

Abstracts of the Immature Beetles Meeting 2011

September 29–30, Prague, Czech Republic

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(editors)

The fourth Immature Beetles Meeting was held in Prague in September 29–30, 2011, two years after the previous meeting (for abstracts see FIKÁČEK et al. (2010)). The meeting took place at the Faculty of Science, Charles University, in cooperation with the National Museum in Prague and the Crop Research Institute in Prague. Altogether 40 participants attended the meeting, including the scientists from Brazil, Canada, China, Cuba and Japan. Similarly as two years ago, the most expected were Cleide Costa and Sergio Vanin who are well known for their life-long studies of beetle larvae of South America, as well as Vasily Grebennikov, who presented the loudest and most general lecture comparing the life style of leaf-mining larvae of beetles and moths. Three lectures were focused on groups with parasitic larvae, including Strepsiptera which are again recognized as sister to beetles based on most recent studies. The friendly and unofficial form of the meeting also provided excellent opportunity for three students to present the results of their M.Sc. theses: Albert Deler-Hernández from Cuba, Haruki Suenaga from Japan and Kateřina Jůzová from the Czech Republic. During both days, attendants presented 19 short lectures (including one unofficial by Petr Švácha) and four posters (including one unofficial by V. Grebennikov). Abstracts of the official ones are presented below in alphabetical order (lectures first, posters following). Coffee breaks and joint lunches in a nearby restaurant provided a handy opportunity for informal discussions of the lectures and individual research projects and interests of the participants. During both evenings, most people continued in a slightly more relaxed setting in a pub over a glass (or perhaps two) of Czech beer. The next meeting is planned for the autumn 2013 and will be held at the Charles University in Prague again. Details about the forthcoming meeting will be available on the Immature Beetles Meeting web pages at http://www.cercyon.eu/IBM/IBM_2011.htm, together with the photos and abstracts of the past meetings. Please contact us if you need further information.

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The abstracts should be cited as follows:

ANGUS R. B. 2011: Rearing *Helophorus*: egg cocoons & larvae. P. 733. In: FIKÁČEK M., SKUHROVEC J. & ŠÍPEK P. (eds.): Abstracts of the Immature Beetles Meeting 2011, September 29–30, Prague, Czech Republic. *Acta Entomologica Musei Nationalis Pragae* **51**: 731–756.

PRESENTATIONS

Rearing *Helophorus*: egg cocoons & larvae

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Adult *Helophorus* may be kept in small aquaria (sandwich boxes) with a bank of sand at one end, and water to a depth of about 1 cm. They are fed with algae (typically *Spirogyra*), moribund grass or occasionally freeze-dried peas. Decomposing vegetation should be removed.

Egg cocoons are usually placed in the bank, but occasionally among the vegetation in the water. They consist of an egg bag about 3–5 mm long, topped by a silk mast of three main forms: 1. Erect, leaf-like; 2. Tubular; 3. Thin ribbon-like, corresponding to the leaf-like masts of type 1 or the back of the tubes of type 2; 4. Long tubular ribbon-like masts corresponding to the entire tubes of type 2. It is suggested that the form of the mast may be important in supplying oxygen to developing eggs, erect leaves and ribbons floating upwards because of trapped air will act as physical gills if cocoons are flooded, while the slightly deeper burial of cocoons with tubular masts could delay desiccation of the cocoon in hot dry conditions. One species, *H. asturiensis* Kuwert, has been found to make two distinct types of cocoon (types 2 and 4).

Egg cocoons are harvested daily and kept on damp filter paper in Petri dishes.

Larvae are normally fed on *Tubifex* worms (available from aquarists' suppliers). In the wild it is possible to improvise – in West Siberia I used chopped up *Gammarus lacustris*, abundant locally. Larvae are given their first feed in the dish with the cocoon, but after one day are transferred to individual pill boxes, on four sheets of damp filter paper. The filter paper must be fully damp, but without any loose water. Food is supplied daily and uneaten food from the previous day removed. Hygiene is essential, and soiled filter papers are changed as necessary.

There are normally three larval instars (but only two in *H. kirgicus* Knisch and *H. kervillei* d'Orchymont), and at temperatures of about 23°C the larvae are ready to pupate in about two weeks. Larvae pupate in banks of damp sand in the pill boxes. Pupation takes about two weeks.

I kept larvae as cleared mounted preparations in Canada balsam on microscope slides. I have found that such preparations keep their colour.

Some aspects of larval morphology are discussed.

Primary larvae of some Ripiphorinae: their phoresy and dispersal (Coleoptera: Ripiphoridae)

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Dispersal abilities of Ripiphorinae have never been studied in the past. Although all members of the subfamily are well known for their phoretic triungulinid primary larvae similar to those in some Meloidae (Coleoptera) or in Strepsiptera, their capability to colonize distant

localities has been investigated only recently (BATELKA 2011, BATELKA & STRAKA 2011). The main features and factors allowing members of two Ripiphorinae genera (*Macrosiagon* Hentz, 1830 and *Ripiphorus* Bosc, 1791) to reach a distant and even very isolated habitats (like oceanic volcanic islands) by the long-range dispersal are shown and discussed. Results will help with future evaluation of biogeography of these two genera.

Primary larvae (so called 'triungulinids') of *Macrosiagon* and *Ripiphorus* show remarkable adaptations for phoresy. Besides their streamlined body shape similar to other phoretic larvae, their pretarsal segments are modified into leaf-shaped pulvilli (or inflatable lobes) which probably help them to crawl in the blossoms to reach their host bees or wasps when they are approaching, their mandibles are sharp and pointed to be able to penetrate soft cuticle or wings of their vectors during the transport, and finally their terminal abdominal segment is modified into retractile sucker capable of adhesion to smooth substrates (TOMLIN & MILLER 1989).

Several genera and species of flowering plants visited by adults of certain species of *Macrosiagon* and *Ripiphorus* in the Arabian Peninsula and Africa were identified. Importance of these plants for phoresy of ripiphorine free-living primary larvae is discussed. The term 'transfer plants' has been introduced to highlight their significance in the life cycle of the associated ripiphorine species. Ovipositing in the inflorescences of these transfer plants in some species was found out to be the reason of the multiple triungulinid load on their hymenopteran host species (i.e., more than one primary larva on a single vector). Phoretic adaptations of primary larvae, widely distributed transfer plant taxa (either on the tribal or generic level) and the multiple triungulinid load mechanism seem to be responsible for a wide distribution of some ripiphorine species and successful colonization of remote places such as arid areas, high mountain ranges or oceanic volcanic islands by the members of this subfamily.

