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What is a moth doing under water? Ecology of aquatic and semi-aquatic Lepidoptera

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Abstract – This paper reviews the current knowledge on the ecology of aquatic and semi-aquatic moths, and discusses possible pre-adaptations of the moths to the aquatic environment. It also highlights major gaps in our understanding of this group of aquatic insects. Aquatic and semi-aquatic moths represent only a tiny fraction of the total lepidopteran diversity. Only about 0.5% of 165,000 known lepidopterans are aquatic; mostly in the preimaginal stages. Truly aquatic species can be found only among the Crambidae, Cosmopterigidae and Erebidae, while semi-aquatic forms associated with amphibious or marsh plants are known in thirteen other families. These lepidopterans have developed various strategies and adaptations that have allowed them to stay under water or in close proximity to water. Problems of respiratory adaptations, locomotor abilities, influence of predators and parasitoids, as well as feeding preferences are discussed. Nevertheless, the poor knowledge on their biology, life cycles, genomics and phylogenetic relationships preclude the generation of fully comprehensive evolutionary scenarios.

Keywords: Lepidoptera / Acentropinae / caterpillars / freshwater / herbivory

Résumé – Que fait une mite sous l'eau? Écologie des lépidoptères aquatiques et semi-aquatiques. Cet article passe en revue les connaissances actuelles sur l'écologie des mites aquatiques et semi-aquatiques, et discute des pré-adaptations possibles des mites au milieu aquatique. Il met également en lumière les principales lacunes dans notre compréhension de ce groupe d'insectes aquatiques. Les papillons aquatiques et semi-aquatiques ne représentent qu'une infime fraction de la diversité totale des lépidoptères. Seulement 0,5% environ des 165,000 lépidoptères connus sont aquatiques, principalement aux stades préimaginaux. On ne trouve des espèces véritablement aquatiques que chez les Crambidés, les Cosmopterigidés et les Erebidés, tandis que les formes semi-aquatiques associées aux plantes amphibies ou des marais sont connues dans treize autres familles. Ces lépidoptères ont développé diverses stratégies et adaptations qui leur ont permis de rester sous l'eau ou à proximité de l'eau. Les problèmes d'adaptation respiratoire, les capacités locomotrices, l'influence des prédateurs et des parasitoïdes, ainsi que les préférences alimentaires sont discutés. Néanmoins, le manque de connaissances sur leur biologie, leur cycle de vie, leur génomique et leurs relations phylogénétiques empêche l'élaboration de scénarios évolutifs complets.

Mots-clés : Lépidoptères / Acentropinae / chenille / eau douce / herbivorie

Introduction – from the water onto the land and back again

All insects are primarily terrestrial. However, it is worth bearing in mind that they have evolved from aquatic invertebrates. According to the pancrustacean theory, insects evolved from crustaceans, with the Remipedia being the most probable sister group of the Hexapoda. Therefore, crustaceans can be said to have colonized the land as insects. According to the latest estimates the terrestrial colonization happened sometime between the late Cambrian and early Ordovician (Schwentner *et al.*, 2017). The enormous radiation of insects in the terrestrial ecosystems resulted in a high level of adaptation to life on land. These adaptations included the ability to fly and the development of a tracheal system. However, all those fantastic adaptations that made the insects the most successful terrestrial animals on our planet imparted important restrictions on the exploration of waters; a process certainly

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associated with substantial modifications of locomotor abilities, mating systems, feeding modes, respiratory and sensory adaptations. In addition, these early insect colonists had to compete with already established inhabitants of the water world (Ward, 1992; Vermeij and Dudley, 2000).

Aquatic or semi-aquatic species can be found in 16 orders of insects (Ward, 1992). All of them have terrestrial ancestors, which have independently colonized the waters. Sometimes, the aquatic mode of life has evolved multiple times within an insect order (Grimaldi and Engle, 2005). Although as few as about 6% of all insects are found in the aquatic environment, they account, according to the latest estimates, for 60%–80% of all the freshwater animals (Dijkstra *et al.*, 2014). The Lepidoptera are represented by a relatively low number of species compared with other aquatic insect orders. Although our knowledge on their diversity and taxonomy is constantly increasing (Landry and Roque-Albelo, 2006; Mey and Speidel, 2008; Chen *et al.*, 2010; Agassiz, 2012, 2014; Scholtens and Solis, 2015), there is a lot yet to be learned about the ecology and possible evolutionary scenarios or phylogenetic relationships that exist among the aquatic and semi-aquatic Lepidoptera.

What are aquatic and semi-aquatic moths?

