.571 g and 7.0 mm; females: 3.2425 g and 5.8 mm) than in the urban population (males: 4.468 g and 6.2 mm; females: 2.916 g and 5.5 mm). The male stag beetles in urban population may shorten the developmental time during the third instar to respond to the removal of tree logs in urban landscape by human thus depriving them with the intake food quantity.
Description of the third instar larva of white grub, *Brahmina coriacea* – an endemic pest on potato in India 
*(Coleoptera: Scarabaeidae: Melolonthinae)*

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The white grub, *Brahmina coriacea* (Hope) is a serious pest of potato in Himachal Pradesh, India, resulting in nearly 60–75% damage to the tubers in endemic areas. The pest is an annual belonging to Melolonthinae of Scarabaeidae (Coleoptera). The immature stage *viz*., larvae feed on the roots and tubers of the plant resulting in initial drying of the plant and subsequent potato tuber damage. The adults are medium sized, black to dark reddish brown beetles whereas the larvae are dull white coloured and are the damaging stage. The identification of the white grub at larval stage itself facilitates the early initiation of pest management programmes. The description of larva of *B. coriacea* has not been attempted so far and hence a study has been conducted at Insect Systematics laboratory, Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi during 2014–2016 to document and describe the morphological characters of the larvae. The adults were collected from Potato Research Station, Kheradar, Sirmour dt, Himachal Pradesh, India (31°19′N Latitude; 77°10′E Longitude) through manual scouting during the night on their host plants, *Robinia*, *Polygonum* and *Indigofera* sp. The collected adults were brought to the laboratory, Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi and reared in plastic jars. The eggs deposited in the moist soil were collected and transferred to Petri plates and the hatched neonates were later transferred to plastic jars containing cowpea seedlings. As the larvae grew, potato pieces were provided as food and reared till pupation. There were three larval stadia differentiated by moulted skin and size of the head capsule. The third instar larvae drawn from the rearing lot were used for the taxonomic studies. The third instar larva measured about 21–25 mm. Each larval specimen was studied for 54 characters and documented the characters specific to the species. Likewise five specimens were studied to record the consistency in the characters. The distinguishing characters included spiracle structure, anal slit, raster pattern, legs structure, mouth parts, etc. The mouth parts formed important diagnostic characters where antenna, epipharynx, mandibles and maxillae showed distinct characters that aid in species delineation. Antenna was four segmented and possessed one dorsal sensory spot and two ventral sensory spots in the terminal segment. The raster pattern observed is typical in distinguishing *B. coriacea* from other melolonthines. The palidium (comb like structure on last ventral segment) was shorter with wider septula with 9–10 linear long pali on each side of the central line. The pali were slender and pointed at the distal end. The pali of two linear palidia overlapped with each other at their distal ends. The stridulatory teeth on maxillae and characters in epipharynx were distinct for the species delineation. Proplegmatia were distinct and prominent in epipharynx with 6 to 10 plegmata on each side. The larval diagnostic characters of *B. coriacea* are described for the first time from India and discussed in detail.
Morphology of the larva of Cypress jewel beetle *Lamprodila (Palmar)* festiva and a problem of delimitation of Poecilonotini and Dicercini using larval characters (Coleoptera: Buprestidae)

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Cypress jewel beetle (CJB), *Lamprodila (Palmar)* festiva (Linnaeus, 1767), is a new invasive species of Mediterranean origin. Numerous reports announcing CJB range expansion to the new areas of Central and Eastern Europe triggered by transition from natural ecosystems to urban landscapes were published during the last decades (synopsis: VOLKOVITSH & KARPUN 2017). Under natural condition CJB feeds on native *Juniperus*, *Cupressus*, and *Tetraclinis*, while in the areas of invasion it infests different species and cultivars of ornamental, mostly introduced Cupressaceae in urban plantations and nursery stocks, particularly *Thuja*, *Chamaecyparis*, *Platycladus*, *Cupressus*, and some hybrids (Cupressocyparis).

The higher classification of Buprestidae is controversial, taxonomic position and relations of many genera, subtribes and tribes are still uncertain and based mainly on adult characters, the larvae of many genera and even tribes are unknown. Genera *Lamprodila* Motschulsky, 1860 and *Poecilonota* Eschscholtz, 1829 constitute the subtribe Poecilonotina Jakobson, 1913 (Chalcophorinae: Poecilonotini) and these are only poecilonotine genera with known larvae. It is assumed that Dicercini is a closest and possibly sister group to Poecilonotini. Although there is no problem in distinguishing Poecilonotini from Dicercini based on adult characters (BÍLY ET AL. 2009), their delimitation by use of larval characters is rather confused.

It is believed that the most important diagnostic character of Poecilonotini vs. Dicercini larvae is an absence vs. presence of large, globular, heavily sclerotized asperities along prothoracic grooves which are derivatives of expanded bases of microdenticles densely covering prothoracic plates in the larvae of both tribes. Additional characters used by different researchers such as configuration of prothoracic grooves, ratio of common part to separate branches of the grooves, angles between the ends of separate branches, a number of apical teeth on mandibles, structure of spiracles, etc. are widely variable and thus unreliable.