Morphology of the phoretic primary larval instar of *Ripiphorus caboverdianus* Batelka & Straka, 2011 has been described, that of *R. arabiaefelix* Batelka, 2009 from Yemen will be described in the forthcoming paper (BATELKA in prep.). Original sampling method to obtain *R. arabiaefelix* primary larvae in the field was developed. Larvae were collected by using cut-off PET bottles half-filled by water with several drops of detergent. Inflorescences of the transfer plant were immersed in the liquid for a few seconds. Positive samples with larvae sunken to the bottom of the bottle are detectable by 20× magnifying glass directly in the field. Several tens of larvae may be obtained in a few minutes.

Five long-range dispersal events in the subfamily Ripiphorinae in the Afrotropical Region were documented. *Ripiphorus caboverdianus* from the Cape Verde islands represents the first record of the family Ripiphoridae from the volcanic islands west of Africa and the first record of the genus on an isolated volcanic archipelago worldwide. *Macrosiagon benschi insularum* Schilder, 1923 from the volcanic Comoros belongs to an endemic Malagasy species-group with three Madagascan taxa. Finally, three widely distributed Afrotropical *Macrosiagon* species common to Africa and Madagascar were identified (BATELKA 2011, BATELKA & STRAKA 2011).

BATELKA J. 2011: Contribution to the synonymies, distributions, and bionomics of the Old World species of *Macrosiagon* (Coleoptera: Ripiphoridae). *Acta Entomologica Musei Nationalis Pragae* **51**: XX–XX

BATELKA J. (in prep.): Transfer plants of some Ripiphorinae in Africa and Arabia with remarks on the primary larva of *Ripiphorus arabiaefelix* (Coleoptera: Ripiphoridae).

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The pre-pupa of Mycteridae, Eurypininae (Coleoptera, Tenebrionoidea)

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In 1977, COSTA & VANIN (1977) reared larvae of *Euryypus muelleri* Seidlitz, 1917 (Mycteridae) in the laboratory and observed that, when the last active larval instar stopped feeding, it molted and was transformed into a quiescent instar, named pre-pupa by those authors. This pre-pupa, after a few days, molted again, giving rise to the pupal stage. On the whole there are only two molts between the mature larva and the adult in the Holometabola: one from larva to pupa and the other from pupa to adult. However, in *E. muelleri* three molts occur: the first from the mature larva to pre-pupa, the second from pre-pupa to pupa and the third from pupa to adult. It is important to point out that morphologically the *E. muelleri* pre-pupa differs slightly from the last active larval instar by the hypognathous head (prognathous in the mature larva), shorter and broader and less sclerotized body, tubercles of the ninth abdominal segment with dark brown apices, contrasting with the cream white integument. So, according to the authors' concept, the pre-pupa of *E. muelleri* is a distinct morphological instar resulting from an extra molt, and not at all equivalent to the pharate pupa as defined by HESLOP-HARRISON (1958) and HINTON (1946, 1973), for the latter is the last active larval instar that becomes inactive without suffering a molt.

In 1984, COSTA & VANIN (1984) conducted a research into the life cycle of another Mycteridae, *Stilpnonotus postsignatus* Fairmaire, 1889 and observed for the second time a morphologically differentiated pre-pupal instar, similar to the one that occurs in *E. muelleri*. Again, the pre-pupa differs from the previous larval instar mainly by the shorter and broader body and the head hypognathous (prognathous in the mature larva). The following year, COSTA & VANIN (1985) discussed the possible functions of this kind of pre-pupa in Mycteridae, probably related to the conspicuous morphological differences occurring between the thorax of larva and adults, thus allowing larvae and adults to occupy different habitats. On reviewing the bibliography of the pre-pupa concepts, the authors distinguished three main types of pre-pupa in the Holometabola, showing that the Mycteridae pre-pupa is a distinct instar resulting from an extra molt, followed by a very short period of quiescence before the ecdysis to the pupal stage happens.

POLLOCK *et al.* (2000) described the pre-pupa of *Physiomorphus subcostulatus* Pollock, 2000 and revealed the biological cycles of two more species: *P. melanurus* Champion, 1916 and *P. angustus* Pollock, 2000. The pre-pupae of these species differ from the mature larva by

their more setose, less flattened and shorter body, head deflected (protracted and prognathous in the mature larvae), and abdominal segment VIII narrower and slightly longer than the combined lengths of segments VI-VII.

Some considerations must be made on the habitats of these Euryrinae species: *Eurypus muelleri*, *Physiomorphus angustus*, *P. melanurus* and *P. subcostulatus* have dorso-ventrally compressed bodies, probably related to their life in the axils of palm leaves and under the bark of dead trees, where the larvae feed. The body of the adults is slightly compressed and does not seem morphologically adapted to live in the same habitat as the larvae. *Stilpnonotus postsignatus* has an almost cylindrical larva adapted to burrows in hard wood and is probably fungivorous. This kind of pre-pupa is very probably an autapomorphic character of the Euryrinae (Mycteridae), being possibly related to the diversified habitats occupied by larvae and adults.

Although the presence of this kind of pre-pupa (resulting from an extra molt) is consistent in the three mentioned genera, we find its concept is still poorly understood. Bearing this in mind, we regard it as important that it be presented for discussion again.

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First data on the study of larval morphology and chaetotaxy of the family Hydraenidae from Cuba

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The family Hydraenidae has a worldwide distribution and contains more than 1420 species grouped in 40 genera (JÄCH & BALKE 2008). The family is considered one of the most speciose groups within the aquatic beetles (JÄCH & BALKE 2008), however only four species have been cited from the island of Cuba until now: *Hydraena perkinsi* Spangler, *H. decui* Spangler, *Gymnochthebius fossatus* (Leconte), and *Ochthebius attritus* Leconte. Of these, *Hydraena perkinsi* and *H. decui* are Cuban endemics. *Hydraena guadelupensis* Orchymont is a new record presented in this work.

Different studies have demonstrated the utility of larval chaetotaxy in Coleoptera both for taxonomic and phylogenetic purposes (e.g., ALARIE 1991, KOVARIK & PASSOA 1993, DELGADO & ARCHANGELSKY 2005, BYTTEBIER & TORRES 2009). All these studies assume that each species, or groups of related species, have unique chaetotaxic formula (ALARIE et al. 1990). Although these works have demonstrated the utility of chaetotaxy for taxonomic diagnosis (TORRES et al. 2008), very few studies have been carried out on larval Hydraenidae in America, and Cuba is not an exception.

The low number of published larval studies of Hydraenidae is not surprising as immature stages of many groups of Coleoptera are little known (HANSEN 2000, MEIER & LIM 2009). This explains why most morphological analyses use exclusively the adult data while larval characters are waiting for discovery and probably many larvae are waiting for description in vials deposited in many of our laboratories. There are three main causes of these problems: 1) the usual taxonomic problems that we find in Coleoptera, often with good revisions being totally absent; 2) the difficulty of reliable association of larva with adults, aggravated by the fact that preimaginal stages can be very active and sometimes occupy different habitats than adults, and 3) the lack of detailed descriptive studies useful for identification and comparison of species or genera. Problems 2 and 3 were especially relevant during the study of the immature stages of the family Hydraenidae in Cuba.