Among the 165,000 currently described Lepidoptera, only about 0.5% of the species (representing three families) are considered to be truly aquatic. Their caterpillars are generally believed to live entirely submerged. Most of the species of truly aquatic Lepidoptera belong to the family Crambidae (about 800 species of the Acentropinae, representing over 50 genera, and at least two species in the genera *Samea* and *Niphograpta* of the subfamily Pyraustinae) (Mey and Speidel, 2008). Mey and Speidel (2008) reviewed the information regarding the species richness of aquatic Crambidae, but they did not analyse the problems associated with the ecology of this group. It is worth remembering that the biology of the immature stages of numerous species of Crambidae is completely unknown. It can only be assumed that some species are aquatic based on their systematic position within the subfamily Acentropinae. On the other hand, larvae of some Acentropinae (in the genera *Nymphicula*, *Paracymoriza*, and *Aulacodes*) are terrestrial (Regier *et al.*, 2012), but it is not clear whether they represent reversions or ancestral adaptations. In the case of *Nymphicula*, Yoshiyasu (1980) suggested based on the morphology of the caterpillar tubes that this genus might represent a reversion from an aquatic to a terrestrial mode of life, but without detailed molecular studies it is difficult to confirm the validity of this hypothesis. Some other aquatic crambids like larvae of *Petrophila truckeealis* are able to live for several days outside the water (Lange, 1971), which suggests that the diversity of strategies is probably much higher than we expect. There are also at least four species of aquatic arctiid moths. Larvae of *Paracles laboulbeni* live in the South American lakes and feed on *Oedogonium*, various Bacillariophyta and, at later stages, on *Utricularia olivacea* (Adis, 1983). Three of the other neotropical species of the genus *Paracles*: *P. klagesi* (associated with *Tonina fluviatilis* and some other plants), *P. azollae* and *P. burmeisteri* also develop in freshwater (Meneses *et al.*, 2013). Large numbers of aquatic species, most of which are still undescribed represent the genus *Hyposmocoma* (Cosmopterigidae), which is endemic to Hawaii (Schmitz and Rubinoff, 2011).

Various caterpillars of Lepidoptera live in stems or roots or on exposed and non-submerged leaves of semi-aquatic or marsh plants such as: *Typha*, *Glyceria*, *Carex*, *Phragmites*, *Sparganium* or *Scirpus*. Such species are known from various families and genera (Table 1). Mey and Speidel (2008) treated all similar taxa as semi-aquatic and did not include them in their review. Nevertheless, it is also worth remembering that it is occasionally difficult to clearly differentiate between aquatic and semi-aquatic forms; for example the caterpillar of noctuid *Bellura melanopyga* periodically comes to the surface to renew its oxygen supply (Lange, 1956). On the other hand, some Acentropinae, *e.g.* the common European *Nymphula nitidulata* that lives on *Sparganium erectum* represents a semi-aquatic rather than a truly aquatic Lepidoptera (Vallenduuk and Cuppen, 2004).

According to rough estimates, there are about 500,000 lepidopteran species worldwide (Kristensen *et al.*, 2007; Brito *et al.*, 2016 end references therein). The number of undescribed species is huge. Moreover, the biology and habitat preferences of numerous formally described species, especially tropical lepidopterans, are completely unknown. Therefore, more aquatic and semi-aquatic forms can be expected to be found in other families, in both the Macro- and Microlepidoptera.

From the surface to the depths – evolutionary potential of aquatic caterpillars

Generally, lepidopteran caterpillars are not typical inhabitants of the aquatic environment. However, they are associated with a great variety of habitats, including those that are moist or wet. Some of the caterpillars live in moist soil (Grimaldi and Engle, 2005) or inside pitcher plants (Scoble, 1995), while others – such as some of the Hawaiian *Hyposmocoma* – inhabit streams where they feed on algae covering wet rocks. However, they can also complete their whole life cycle outside of a water body (Rubinoff, 2008). An evolutionary step from such moist habitats to a fully aquatic lifestyle seems to be possible. Even more interesting transitions to the aquatic mode of life have been observed in other insect orders, for example, a nitidulid beetle has changed its habitat from bamboo sap to freshwater (Kovac *et al.*, 2007).

It should not then be surprising to assume that similar events might also have occurred among the Lepidoptera. Some adaptations to moisture or periodic flooding were already reported from the phylogenetically most basal lepidopteran groups such as the Micropterigidae. For example, caterpillars of the genus *Epimartyria* from North America live in swampy woods or boggy ditches and are known to have micropapillae on their cuticle. These micropapillae form a simple plastron-like respiration system (Davis and Landry, 2012). Thus, this suggests that moth caterpillars already had the evolutionary potential to enter the aquatic milieu at the beginning of their evolutionary history.

Various pre-adaptations, typical of many terrestrial caterpillars were most probably very important for the evolution of the aquatic life style. The underwater breathing

Table 1. Moth genera with representants associated with various amphibious and marsh plants.