Study of CJB larva revealed a presence of well-marked, heavily sclerotized, globular asperities surrounding prothoracic grooves. Such asperities were never observed in poecilonotine larvae including known larvae of the species belonging to the same subgenus *L. (Palmar)* though much smaller and poorly sclerotized tubercles along the grooves were found in *L. (Lamprodila) decipiens* (Gebler, 1847) (ZYKOV 1984; as dives Guillebeau, 1889). Presence of well-marked asperities in CJB larva disclaims the principal importance of mentioned character for discrimination of Poecilonotini and Dicercini; in the same time it supports much closer relationship of these taxa than adult characters demonstrate. From the other hand, our study revealed much closer similarity in many larval characters between *Dicerca* Eschscholtz, 1829 and Poecilonotini than these between *Dicerca* and former “psilopterine” genera *Capnodis* Eschscholtz, 1829 and *Cyphosoma* Mannerheim, 1837 (currently in Dicercini). The results of this study demonstrate the importance of larval characters to clarify the controversial aspects
of classification and the need of revision of buprestid higher classification and phylogeny using modern morphological and molecular approaches and phylogenetic analysis based on imaginal and larval characters.

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**Phylogeny of the genus Oxythyrea using molecular, ecological and morphological data from adults and larvae**

(Coleoptera: Scarabaeidae: Cetoniinae)

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Genus Oxythyrea Mulsant, 1842 contains 10 species, but the larval description exists only for three of them. During several last years we collected and successfully reared nine species of Oxythyrea and used this material for the phylogenetic study including various types of data. In this talk, we are presenting the bionomy of adults and larvae of the genus. We found several interesting larval morphological characters, which can be used for the phylogeny of the genus e.g. specific types of setae and their arrangement on cranium and abdomen. We compared the biological and morphological data from adults and larvae with our molecular phylogenetic analyses based on three genes (Cox1, CytB, ITS1) under Bayesian interference method. More than 120 samples were in the dataset including all 10 currently recognized species of Oxythyrea.

Phylogenetic tree was almost congruent with already existing hypothesis postulated by SABATINELLI (1981, 1984) and separated Oxythyrea species in four different clades which can be usually supported by specific set of morphological characters (adults and larvae) as well as by bionomy of species included in the clade. Larval morphological data will be used for (re)description of these stages and in the future we will form a matrix based on morphological characters of adults and larvae for analyses combining these data with molecular ones.
Observations on the pupal stage of *Platycerus caprea* and *P. caraboides* (Coleoptera: Lucanidae)

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Stag beetles (Coleoptera: Lucanidae) are secondary xylophagous insects related to decaying wood (Audisio et al. 2014). Among them, the two Italian *Platycerus* species, *P. caprea* (De Geer, 1774) and *P. caraboides* (Linnaeus, 1758), live within deadwood of different plant species, with a particular preference for small-diameter logs (Franciscolo 1997, Scaccini 2016). Although some studies have already investigated the life cycle of these species, the biology of their pupal stage is still largely understudied, something probably due to the rarity of the beetles, their cryptic life-style (i.e., within the wood), and the short time spent as pupae.

Larvae, prepupae and pupae of both *P. caprea* and *P. caraboides* were collected in forests in hills and mountains from 2012 to 2016 (northern Italy). The date of presence of the pupal stage (only for *P. caraboides*) and the total length of available pupae (measured with a calliper, precision 0.05 mm) were recorded in the field before collection. Then, both larvae and pupae were brought to the lab and reared to understand when the pupal stage occurs, to identify its duration (calculated at 16–18 °C or 20–22 °C), and to record some morphometric data. Data are reported as mean ± st. dev. (min, max, n).

The pupal stage of *P. caraboides* (n = 11) occurred in all years (2012–2016) from mid to end of August. For *P. caprea*, instead, the pupal stage is reported to occur in September–October (Moretto 1984); for *P. caraboides*, Palm (1951) reported the occurrence of the pupae in the middle of July. In lab conditions, the pupation of *P. caprea* (n = 1) and *P. caraboides* (n = 8) occurred from the end of July to the end of September, and, in one case (*P. caprea*), at the beginning of October. It confirms the observations reported by Mulstant & Rey (1871) and Moretto (1984). However, for some specimens (three *P. caprea* and one *P. caraboides*) the pupation occurred in May. It could be possible that in some environmental conditions (i.e., warm springs) the larvae of both species can pupate and eclose just before or during the flight period of adults. The total length of the pupa of *P. caprea* (a male) was 13.90 mm, whereas, for *P. caraboides*, it was $13.48 ± 1.40$ (min = 10.80, max = 15.45, n = 11) mm. The pupal duration in the lab was $18.40 ± 3.78$ (min = 13, max = 22, n = 5) days at 16–18 °C, and $14.75 ± 1.58$ (min = 13, max = 18, n = 8) days at 20–22 °C for both *Platycerus* species. The data confirm the information on the life cycle of *Platycerus* species previously reported for Italy (Franciscolo 1997), with pupation and eclosion occurring from late summer to early autumn, and overwintering carried by adults. Finally, in lab conditions seven pupae were...
observed to build their pupal chamber from 20 to 90° slope, which is different from what is known to occur in the field, where pupal chambers are always built horizontally (pers. obs.)

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