The larvae used in this study were obtained by rearing the adults in the laboratory. The rearing techniques used by us follow those described by DELGADO et al. (1996), with only slight modifications: Plastic 500 ml jars were used as rearing aquaria. These containers were covered with gauze and the walls were covered with filter paper. Water, sand, small rock, mud and organic matter collected at the sampling sites were maintained in quarantine for at least 15 days before they were used in the rearing box. Each container was filled with approximately 25 ml of water and kept in the shade at room temperature. We tried to recreate the original environment in each species reared, in order to keep the rearing conditions similar to those on the collecting site (habitat with lots of fallen leaves, sandy environment, etc.). No more than 20 specimens were used in each rearing experiment. When the first instar larvae hatched, they were moved to small containers with perforated lids using a pencil. The jars were filled with only 2 ml of water and contained the same ecological conditions as in adult rearing containers.

Using this method, we have obtained larvae of four of five known Cuban species, which has allowed us to prepare larval descriptions of most instars and study their larval chaetotaxy. This means a remarkable advance in the knowledge of the morphology of water beetles of Cuba. Until now, larvae of only two species of aquatic beetles, both belonging to the family Dytiscidae, have been described using larval chaetotaxy: *Pachydрус obniger* Chevrolat and *Celina imitatrix* Young (ALARIE & MEGNA 2006, MICHAT et al. 2007).

Of the four species studied, we described all three larval instars of *Hydraena perkinsi*, *H. guadelupensis* and *Ochthebius attritus*. In *Gymnochthebius fossatus*, we were only able to rear first instar larvae but failed to rear larvae of higher instars as all reared larvae died during the first stage. This was surprising as *G. fossatus* is supposed as ecologically adaptive and we initially considered it as non-problematic to rear. However, no larvae reached the second instar under the laboratory conditions. We speculate that the species is susceptible to fungi or bacteria during the rearing.

In the case of *Hydraena decui*, we failed completely in the rearing the larval stages. The species apparently requires precise environmental conditions, most likely special sun exposure

conditions, temperature and food. Evidently, all these specific conditions are present in the mountain ecosystems where *H. decui* occurs but were out of control or difficult to simulate in the laboratory. We suspect that the high temperatures in the laboratory where the rearing experiments were carried out differ excessively from the original conditions of the habitat typical for that species.

In this study, larval chaetotaxy is used for the first time in the Cuban fauna of Hydraenidae. Comparing the two Cuban *Hydraena* with some of the previously described species of the genus (PERKINS 1980, DELGADO & SOLER 1997a, DELGADO et al. 1997), we can observe a common pattern in the primary setae of all of them: head capsule with epicraneal marginal setae Em1 and temporal setae T2, T3 and T4 minute; anterior setae of the pronotum with A1 short, A2 long, A3 short and A4 long; lateral setae with L1 and L2 short and L3 considerably long; and abdomen with notable reduction of the setae compared with other genera (DELGADO & SOLER 1997a, DELGADO et al. 1997).

Hydraena guadelupensis and *H. perkinsi* together with *H. particeps* from Nicaragua are the only three species of *Hydraena* for which all three larval instars have been described. These three species share a common pattern in the subprimary setae in the second and third instars including the presence of subprimary setae Dc'' on the pronotum and DP' on dorsopleural sclerites of the abdomen. The Cuban species bear no secondary setae.

The larva of the first instar of *Gymnochthebius fossatus* is characterized by its small size, presence of a pair of egg-bursters in the cephalic capsule, well developed anal hook and abdominal segment X with a dorsal projection that resembles the cephalic egg-bursters. The latter feature is unique for this species within the Hydraenidae. We consider two hypotheses about the function of the tooth-like structure: if this structure is absent in the second and in the third instar, it is very probable that it could be an accessory egg-burster. However, if this structure is also present in higher instars, its function became a challenge. In any case, it seems an excellent character to be used in phylogenetic studies.

The larval chaetotaxy of *Gymnochthebius fossatus* can only be compared with that of *G. jensenhaarupi*. In the latter species, the epicraneal setae Ed1 are minute while they are of normal size in *G. fossatus*. Also, the prothoracic discal setae Db1 and Dc1 are minute in *G. jensenhaarupi*, but not reduced in size in *G. fossatus*.

The general aspect of the larva of *Ochthebius attritus* is quite similar to the previously described larvae of the genus (DELGADO & SOLER 1997b). A relevant and unique feature found in *O. attritus* is the presence of two clypeal projections on the external clypeal margin, which force the clypeal setae C11 to an unusual position. As these projections can be observed in all three larval instars, it may be hypothesized that these structures are not egg-bursters.

In this work, the larval tentorium of the four Cuban species is described and figured. The tentorial dorsal arms are very slender in two examined species of *Hydraena*, stout and wide in *Ochthebius attritus* and wide but partially unsclerotized in *Gymnochthebius fossatus*.

Worldwide, only 16 species of the family Hydraenidae have been described using larval chaetotaxy and of these, only three from the Western Hemisphere (PERKINS 1980, DELGADO & SOLER 1996a, DELGADO & SOLER 1997c, DELGADO & PALMA 2004, DELGADO & ARCHANGELSKY 2005, PARK & AHN 2008). The study of the Cuban species raises the number of species with known larvae to 20, and to six for America.

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Fossils of the hydrophiloid larvae – what are they good for?

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Most of the described and many undescribed fossils assigned to the superfamily Hydrophiloidea have been examined within last three years in the cooperative project *Revision of the fossil record of the Hydrophiloidea*. The project is focused on three goals: (1) to (re)examine all described and available undescribed material assigned to the Hydrophiloidea, (2) to revise the taxonomic placement of well-preserved fossils and excluding of incorrectly assigned or badly preserved taxa from the Hydrophiloidea, (3) to select the fossil taxa which may be used for reliable dating of nodes in phylogeny reconstructions.

Fossils of two larval species have been found to belong to Hydrophiloidea so far, both originating from the famous early Cretaceous locality of Baissa in Transbaikalian Russia (ZHERIKHIN et al. 1998). Remaining published larvae (early Jurassic *Angarolarva* Ponomarenko, 1985, and unnamed larvae from Crato Formation and Koonwarra Formation) do not belong to the Hydrophiloidea.