Family/genus	Plant genera	References
Coleophoridae: *Coleophora*	*Juncus*, *Polygonum*	Harms and Grodowitz (2009); Sterling and Parsons (2012)
Cosmopterigidae: *Cosmoptrix, Limnaecia*	*Phragmites*, *Typha*	Harms and Grodowitz (2009); Sterling and Parsons (2012)
Cossidae*: Phragmatecia*	*Phragmites*	Carter and Hargreaves (1994)
Crambidae (Crambinae): *Acigona, Calamotropha, Chilo, Occidentalia,Thopeutis*	*Eleocharis*, *Juncus*, *Schoenoplectus*, *Scirpus*, *Typha*	Slamka (1997); Harms and Grodowitz (2009); Sterling and Parsons (2012)
Crambidae (Schoenobiinae): *Donacaula, Schoenobius, Scirpophaga*	*Carex*, *Glyceria*, *Phragmites*, *Scirpus*	Slamka (1997); Vallenduuk and Cuppen (2004)
Elachistidae*: Elachista*	*Phragmites*	Sterling and Parsons (2012)
Erebidae (Arctiinae): *Estigmene*	*Polygonum*	Harms and Grodowitz (2009)
Erebidae (Herminiinae): *Palthis*	*Polygonum*	Harms and Grodowitz (2009)
Erebidae (Hypenodinae): *Hypenodes*	*Carex*, *Juncus*, *Sparganium*	Nowacki (1998)
Erebidae (Lymantriinae): *Laelia*	*Cladium*, *Phragmites*, *Sparganium*	Carter and Hargreaves (1994)
Gelehiidae: *Aristotelia, Brachmia Chionodes*	*Phragmites*, *Polygonum*	Harms and Grodowitz (2009)
Glyphipterigidae: *Glyphipterix*	*Juncus*	Sterling and Parsons (2012)
Nepticulidae: *Stigmella*	–	Lange (1956)
Noctuidae: *Acronicta*, *Apamea*, *Archanara*, *Argyrogramma*, *Bellura*, *Capsula*, *Celaena*, *Cerapteryx*, *Chilodes*, *Coenobia*, *Homophoberia*, *Neoerastria*, *Nonagria*, *Oligia*, *Plusia*, *Rhizedra*, *Sedina*, *Simyra*, *Spodoptera*	*Carex*, *Eichhornia*, *Glyceria*, *Juncus*, *Nelumbo*, *Nuphar*, *Nymphaea*, *Phragmites*, *Pistia*, *Polygonum*, *Pontederia*, *Sagittaria*, *Scirpus*, *Sparganium*, *Typha*, *Zizania*	McGaha (1954); Carter and Hargreaves (1994); Nowacki (1998); Wheeler and Halpern (1999); Center and Hill (2002); Harms and Grodowitz (2009)
Pyralidae: *Dicymolomia, Sylepta*	*Polygonum, Typha*	Harms and Grodowitz (2009)
Sphingidae: *Eumorpha*	*Ludwigia*	Harms and Grodowitz (2009), Lange 1956; Lange (1971); Ward (1992)
Tineidae	–	Lange (1956); Lange (1971); Ward (1992)
Tortricidae: *Argyrotaenia*, *Bactra*, *Choristoneura*, *Platynota*, *Sparganothis*	*Juncus*, *Polygonum*, *Schoenoplectus*, *Scirpus*, *Typha*	Harms and Grodowitz (2009); Sterling and Parsons (2012)
Yponomeutidae: *Orthotaelia*	*Schoenoplectus*, *Sparganium*, *Typha*	

mode most probably began to develop from the aforementioned cuticle pre-adaptations. A collapsible air bubble (a physical gill) that allows diving and requires regular air supply restoration is a very common adaptation in this group (Lange, 1956; Speidel, 2002). A further improvement of this mechanism could have led to the evolution of a more efficient plastron structures which allowed for further exploration of the aquatic environment and may have enabled longer stays under water. For example, caterpillars of the genus *Paracles* developed a unique plastron system from long clavate hairs that covered the larval body (Messner and Adis, 1987; Meneses *et al.*, 2013). Cuticle hydrophobicity can be enhanced by various waxy substances, hairs, or cuticular surface structures (Reichholf, 1976; Ward, 1992). Although the hydrophobic cuticle is known in aquatic moths larvae, such adaptations can be found in many typically terrestrial caterpillars representing various families of Lepidoptera. The hydrophobic cuticle prevents the caterpillar from getting and staying wet since the water can simply slide off the body (Balmert *et al.*, 2011). Developing a relatively stable air bubble around the body can be facilitated by the presence of tubes made of leaves of the host plants or made from the debris of various plants (Pabis, 2014). This is another typical feature of many terrestrial lepidopteran larvae. These tubes of aquatic caterpillars enhance respiration and protect the caterpillar from UV radiation (Dorn *et al.*, 2001). These tubes also provide at least some protection from predators or parasites (Müeller and Dearing, 1994).

Development of the hydrophilic cuticle and of the closed spiracle system allowed for respiration based on water-dissolved oxygen diffusing through the cuticle. This adaptation enhanced exploration of the deeper areas, like in the case of *Acentria ephemerella* (Berg, 1941). It is still not clear which adaptation appeared earlier and which can be treated as a more advanced. There are species of Acentropinae that are hydrophilic during the first stages of development and become hydrophobic later on during development. Caterpillars of some other species are hydrophilic during all the larval stages (Speidel, 2002). Moreover, typical hydrophilous caterpillars may also construct protective cases (Berg, 1941). Some lepidopteran larvae developed tracheal gills that can be aided by periodic vibratory movements, which probably enhances the air supply (Welch and Sehon, 1928). Hawaiian aquatic *Hyposmocoma* most probably breathe directly through the cuticle and need well oxygenated running water. They will die if they are in still water (Schmitz and Rubinoff, 2011).

In contrast to the respiratory systems, aquatic caterpillars did not develop any special or particularly efficient locomotor adaptations to living in the aquatic environment. Generally, caterpillars are not very good swimmers. Although larvae of the crambid *Ostrinia penitalis* may swim on the water surface and may also use a dragline made of silk (Welch, 1919). Aquatic caterpillars generally move in a manner that is very similar to that seen in the terrestrial forms (they use thoracic legs and prolegs with crochets). Aquatic caterpillars can be found almost exclusively on plants they feed on, or on algae-covered surfaces. None of the known caterpillars found associated with water developed any special swimming legs such as are evident in many aquatic adult beetles or aquatic hemipterans. Despite the very diverse caterpillar morphology, the basic body plan is very conservative and the legs even if modified for some reason (*e.g. Stauropus fagi*, or carnivorous Hawaiian caterpillars) do not differ radically in their locomotor functions (Grimaldi and Engle, 2005). Perhaps this is one of the most important evolutionary limitations that did not allow for the evolution of active swimming. Furthermore, the general caterpillar body plan probably precludes the development of a more streamlined shape. In addition, insect bodies tend to sink in water because their density is only slightly higher than that of water (Flynn and Bush, 2008). To be able to actively swim under water insects should combine morphological adaptations (*e.g.* swimming legs) with air bubbles that enhance their buoyancy. Aquatic caterpillars are often associated with stagnant waters or slow-flowing rivers. Even when they live in streams, they do not develop any swimming adaptations that would enable them to move actively through the water column (Lange, 1956; Ward, 1992; Stoops *et al.*, 1998). Some, like the North American species of *Petrophila* and *Argyractis*, do inhabit streams, but they are protected from being carried away by the currents by having types of silken tents that are attached to the stones on the bottom of the stream (Lange, 1956; Lange, 1971).

Adaptations associated with diet were also probably very important for the evolution of an aquatic mode of life in the caterpillars. Exactly like truly terrestrial forms, aquatic and semi-aquatic caterpillars include scrapers (often with flattened and enlarged mandibles), algae feeders and typical leaf shredders associated with angiosperms (Lange, 1956; Mey and Speidel, 2008). Some free-living caterpillars that are algae scrapers could have evolved from soil-dwelling forms (Grimaldi and Engle, 2005; Davis and Landry, 2012). Of the typical plant-feeding lepidopteran larvae, stem borers and typical external feeders were probably among the first colonizers of aquatic environment (Ward, 1992; Grimaldi and Engle, 2005). Is often assumed that the first aquatic plant feeders had initially no real contact with water since they were hiding inside of plant tissues or foraging only on the emergent parts of plants that were above the water surface (Hannemann, 1967; Ward, 1992; Mey and Speidel, 2008). Some known terrestrial species possess unusual abilities that could be similar to the first basic adaptations that occurred in the aquatic environment. For example, caterpillars of the arctiid moth *Rhyparioides metelkana* feed on *Caltha palustris* and are able to swim to another plant when they accidentally fall into the water (Hannemann, 1967). Larval stages of the arctiid moth, *Spilosoma lubricipeda* that normally feed on *Menta* or *Rubus* were also occasionally observed on the water pineapple, *Stratiotes aloides*, and were also able to swim to another plant. However, all the pupae died at the end of the season when the water pineapple sank to the bottom of the water body (Smolders and van der Velde, 1996). A common polyphagous pest *Duponchelia fovealis* is known to consume various plants from 38 families, including at least one aquatic plant – a water-trumpet (*Cryptocoryne*) (Brambila and Stocks, 2010). This suggests that polyphagy might have been an important first step in the early evolution of aquatic moths and probably allowed caterpillars to switch to the aquatic plants as a food source.