Cretotaenia pallida Ponomarenko, 1977 was originally described as belonging to the Adephaga, but already CROWSON (1981) mentioned that it is actually similar to modern larvae of *Helophorus* Fabricius, 1775 (Hydrophiloidea: Helophoridae). Examination of several dozens of specimens confirmed this opinion (shared characters are e.g. large meso- and metathoracic tergites, large abdominal tergites, shape of anterior portion of the head, morphology of labium and mandible, arrangement of ommatidia and presence of long segmented urogomphi). Differences from *Helophorus* larvae were also found: occipital foramen is shifted dorsally as in Hydrophilidae (situated more or less posteriad in *Helophorus*), laterotergite is divided into two minute sclerites (one large sclerite present in *Helophorus*) and urogomphi bear four segments (three in *Helophorus*). The phylogenetic analysis combining modern and fossil Helophoridae confirmed basal position of *Cretotaenia* and moreover supported the hypothesis by ZHERIKHIN et al. (1998) that *Cretotaenia* is larval form of the extinct genus *Hydrophilopsia* Ponomarenko, 1985. By this association, *Cretotaenia* provides sound arguments that *Hydrophilopsia* represent a separate extinct lineage of the Helophoridae rather than the stem group of modern *Helophorus*.

The second fossil species, an undescribed larva from the same deposit, is surprisingly well preserved and clearly belongs to the family Hydrophilidae, which nowadays contains the vast majority of hydrophiloid beetles. Preserved characters (nasale with five teeth, mandible with 3 inner teeth, size and arrangement of tergites on thorax and abdomen) suggest, that this larva is morphologically close to modern tribe Hydrobiusina, which seems to be confirmed even by a preliminary phylogenetic analysis. Several, mostly undescribed fossil adults are known from early Cretaceous localities in Spain, Germany, China and Australia, but adult characters did not allow for their unambiguous taxonomic placement as the adult morphology of most aquatic hydrophilids is rather uniform. However, morphology of most of them is congruent with their possible placement in the Hydrobiusini, in agreement with the presented larva.

Both presented fossil larvae bear characters which are more decisive for reconstructing the higher level phylogeny of the extinct Hydrophiloidea than those of many adult forms. Hence, they seem to be crucial for understanding the early evolution of the Hydrophiloidea.

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Life in two dimensions or ways of staying low: lateral exuvial split in leaf-mining larvae of *Pachyschelus* (Coleoptera: Buprestidae) and *Cameraria* (Lepidoptera: Gracillariidae)

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The necessity to split and shed the overgrown exoskeleton is one of the most universal challenges repeatedly faced by nearly all immature individuals of Arthropoda and few other phyla. With a few exceptions like the front-moulting scorpions, the split of the old cuticle occurs dorsally along the antero-posterior body axis closer to the anterior body end. Such a pattern is almost universally found among immature holometabolous insects, at least in those with a distinguishable dorso-lateral axis and with moderately to strongly sclerotised body, like the vast majority of Coleoptera and Lepidoptera. We report an alternative and apparently previously undetected lateral cuticular split in leaf-mining larvae of *Pachyschelus* (Coleoptera: Buprestidae) and *Cameraria* (Lepidoptera: Gracillariidae). In these species the first exoskeletal split takes place on the lateral body sides, thus permitting the larva to leave the exuvium side-wise. This discovery of a lateral exuvial split in leaf-mining Coleoptera and Lepidoptera suggests that this previously overlooked phenomenon has evolved independently as an adaptation to a lifestyle in vertically limited mine space and, therefore, might be found in other organisms living under similar constraints.

Prey preferences and feeding strategies of larval *Scydmaeninae*

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Species of the subfamily Scydmaeninae of Staphylinidae are commonly believed to be specialized predators feeding on armored mites (Oribatida) (e.g., NEWTON 1991, NEWTON & FRANZ 1998, O'KEEFE 2005). Most published observations of the behavior associated with feeding were focused on adult ant-like stone beetles; data on larvae are available only for 4 genera (out of nearly 100 currently known) in 3 tribes: *Cephennium* Müller & Kunze, *Stenichnus* Thomson, *Scydmorphes* Reitter and *Palaeostigus* Newton (SCHUSTER 1966, SCHMID 1988, DE MARZO 1983).

In the present study, new data on feeding preferences are provided for genera *Scydmaenus* Latreille (Scydmaenini), *Euconnus* Thomson and *Stenichnus* Thomson (Cyrtyoscydmini). While larvae of the two cyrtoscydmine genera seem to be strict predators on Oribatida, larvae of *Scydmaenus tarsatus* Müller & Kunze feed only on soft-bodied soil animals as Collembola and acaridid Acari, ignoring armored mites. Not only predation on live prey, but also scavenging on dead arthropods was observed. These findings and morphological adaptations for this type of feeding are compared with those of adults of *Scydmaenus*, leading to conclusions that remarkably different structures of mandibles do not imply different prey preferences or different prey capture strategies.

New data on unique morphological adaptations of *Cephennium* larvae for feeding on oribatid mites are presented. Both adults and larvae of this genus have the labium strongly modified and bearing paired adhesive discs used to immobilize even a very large prey. Strategies used by *Cephennium* larvae for capturing prey and feeding through a small hole “drilled” in the mite cuticle are reviewed.

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First larval instars of Strepsiptera

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Strepsiptera is an order of obligatory parasitic insects. They are parasites of seven insect orders (Thysanura, Blattodea, Mantodea, Orthoptera, Hemiptera, Diptera, Hymenoptera) (KATHIRITHAMBY 1989). In the light of the latest studies, Strepsiptera appears to be closely related to Coleoptera (WIEGMANN et al. 2009, FRIEDRICH & BEUTEL 2010, LONGHORN et al. 2010, BEUTEL et al. 2011).

During the evolutionary progress, first instar larvae of Strepsiptera, often called ‘triungulinids’, got through the extreme degree of miniaturisation (POHL & BEUTEL 2008). In spite of this, it has preserved many morphological features.

Complicated microtrichia distribution, simple and stable chaetotaxy as well as the other morphological features can provide us a suitable tool to distinguish particular species, but we can also proceed a phylogenetic study of the Strepsiptera based on morphological data of the first instar larvae (POHL 2002). Considering to very simplified morphological characters of females and frequently unknown males, the morphology of first instars could be very helpful in strepsipteran phylogeny.

Using morphological data of Strepsiptera triungulins we have recognized a new genus and put it to tribal relationship within the Strepsiptera family Stylopidae. We also revealed four new species of Strepsiptera with unique autapomorphies within the tribe Crawfordiini. This tribe is unique in bifid femoral spurs as well as bifid setae in some species. Their caudal filaments are very long and in one species are almost twice longer than body. Reversal state in chaetotaxy is found in one undescribed species within this tribe. This unusual species is very similar to basal Strepsiptera first instars in distribution of body setae.

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Systematics of the rove beetle tribe Staphylinini: will larvae help us?