The influence of a caterpillar's feeding experience (first species of plant used by newly hatched caterpillar) on its host plant preferences (host plant induction, level of specialization and its relation to plant chemical defences) could also be important for the evolution of aquatic and semi-aquatic moths, but there are almost no data on such processes (Litsinger and Chantarapraha, 1995; Wheeler and Halpern, 1999; Dorn *et al.*, 2001; Erhard *et al.*, 2007; Petit *et al.*, 2015). Walenciak *et al.* (2002) and Choi *et al.* (2002) reported that macrophytes containing tannin may possibly alter the performance of *A. ephemerella* caterpillars indirectly by an inhibitory effect on their gut microbiota. Since symbiotic bacteria can be very important in the evolution of Lepidoptera (Russell *et al.*, 2012), further studies in this area are urgently needed in aquatic moths. Both, prior feeding experience, and plant chemical cues have increased the preference of the *Munroessa gyralis* caterpillar for *Nuphar*. However, protein content, concentration of polyphenols and leaf toughness were found to not be as important in influencing food preference in *Munroessa gyralis* (Dorn *et al.*, 2001). At the same time none of the larvae managed to pupate, neither on *Nuphar* nor on the normally preferred *Nymphaea*. This might suggest that larvae require a mixed diet or that the conditions provided in the experiments were inappropriate. Authors also speculated that *Nuphar* petioles might be too small to serve as a pupation site for the caterpillars. This study of the one species shows how complex such interactions might be. Caterpillar preferences can depend on many factors, including the influence of predators, development time of the plant, or its various chemical or morphological features. Such relationships may vary depending on the species or genus of moth; moreover, the first generation caterpillars might have different preferences compared with the second generation caterpillars. *Elophila obliteralis* may feed on about 60 species of plants, including such different taxa as *Lemna*, *Sagittaria*, *Myriophyllum* or *Hydrochloa* (Habeck *et al.*, 2017). However, we do not know much about the mechanisms involved in shaping preferences for a specific plant species. We also do not know about the caterpillar development time and survival rates on different plant species. On the other hand some oligophagous species, like *Cataclysta lemnata*, a crambid that was generally found to be associated with Lemnaceae, may occasionally consume other macrophytes including *Stratiotes aloides*, or even *Typha latifolia* and *Glyceria maxima* (van der Velde, 1988), as well as water ferns of the genus *Azolla* (Farahpour-Haghani *et al.*, 2017). Stoops *et al.* (1998) suggested, based on their own results and literature data that most of the aquatic crambids are polyphagous since they feed on more than four species of plants from a minimum of three plant families. A wide host range of aquatic caterpillars might have been important in the evolution of the aquatic and semi-aquatic moths taking into account the fact that the number of aquatic angiosperms in freshwater is much lower than is found in terrestrial environment (Chambers *et al.*, 2008). On the other hand such generalisations should be made with caution, since we do not know much about the diet of the majority of the aquatic moths.

Ecological interactions

There is a common notion that aquatic caterpillars play a relatively minor role in the ecological interactions of freshwater ecosystems. However, those opinions are often based on the underestimations of the importance of Lepidoptera and there is also a lack of even basic knowledge about their diversity and abundance. Aquatic caterpillars are definitely an important group of aquatic herbivores. In fact, some species were noted to occur at very high densities in aquatic ecosystems. For example, the abundance of *A. ephemerella* caterpillars may sometimes reach 10,000 ind./m^2 (Gross *et al.*, 2002). Lepidopteran caterpillars may also influence the species composition of macrophytes, which might result in important changes in the functioning of the ecosystem (Gross *et al.*, 2001). Some of the caterpillars can probably also be used as indicators of changes in natural ecosystems. Such ecosystems could include the Hawaiian streams, a habitat that lacks typical aquatic insect indicators such as trichopterans and ephemeropterans (Schmitz and Rubinoff, 2011). It was also demonstrated that larvae of *Parapoynx stratiotata* may stimulate nutrient release and alter water quality (Grutters *et al.*, 2016). These above mentioned examples demonstrate that the role of Lepidoptera in the functioning of freshwater ecosystems is probably vastly underestimated.

Our knowledge about the interactions of aquatic caterpillars with other animals, especially predators and parasites, is also very limited, but studies suggest that the caterpillars play an important role in the diet of some fish and invertebrates. Larvae of some beetles and dragonflies are also known to attack aquatic caterpillars, although there is no information about specific species or genera that prey on lepidopteran larvae (Agassiz, 1996). There is a single observation of *A. ephemerella* caterpillars that were attacked by hemipterans, water mites, and spiders (Buckingham and Ross, 1981), while eggs of this species were eaten by planarians. However, this observation was made in North America which is outside native European range of *A. ephemerella* (Batra, 1977). Tuskes (1977) reported high fish predation pressure on the algae-scraping larvae of *Petrophila confusalis*. In addition, caterpillars of the closely related species *P. truckeealis* were found in the stomachs of perch (Lange, 1971). Some aquatic caterpillars were also recorded in the diet of a rainbow trout – a species that was introduced to Hawaii (Englund and Polhemus, 2001). The larvae of *C. lemnata* and *Elophila nymphaeata* kept in the laboratory were eaten by carp, tench, roach, gudgeon or common bleak (Wojtusiak and Wojtusiak, 1960). It is worth remembering that laboratory observations may produce different results than those obtained under natural conditions. For example, Dorn *et al.* (2001) observed that caterpillars outside their tubes were eaten more often than those protected by cases, although results were different in the laboratory. What is more important is that these observations were based on a single experiment with only a small number of caterpillars. At the same time these observations showed that some fish are in fact able to consume caterpillars without swallowing the protective cases.

There is also very little data on the effects of parasitic hymenopterans (Ichneumonidae) and flies (Tachinidae) on aquatic caterpillars (Lange, 1956; Lange, 1971; Resh and Jamieson, 1988; Yoshida *et al.*, 2011). No study has comprehensively analysed the pressure of fish or other predators and parasitoids on the populations of different moth species, or compared the predation on tube building species with those that do not hide inside any protective case. In at least some aquatic crambids the time needed for the construction of a protective case and the type of the material used can be very important as an element of a predator avoidance strategy (Müeller and Dearing, 1994).

Moreover, macrophytes themselves can provide good shelter from various threats (Dorn *et al.*, 2001). In view of all the incomplete evidence, it is difficult to assess the importance of predation pressure during the early stages of evolution of the aquatic life style in Lepidoptera. It is equally difficult to theorize how the predation pressure could have influenced the development of defensive strategies, host plant preferences or the distribution along environmental gradients or within various microhabitats. Furthermore, information is lacking on the inter- and intraspecific competition in aquatic moths.

Adults, eggs and pupae – life cycle under the water

Many aquatic moths stay underwater during all the preimaginal stages. Adults of almost all these species are typical terrestrial insects. Females of some Acentropinae (*e.g.* genus *Petrophila*) may enter the water to lay eggs and stay submerged for a few hours, but this does not make them fully aquatic (Lange, 1956). Many aquatic moths lay eggs on the submerged side of floating leaves or stems by placing the abdomen beneath the water surface (Reichholf, 1970; Pabis, 2014). A truly aquatic adult form is found in only one species, *A. ephemerella*, the only species in the genus. In this species, aquatic brachypterous females swim using the last pair of legs, and they also have plastron structures for respiration. Along with hemipterans of the genus *Aphelocheirus* and some aquatic cave beetles, *Acentria ephemerella* is one of only a few insects that can stay under water throughout its entire life span (Carbonell *et al.*, 2011; Miller and Bergsten, 2016). Such a mode of life strongly affects the dispersal ability of the moth; however, the second form of *A. ephemerella* female and all males are terrestrial and have fully developed wings. This unique mode of life is difficult to explain because, despite the relatively good knowledge about the host plants and life cycle of the species (both forms of females lay eggs on *Potamogeton*, *Chara* and *Elodea*; caterpillars are hydrophilous; copulation of the brachypterous females takes place close to the water surface; adult females live for only 1–2 days) (Berg, 1941; Kokociński, 1963; Choi *et al.*, 2002; Speidel, 2002), there have been no detailed studies on factors affecting the development of these two different forms of *A. ephemerella*. In addition, no molecular or physiological research has been conducted on these morphotypes. Virtually nothing is known about the effects of physical and chemical factors (*e.g.* dissolved oxygen content or temperature in water) on the development time and divergence in the adult female morphology of this species. Some studies suggest that development of these two morphotypes is a relatively recent adaptation because the morphology of the compound eyes in the aquatic form is similar to the eye morphology of the terrestrial form; despite the obvious differences in the physical characteristics of the environment and biology of the two forms of the moth (Lau *et al.*, 2007). The presence of the two morphotypes might be related to divergence in dispersal strategies. *A. ephemerella* is a small, delicate moth with limited flying ability, and can thus be blown far from the water by the wind (Berg, 1941), although adults have been observed engaging in active flight at relatively large distance of 1 km from water bodies (Pruffer, 1957). While the winged form allows for dispersal, the presence of the aquatic form minimizes the risk of being lost. Brachyptery can also be associated with the larger number of eggs produced (Roff, 1994), but in no study were the two forms compared with respect to this.