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With more than 200 genera and ca. 5000 described species, the rove beetle tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae) is one of largest global terrestrial animal groups. Paleontological and biogeographical data suggest that earliest Staphylinini appeared in Late Jurassic, while youngest radiations within this tribe occurred 50–30 mya. With such a long time span of molecular and morphological evolution, finding right markers for phylogeny reconstruction and proposing a natural classification of this group are a difficult task.

Unlike morphology of adults and DNA sequences, larval morphology has never been explored for this purpose. Based on detailed morphological examination of larvae of *Quedius antipodum* Sharp from New Zealand, and *Holisus* sp. from Mexico in a broader phylogenetic context of Staphylinini, we explore diagnostic and phylogenetic value of larval characters of Staphylinini. Both taxa have been chosen for study because their systematic position inferred from adult morphology and DNA-sequences is most controversial, and because their larvae became available.

First record of bioluminescence in larvae of *Alampoides alychnus* (Kirsch, 1873) (Elateridae: Agrypninae)

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During a scientific trip to Campo Novo dos Parecis, Mato Grosso, Brazil (S13°36'33.8" W57°52'9.5") from July 25 to August 04, 2008, S. P. Rosa collected two elaterid larvae. They were found in the soil, at an altitude of 528 m, between a region of sugarcane crop and the gallery forest of the Membeça river.

These larvae were bioluminescent and were kept in the laboratory in a 'Germination Camera Fanem mod. 347' at 26°C and were weekly fed with termite workers. One larva pupated on October 5, 2009 and the adult appeared two weeks later. The second larva died before pupation. Larvae and pupa were photographed and the luminescence patterns could be seen in a dark place. The larvae showed bioluminescence in one pair of luminous spots on the mesonotum and a longitudinal series of median spots on the metanotum and on all abdominal segments. The mesothoracic spots were larger and brighter than the metathoracic and abdominal luminous organs. The pupa illuminated the same spots as in the larva and also showed a diffuse glow over the entire body.

At first we identified the larvae as a Pyrophorini. But it was surprising to see that the newborn adult, identified as *Alampoides alychnus* (Kirsch, 1873), did not present bioluminescence at all or vestigial trait of luminous organs.

Alampoides was originally described by Schwarz in 1902 (type-species *Pyrophorus submaculatus* Schwarz, 1902; Hyslop's designation, 1921). The genus has five known species, which occur in Colombia, Ecuador, Peru, Bolivia and Brazil (Amazonas and Mato Grosso). Adults are characterized by the mandibles with teeth, antennal segment 3 usually twice as long as 2 and mesosternal cavity open and slightly raised behind. It was located in the Heligmini and Alampina (COSTA 1975). JOHNSON (2002) replaced the name Heligmini Costa, 1975 by Cleidecostini because of the homonymy of the type genus.

The larval bioluminescent pattern of *A. alychnus* differs from the luminescent patterns presented by Pyrophorini species (COSTA 1970, CASARI-CHEN & COSTA 1986, ROSA *et al.* 2010) especially in the absence of luminescent spots on prothorax. The median luminescent spots of metanotum and abdominal segments are similar to those of *Pyrearinus janus* (Herbst, 1906), although the latter has an additional pair of lateral spots.

Larva and pupa of *A. alychnus* are very similar to those of the Pyrophorini. The larva is more similar to the well-known *Pyrophorus* larvae for its mandible with two setae, abdominal terga 1–8 with one anterolateral and two posterolateral pairs of setae and for its abdominal tergum 9 with four pairs of tubercles forming two lateral rows anteriorly to the bifurcate urogomphi. The antenna has one AS3 as in *P. noctilucus* Linnaeus, 1758 and *P. punctatissimus* Blanchard, 1843.

The similarities and the presence of bioluminescence in *Alampoides alychnus* suggest a close phylogenetic relationship between Pyrophorini and Cleidecostini and also indicate that the luminescent organs can have been lost in the adult stage of the later species.

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Immature stages and biology of *Diamesus* (Coleoptera: Silphidae)

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A brief summary on the morphology of immature stages (egg, all three larval instars and pupa) of *Diamesus* Hope, 1840 (Coleoptera: Silphidae: Silphinae) is provided. Although mature larva of *D. osculans* (Vigors, 1825) was formally described twice (PORTEVIN 1922, TUNG 1983), in both cases it is considered a misidentification with other beetle groups: larviform female ('trilobite larva') of Lycidae: *Duliticola* sp. in the former and unidentified beetle larva (but certainly not of Silphidae) in the latter case.

Systematic position of *Diamesus* and closely related *Necrodes* Leach, 1815 is briefly discussed. Detailed distribution of *Diamesus* is commented (based on literary data, incl. PECK 2001, and material from 33 public and private collections), with widely distributed *D. osculans* (known from India to south-east Australia) and endemic *D. bimaculatus* Portevin, 1914 (restricted only to Taiwan).

Biology of *Diamesus* is summarized, attraction to light traps and baited pitfall trap is general way how adults are mostly collected (as already reviewed by PECK 2001). Association with Titan arum (*Amorphophallus titanum*, Plantae: Araceae) is documented, chemical composition of its rotting animal-like odor (SHIRASU et al. 2010) is similar to sulphur-containing volatile organic compounds released by real carrion (KALINOVÁ et al. 2009). Well developed hind wing of *D. osculans* is compared with that of *Necrodes littoralis* (Linnaeus, 1758), main differences are found in better developed venation of medium part of the wing and enlarged anal area.

Immature stages of *D. osculans* were reared in the laboratory; best results were obtained if larvae are reared together on a large piece of decaying fish meat, from first larval instar to mature larva, pupation take part in chamber in the soil. However, contamination with Nematoda was observed on carrion and larvae in most cases. Time span from egg to teneral adult is 38–40 days, longest life stage being the 3rd larval instar (developing for three weeks).

Larva of *D. osculans* is compared with larva of *Necrodes littoralis*, both genera share pale median line on tergites and laterally divided second abdominal ventrite. Larva of *Diamesus* differ by more compact and more flattened body, relatively larger and more robust head, shorter and more robust legs, round lighter spots on laterotergites of abdominal segments (oval to elongate spots are developed in *N. littoralis*) and only short praescutum and scutellum on dorsum of abdominal segments (elongate praescutum and scutellum in *N. littoralis*). Important morphological characters are documented by macrophotography.

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Host utilisation by *Brachinus*, coleopteran parasitoids

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In insect larvae, optimising food utilisation with respect to available meals and time is essential for achieving maximum adult body size, which is a relevant proxy of fitness. We studied the efficiency of food conversion, body size, mortality and development time in a solitary idiobiont ectoparasitoid, *Brachinus explodens* (Coleoptera: Carabidae), reared in the laboratory on the pupae of another carabid genus, *Amara*.