Most of the knowledge on adaptations of Lepidoptera to the aquatic environment concerns caterpillars. In only one study were egg adaptations examined. In *E. nymphaeata* air-filled structures located under the chorion and a mucus layer of the egg allowed for the uptake of air directly from plants (Barbier and Chauvin, 1974). Pupae are often hidden in various air-filled cocoons or in stems of aquatic plants (Lange, 1956; Reichholf, 1970; Speidel, 2002; Pabis, 2014). However, we do not know anything about the oxygen requirements and/or tempo of the developmental and metabolic processes of these pupae.

So many or so few?

There are at least 800 species of aquatic lepidopterans. On the other hand, when the number of evolutionary transfers from land to water is taken into account (members of three families only!), the number of truly aquatic moths is actually low compared to other groups of aquatic insects such as the Hemiptera, Coleoptera and Diptera (Jach and Balke, 2008; Polhemus and Polhemus, 2008). The number of evolutionary entries to the freshwater by insects is estimated to exceed 50 based on the review of the available phylogenetic studies (Dijkstra *et al.*, 2014; Mitterboeck *et al.*, 2016).

Knowledge of the phylogeny of the aquatic crambids is increasing (Solis, 2007; Regier *et al.*, 2012; Liu *et al.*, 2016), although it is still not detailed enough to enable us to develop scenarios concerning the natural history of aquatic species. It cannot be ruled out that similar adaptations occurred multiple times within the Crambidae. A recent study by Chen *et al.* (2017a), involving molecular data, suggests that the *Nymphula*-type caterpillar (with hydrophobic cuticle and open spiracle system) evolved from the *Parapoynx*-type larva (with tracheal gills and closed spiracles). Although the current state of biodiversity inventories in different regions of the world preclude the completion of any comprehensive zoogeographical studies; it is worth mentioning that only two genera, *Parapoynx* and *Elophila*, are cosmopolitan (Mey and Speidel, 2008). Since these two taxa probably represent the key evolutionary lines among aquatic moths, they should be in the focus of phylogeographic studies.

The most recent molecular analysis strongly supports monophyly of the Acentropinae (Regier *et al.*, 2012). Moreover, the crambid subfamilies that can be defined as semi-aquatic or associated with moist habitats (Schoenobiinae and Midilinae) are very closely related to the Acentropinae, together forming, in the terminology of Regier *et al.* (2012), a “wet clade”. The crambid subfamily Pyraustinae and the genus *Paracles* represent independent evolutionary events. Interesting results based on the analysis of molecular data showed that the semi-aquatic Hawaiian *Hyposmocoma* represent multiple entrances to and reversions from the aquatic life style. Although in this case the isolated nature of the Hawaiian ecosystem could have substantially influenced the evolution of these moths, since they most probably represent one of the early colonisers of the Hawaiian archipelago (Rubinoff, 2008). There are no other similar studies on semi-aquatic members of other families, but most of them probably represent relatively recent adaptations to the aquatic environment, which are observed in single species or genera only.

The near absence of adult aquatic moths can be relatively easily explained. Unlike the robust bodies of beetles and hemipterans which have a second pair of wings covered by the elytra, delicate wings of the moths are not a very good preadaptation to the aquatic environment. In the case of the Lepidoptera, still another important aspect of their biology could have affected their evolution in the aquatic environment – almost all caterpillars are phytophagous. Co-evolution with the angiosperms was most probably a key element of lepidopteran evolution for millions of years (Grimaldi and Engle, 2005). At the same time less than 1% of the flowering plants can be considered aquatic (Vermeij and Dudley, 2000; Chambers *et al.*, 2008), which substantially reduces the potential food base for the caterpillars. In fact, only a few of the Brazilian Acentropinae are carnivores that consume larvae of the Simuliidae (Solis, 2007). Representants of other aquatic insect orders are mostly detritivores, carnivores or parasitoids and are not dependent on the availability and diversity of macrophytes (Ward, 1992). In addition to the obvious osmotic limitations, the lack of appropriate food likely reduced the possibility of the marine environment being colonized by lepidopteran caterpillars; in general, the number of insects in the seas is very low and most of them are associated with the near shore zone (Ward, 1992). Some aquatic moth caterpillars such as *E. nymphaeata* were reported from brackish waters of a small Black Sea lagoon (Kovachev *et al.*, 1999). Some other caterpillars of Acentropinae were recorded in estuaries or in brackish lakes (Ward, 1992).