The efficiency of conversion index (ECI – ratio of ingested to assimilated food) was, on average, 54.1 ± 1.1 % ($n = 76$), with a minimum of 26.9 % and a maximum of 81.6 %. The rate of increase in biomass gained (W_{gained}) with biomass of the host was constant in females, but it decreased in males over the range of host body mass. Females, therefore, grew heavier from hosts of the same mass compared to males. Body length increased with the host mass and was correlated with W_{gained} identically for both genders. Mortality was unaffected by the host mass, but it significantly increased below 20 °C. In contrast, the development time of the feeding phase of the larva increased with the host mass at 20.3 and 23.7°C, but it remained unaffected at 26.9°C and in all three temperatures considering pupal development. W_{gained} increased with development time up to ca. 8 days of larval feeding at 23.7°C, above which it began to decrease.

To our knowledge, our data are the first on food utilisation in solitary idiobiont coleopteran ectoparasitoids, and they present the highest values of ECI in insects.

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Larvae of case-bearing leaf beetles (Coleoptera: Chrysomelidae: Cryptocephalinae)

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The larvae of leaf beetles in the subfamilies Lamprosomatinae and Cryptocephalinae with its three tribes Clytrini, Cryptocephalini and Chlamisini wear a case, for this reason they are called ‘case bearers’. This case is based on an extrachorion produced by the parental females which cover their eggs with a case made by faeces and secretes. The egg case is subsequently kept and enlarged by the larva with faeces and soil as they grow. Pupation takes place within the larval case (ERBER 1988).

On a world-wide scale, the larvae of about 6 % of the Cryptocephalinae were described, however, the quality of the descriptions is quite variable because the descriptions partly date back to the 19th century. The knowledge of the Central European fauna is much better, mostly due to the publications of W. Steinhausen (e.g., STEINHAUSEN 2007), the keys allow to determine approximately 90 % of the species.

Larval characters used for determination include the shape and microsculpture of the head capsule, the stigmal plates, and setae of the tibiotarsus and the head capsule. While late-instar larvae are needed for determination, first instar larvae provide characters of importance for phylogenetic studies like spatulate and papillate head capsule setae (REID 1995).

The larvae of most Cryptocephalinae feed on leaf litter contrary to the adults that feed on green parts of the plants. Consequently the subfamily is well represented in semi-desert and steppe biotopes, where green leaves may not be present all year round. However, there are also many Cryptocephalinae present in tropical rainforests.

The larval cases provide some protection from generalist insect predators, but parasitoid natural enemies are known (SCHÖLLER 1999), and Carabid beetles and mammalian insectivores have been shown to prey on Cryptocephalinae larvae (OWEN 2003).

Several species in the tribe Clytrini and few in the tribe Cryptocephalini are known to be associated with ants. The larvae of these myrmecophilous species were collected in the vicinity or even within the nest of ants. However, the life-history of these species is only poorly known and controversial information can be found in the literature, ranging from nest materials as feeding substrate to predatory behaviour. In one study, the Clytrini *Macrolenes dentipes* (Olivier) was experimentally shown to feed on both dry and fresh insect fragments (zoosaprophagy) as well as leaf litter (phytosaprophagy) (SCHÖLLER 1998). Recently another species, *Clytra laeviuscula* Ratzeburg, was shown to be zoosaprophagous (Schöller, unpubl. data). The larvae are presumably actively transported into the nest by the ants. Foraging *Lasius emarginatus* (Olivier) ants were experimentally offered eggs and first instar larvae of *C. laeviuscula*. First instar larvae were instantly picked up and transported by the worker ants, while eggs were only picked up in 30 % of the observations (Schöller, unpubl.).

The future study of larvae of especially tropical Cryptocephalinae is a promising field for both research on phylogeny and life-history of this species-rich leaf beetle subfamily.

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Biology and larval morphology of four *Larinus* species (Coleoptera: Curculionidae: Lixinae), possible biological control agents

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The weevil genus *Larinus* Dejean, 1821, belonging to the tribe Lixini Schoenherr, 1823, includes approximately 180 species (GÜLTEKIN 2006). *Larinus* species have different habitat preferences; some of them are associated with xerothermic communities, whilst others inhabit wet meadows, pasture or ruderal communities. The studied species are generally monophagous

or oligophagous, and they are associated with plants from the tribe Cardueae of the genera: *Arctium* L., *Carduus* L., *Carlina* L., *Centaurea* L., *Cirsium* Mill., and *Onopordum* L. (KOCH 1992). The majority of *Larinus* species could be considered as potential biological control agents of weeds (NIKULINA et al. 2004). Importance and usefulness of weevil larvae as biological control agents for thistles (LOUDA et al. 2003) is suggested by their life strategies. Weevil larvae are able to destroy almost the whole receptacle and could prevent seeds from maturing, which will be tested in future studies (SKUHROVEC et al. 2008). Life strategies including type of oviposition and development of these weevils are described and photographs are provided of immature stages, adults, host plants, biotopes and parasitoids.

Detailed descriptions of immature stages of *Larinus* species are important for further studies of generic and subgeneric taxonomic relationships inside the Lixini tribe, to effectively protect endangered species, and to promote the use of larvae of *Larinus* species as a potential biological control agent against weeds (e.g. *Carduus*, *Cirsium*). We presented detailed descriptions of four species in the genus *Larinus*, which demonstrates the possibility of identifying mature larvae as pupa in these species, as has been done in other groups (Hyperini: SKUHROVEC 2007, *Bagous*: GOSIK 2008). Species identification of larvae with chaetotaxy is relatively easy, and it is generally much cheaper than identification by molecular methods (HIRSCH et al. 2010). The largest problem in identifying these species, missing of larval descriptions, occurs at the beginning of describing them, but this is also problem in many other groups and not only in weevils.

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Morphology of the larva and pupa of the genus *Notosacantha* (Coleoptera: Chrysomelidae: Cassidinae: Notosacanthini) from Japan

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Cassidinae beetles are well studied on various evolutionary and biological subjects: i.e., their evolution with the host plants (DUENE & FARRELL 2005), the fossil record (CROWSON

1981), their parental care as a subsocial insect (WINDSOR 1987), their biology of larvae and adults (KIMOTO & TAKIZAWA 1994), the morphology of adults (CHABOO 2007) and reconstruction of the phylogeny (BOROWIEC 1995, HSIAO & WINDSOR 1999, CHABOO 2007). Their larval morphology has also been elaborately studied, and reviewed, and the chaetotaxy system has been recently established by BOROWIEC & ŚWIĘTOJAŃSKA (2003). As mentioned above, the beetles of the subfamily Cassidinae are provided with numerous data regarding their biology and are considered to be suitable for the study of evolutionary biology.