Concluding remarks

Detailed phylogenetic studies, as well as studies on life cycles and evo-devo research are needed to understand the evolutionary processes that shaped the diversity and biology of aquatic and semi-aquatic moths. Genome sequencing of at least some taxa representing various ecological groups, especially from the Acentropinae, could also supply relevant data (Park *et al.*, 2014; Ye and You, 2016; Chen *et al.*, 2017a). To answer many important questions about the ecology and evolution of aquatic moths, life cycles should be studied and linked with the results of phylogenetic studies (genus and/or species level). Phylogenetic studies should include divergence time estimates using the molecular clock. Such studies would help us to understand the rate of evolutionary events, the order of appearance and importance of key morphological and behavioural adaptations, and enable recognition of the most important radiation centres. Studies of this kind should enhance our understanding of the colonization of remote islands since there are endemic species of the Acentropinae known from the Galapagos (Landry and Roque-Albelo, 2006) or Wallacea (Mey and Speidel, 2008). At the same time we do not know the life cycles of even some European species (Slamka, 1997; Speidel, 2002).

Even studies on distribution patterns, abundance or activity levels in relation to basic environmental factors (*e.g.* water chemistry, temperature, pH, and food availability) and research on dispersal abilities are rare (Stoops *et al.*, 1998; Wheeler and Halpern, 1999; van der Heide *et al.*, 2006). For example, studies of the influence of temperature on grazing pressure can be very important in the context of climate warming (van der Heide *et al.*, 2006); especially since moth caterpillars are a major group of aquatic herbivores. All these processes were probably important for the radiation and diversification of species in various microhabitats and for the selection of food plants. There is very limited knowledge on possible shifts between habitats or different types of water bodies (lotic or stagnant waters) and the related evolutionary processes. Semi-aquatic forms should receive particular attention, because they represent the basic stages of adaptation to the aquatic environment and thus may serve as proxies of the early evolutionary processes.

Most ecological and life cycle studies of aquatic moths were carried out between the 1940s and 1980s, primarily on the European or North American faunas (*e.g.* Berg, 1941; Berg, 1950; McGaha, 1954; Lange, 1956; Reichholf, 1970; Barbier and Chauvin, 1974; Tuskes, 1977; Buckingham and Ross, 1981; Habeck, 1988 and references therein). Some of the studies date back to the beginning of last century (*e.g.* Welch, 1919; Welch and Sechon, 1928). Modern hydrobiologists seem to have neglected ecological studies of freshwater caterpillars. Most of the recent studies focus on taxonomy and biodiversity inventories, although some regions remain poorly explored (*e. g.* Chen *et al.*, 2010; Schmitz and Rubinoff, 2011; Agassiz, 2012, 2014; Scholtens and Solis, 2015; Irungbam *et al.*, 2016). The few ecological studies that have been published during the last 15 years often addressed the biology of the already relatively well-studied and common, mostly European species such as *C. lemnata* or *A. ephemerella* (*e.g.* van der Heide *et al.*, 2006; Erhard *et al.*, 2007; Miler *et al.*, 2014; Pabis, 2014) or species treated as pests of cultivated aquatic plants, such as the common *Parapoynx crisonalis* (Li *et al.*, 2017; Chen *et al.*, 2017b). This situation might be due to the paucity of specialists, or the relative difficulty of carrying out long-term laboratory observations, and perhaps also due to the relatively minor economic importance of the insects in question, although they are sometimes used for biological control of selected macrophytes (Center and Hill, 2002; Bownes, 2010). Some of the aquatic caterpillars may also be regarded as pests of rice (Lange, 1956), but have still received rather minor attention (*e.g.* Pulin and Khound, 2000). Larvae of *C. lemnata* can drill holes in PVC foil (van der Velde, 1991) and therefore may have the potential to be used for plastic waste biodegradation, as recently proposed for the pyralid *Galleria mellonella* (Bombelli *et al.*, 2017).

There is also a great need for further taxonomic studies. Since identification of larvae is very difficult, descriptions of most species are based on the traditional morphotaxonomy of adult stages (Mey and Speidel, 2008). This results in erroneous placement of some species, belonging to other crambid subfamilies, within the Acentropinae (Yen *et al.*, 2004; Mey and Speidel, 2010). Studies which provide detailed descriptions of caterpillars together with identification keys and good drawings are very scarce and tend to analyse only a very small number of species (Krampl, 1980; Vallenduuk and Cuppen, 2004; Habeck and Balciunas, 2005). A larger number of caterpillar descriptions together with studies of the biology of Australian Acentropinae were done by John Hawking, but the results are still unpublished (Agassiz, 2014). It is very important to include the integrative taxonomy methods (including barcoding) so that not only potential cryptic species are found, but so that caterpillars are linked with their respective imaginal stages. This would result in more comprehensive descriptions of species that would help ecologists in field and laboratory studies of the biology and life cycles. It will also allow to trace the origin of at least some non-indigenous species. At present there is only one similar integrative study that only focused on two species of Acentropinae (Solis *et al.*, 2018). Aquatic and semi-aquatic moths are probably one of the most poorly studied ecological groups within the Lepidoptera. The potential for various studies on their ecology and evolution is great and untapped.

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