Seven tribes, 15 genera and 43 species from the subfamily Cassidinae are known from Japan; of these, 32 species are described and studied concerning their immature stages (KIMOTO & TAKIZAWA 1994). About 75 % of the Japanese species of Cassidinae have already been studied regarding their biology and morphology of their immature stages. The remaining species are usually very rare and not easily accessible for study. The larvae of the Japanese species of the genus *Notosacantha* have never been studied before, probably because their distributions are restricted and they are endemic to small islands.

In this presentation, I report the comparison of morphologies of the first and last instar larvae and pupae from the Japanese species of the genus *Notosacantha*, especially focusing on their chaetotaxy of the head capsule. I show the fragmentary knowledge, which has resulted from the comparison of the chaetotaxy among three genera of the tribe Oncocephalini which are the leaf-mining Cassidinae.

Species examined: *N. ihai* Chûjô, 1958, *N. loochooana* Chûjô, 1961 and *N. nishiyamai* Komiya, 2002; all originating from the Ryukyu Islands, southwestern Japan. Their larvae are the leaf-miners.

Methods: I examined following characters: chaetotaxy of the head capsule, mouthparts, spiracles and 8 – 9th abdominal segments. Terminology follows that of BOROWIEC & ŚWIĘTOJAŃSKA (2003).

Results: (1) 1st instar and mature larvae can be distinguished based on the shape of the lateral scoli, 8 – 9th abdominal segments, but their chaetotaxies are close and undistinguishable. The mature larva of *N. ihai* can be distinguished from *N. nishiyamai* and *N. loochooana* by (1) the length of spiracle; (2) lateral projections of 8 – 9th abdominal segments and coloration of 7th abdominal segment that are different from those of *N. nishiyamai* and *N. loochooana*. The chaetotaxies of their head capsules are likewise similar to each other. In particular, *N. nishiyamai* and *N. loochooana* are so similar and that they are almost impossible to distinguish. The pupae of *N. ihai* and *N. nishiyamai* can be distinguished by (1) the shape of their pronota; (2) length of their spiracles; (3) branching of lateral projection: present or absent; (4) elytral projection: present or absent. The genus *Notosacantha* is distinguished from the genera *Prionispa* and *Chaeridiona* by the absence of the fronto-clypeal suture, and its head capsule is furnished with more (18–19) setae (15–17 setae in other three genera).

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What to do with dried-up larvae

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Almost every one has the painful experience of finding one of its most important samples from spirit collection dried-up. Dried-up vials with alcohol samples can be occasionally found in museum collections, alcohol evaporates quickly and especially old vials may not seal perfectly. Sometimes are dry pinned larvae also found in the same box with adult beetles. Most people consider a dried-up larval sample useless for any studies. However there is a good chance to recover such material with the use of trisodium phosphate solution. The method is very easy and was originally published by VAN CLEAVE & ROSS (1947). The specimen is soaked in 0.5% solution of trisodium phosphate (Na_3PO_4); length of soaking depends on the size of specimen, from a few hours to several days. Specimens may initially float on the solution; however this is not the rule. Sinking of the specimen often indicates a sufficient stage of rehydration. When the specimens are soaked enough, they can be transferred into 75% alcohol by soaking them in 30% and 50% alcohol for few minutes. The method can be applied also for the rehydration of other dried-up spirit samples as adult Heteroptera (P. Banař pers. comm.), spiders, mites (M. Řezáč, pers. comm.) or in helmitology. Some attention should be paid if rehydrating females which may contains eggs, as these might swell too much and cause the specimen virtually to explode (J. Gruber, pers. comm.).

Trisodium phosphate is used as a cleaning agent, food additive, stain remover and degreaser, therefore it can be considered safe to use. The chemical comes in various hydric forms from anhydric trisodium fosfate to dodecahydrate. For re-hydration of larval samples we successfully use the dodecahydrate of trisodium fosfate ($\text{Na}_3\text{PO}_4 \cdot 12\text{H}_2\text{O}$).

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The current advance in immature ‘Trichiinae’

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After the description of the *Coleocorynus* larvae (ŠÍPEK et al. 2009), the total number of described immature taxa of ‘Trichiinae’ (sensu KRIKKEEN 1984; including Cryptodontini, Incaini, Osmodermatini, Platygeniini and Trichiini) has risen to 48, in 14 genera. Analyses based on larval and adult morphological characters have corroborated the hypothesis about

the polyphyly of Trichiinae. Since 2009 some more material was available for further study. In collaboration with Renzo Perissinotto and Enrico Richiardi we currently finalize the description of two immature *Stripsipher* species from South Africa. Moreover three dry pinned larvae of *Platygenia* were found in the Smithsonian collection of Scarabaeoidea in Lincoln (Nebraska, USA). These larvae were successfully re-hydrated and can be used for further studies. The larvae of *Stripsipher* are similar to other larvae Trichiini sensu stricto, e.g. *Trichius*, *Gnorimus*, however they differentiate slightly in the morphology of the epipharynx. The most remarkable feature of *Platygenia* larvae is the fusion of abdominal tergite IX and X found only in *Osmoderma* and Cetoniinae sensu stricto. With no surprise, parsimony analyses based on the morphological dataset of ŠÍPEK et al. (2009) have shown a sister-group relationship of *Stripsipher* and *Trichius* + (*Gnorimus* + *Iridiosoma*). The inclusion of *Platygenia* into the current dataset has caused dramatic changes in the overall topology of the phylogenetic tree. While *Platygenia* was identified as sister group of *Valgus*, the most significant result was the inclusion of the Inacaini genera *Inca* and *Archedinus* into a clade composed of *Valgus*, *Platygenia*, *Coelocorynus* and Trichiini sensu stricto. Although these results are preliminary and weakly supported they indicate the necessary direction of future research.

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Immatures of *Phelypera schuppeli* (Boheman, 1834) with comments on natural history (Coleoptera: Curculionidae: Hyperinae)

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The knowledge on taxonomy and natural history of the Cepurini, tribe to which the genus *Phelypera* Jekel, 1865 is assigned, is scanty. As immatures of *Phelypera* are poorly described, we decided to provide a detailed morphological description of the last instar larva and the pupa of *P. schuppeli* (Boheman, 1834) and compare with immatures of Hyperini described. The material studied was collected in the Midwest (Dourados, MS and Pirenópolis, GO) and Southeast Brazil (Bauru, SP). Unlike other groups of Curculionidae, the larvae of Hyperinae do not leave inside plant tissue, but instead they spend all their development time on or under their host leaves surface (CAPIOMONT 1868, LIMA 1956, BONDAR 1943). The known larvae of *Phelypera* species are exophytic, brightly colored, eruciform, provided with abdominal ambulatory ampullae, and resemble larvae of Lepidoptera. The mature larvae can

spin globular wide-laced cocoons where pupation takes place. The host plant of *Phelypera schuppeli* is *Pachyra aquatica* Aubl. (Bombacaceae) (LIMA 1956, BONDAR 1943). Some data achieved during field work, and also obtained under laboratory conditions, confirmed previously published biological observations on *P. schuppeli* (FERREIRA & CAMARGO 1989, DINIZ & MORAIS 1996). Furthermore, additional information is reported, mainly on defensive behavior, process of cocoon construction and natural enemies that contribute to the natural regulation of *P. schuppeli* populations, as the larva predator *Supputius cincticeps* (Stål, 1860) (Hemiptera: Pentatomidae) and the prepupa and pupa parasitoid *Jeliscoa* sp. (Hymenoptera: Pteromalidae).

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POSTERS**The van Emden larval collection of Coleoptera housed
in the Natural History Museum, London**

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The spirit preserved coleoptera collection of Dr. F. I. van Emden (1898–1958) was presented to the Natural History Museum, London in 1977 by his son, Dr. H. F. van Emden. The collection comprised of 6,500 spirited tubes and 2,400 slides, principally of Coleoptera larvae. The collection is investigated, and a summary of notable taxa listed, with particular reference to van Emden's seminal works (VAN EMDEN 1941, 1943).

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**Maintaining concentration: a new practical method for profiling and
topping up spirit collections**

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A new method of profiling alcohol-preserved collections is presented and its use as a diagnostic tool is discussed. Some previous methods for topping up are reviewed and a new method is proposed. A novel tool is presented – a reference table for calculating the concentration of topping up alcohol – which allows the regulation of preservative alcohol concentration within close limits. The method can be used for remedial and routine topping up and can be adapted to the needs of different collections.

**Development of the epipharynx in two aphodiid species of the genus
Amidorus (Coleoptera: Aphodiidae)**Angela ROGGERO, Claudia TOCCO & Claudia PALESTRINI

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Coleoptera development leads to profound modifications of tissues and organs. The mouthparts are always present, being functional in larval instars and adult, though not in pupa. Among these structures, the epipharynx is almost unique and, in adults, is differentiated to the extent that it is reliable for taxa identification. Although less well characterized, the epipharynx is also widely studied in larvae, but it is not usually examined in pupa.

The aim of our work was to study the ontogenetic trajectories of the epipharynx development in *Amidorus immaturus* and *A. obscurus* (Coleoptera: Aphodiidae), two closely related Palaearctic species that are almost indistinguishable on the basis of external traits (DELLACASA & DELLACASA 2006, TARASOV 2008, TOCCO et al. 2011). The pupal epipharynx of *A. obscurus* is shown for the first time and the features of the structure in adult, pupa and larvae are compared.

Adults of both species were collected in Val Ferret (Val d'Aosta, NW Italy) and reared in the laboratory to hatch the preimaginal instars. The larvae were identified according to species, gender and instar (ROGGERO et al., submitted), then the epipharynges were dissected, mounted on slides and photographed (TOCCO et al. 2011); the dataset included adults and larvae of both sexes ($N_{TOT} = 168$). Through landmark-based geometric morphometrics the phenotypic differences and ontogenetic trajectories of the two species were analyzed. Seven landmarks were placed on the epipharynx by tpsDig 2.16 (ROHLF 2010a), according to functional homology criteria. Generalized Procrustes Analysis was carried on by tpsRelw 1.49 (ROHLF 2010b), retaining the Relative Warp values (RWs) for the further analyses. To define the size measurement, the centroid size value of the epipharynx (CS_epi) was chosen. We drew the scatterplots of RW scores pairs to summarize the shape variation within the sample, identifying the different groups (PASW Statistics 18, IBM SPSS). The classifications based on species, instars and species/instars together were tested by the Multivariate Test of Significance as implemented in tpsRegr 1.37 (ROHLF 2009), and the statistical results were compared to choose the better-fit hypothesis.

A non-significant difference in body size between the two species has already been observed at each larval instar (ROGGERO et al., submitted). Hence, shape variation during development was tested here. To check whether *A. immaturus* and *A. obscurus* share the same ontogenetic trajectories, the shape space was examined in the plot of RWs score pairs, then a MANOVA was performed on the RWs scores (species and instars as fixed factors). To examine the relationship between shape and size in each species, the RWs 1 and 2 were regressed separately on size (expressed by the CS_epi), then the covariation in shape and size was tested by ANCOVA. Subsequently, to examine the relationship between shape and size during development, a MANCOVA was employed with RWs scores as the dependent variables (species and instar as fixed factors and the CS_epi as a covariate).

In the Relative Warps analysis (a.k.a. PCA) the first three out of ten RWs explained about the 98 % of the overall shape variation (RW_1 = 95.35 %). The separation between the species was well-resolved for adults, but was poor for the preimaginal instars that were largely superimposed in any plot of pairs of the first three RWs. The Multivariate Tests of Significance based on species and instars separately gave significant results, although the percent unexplained value (used as an overall measure of fit) was high for both the classifications. A better result was achieved using the species/instars classification together, obtaining significant statistics and the lowest value of percent unexplained.

The MANOVA results confirmed that the shape of the epipharynx differs significantly both in species and in instars. For each species, a significant relationship of size and shape was assessed through Regression Analysis. In the development of the two species, often a similar pattern of changes affect the same parts (i.e. the apotormae), which differ exclusively in the growth ratio, as was established through the ANCOVA on RW_1. Besides, the development

acts differently on other parts of the epipharynx, giving diverging patterns of shape variation, as was shown through the ANCOVA on the RW_2. According to the MANCOVA results, the overall shape variation was not significantly related to size variation between the species, although a significant result was given for the instars, irrespective of species classification.

In the pupa, the epipharynx is not trilobate (as in the larval instars), but is more similar to that in the adult, and some of its anatomical parts can be easily identified, such as the tylus, with the fore margin slightly folded downward, the enlarged area of the crepis or the chaetopariae. Also the haptomerum area is recognizable, although it is far less sclerotized than in the adult.

On the basis of our present findings, it appears that both species invest more in allometric changes in the epipharynx than in its diversification at preimaginal instars. In the larvae, the epipharynx moves freely, being joined to the clypeus (head capsule) only at the base, and the structure can grow in size without being constrained by the surrounding mouthparts. Thus, in the early instars the developmental pattern is focused essentially more on size than on shape variation. In the pupa, the epipharynx changes its position, being placed under the clypeus. Thus, in the adult the epipharynx's size is constrained by the clypeus' size, and shape diversification became the main factor of developmental pattern in both species. The ontogenetic trajectories of the two species show similar developmental patterns.

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