Hydrobiologia (2008) 595:521–528
DOI 10.1007/s10750-007-9038-9

FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of butterflies (Lepidotera) in freshwater

Wolfram Mey · Wolfgang Speidel

Abstract In Lepidoptera, the subfamily Acentropinae and Pyraustinae of Crambidae (Pyraloidea) and the family Arctiidae (Noctuoidea) contain species with true aquatic larvae, which live submerged during larval development. In Pyraustinae and Arctiidae only a few species exhibit an aquatic life-history. From the latter, aquatic larvae are known from the Neotropical genus *Paracles*. The number of aquatic *Paracles* species is unknown. The Acentropinae are predominantly aquatic. They are distributed worldwide, and reach the highest diversity in tropical regions of South East Asia/Malesia and in the Neotropical Region. At present, the Acentropinae include a total of 50 genera and 737 described species. All genera, assigned to the subfamily, are listed in a table, and the numbers of included species are indicated. The taxonomy and phylogeney of the genera are inadequately known. The species have a minor economic importance, however, they are very sensitive to degradation of water quality and habitat destruction.

Guest editors: E.V. Balian, C. Lévêque, H. Segers & K. Martens
Freshwater Animal Diversity Assessment

W. Mey (✉)
Museum für Naturkunde, Humboldt-Universität Berlin, Invalidenstr. 43, 10115 Berlin, Germany
e-mail: wolfram.mey@museum.hu-berlin.de

W. Speidel
Museum Witt, Tengstrasse 33, 80796 Munchen, Germany

Keywords Lepidoptera · Acentropinae · Pyraloidea · Arctiidae · Diversity · Distribution · Taxonomy · Genera · Species numbers

Introduction

For an outsider it is surprising to learn that there are indeed some Lepidoptera which are aquatic. Even for limnologists or aquatic entomologists aquatic moths do not belong to the well known and instantly recognised types of aquatic insects. There is a special reason for the poor recognition of aquatic Lepidoptera: the handling of the adult moths during sampling and processing differs completely from the methods used for other freshwater insects. The wing patterns provide features, which are diagnostic at the species level and, therefore, must be preserved intact, i.e. in a dry state. As a consequence, individuals have to be treated very carefully. Correct handling needs to use killing jars, pins, pinning boxes, setting boards, and insect drawers. These tools do not belong to the regular equipment of aquatic entomologists or limnologists. However, they are regularly used by lepidopterists, who are usually specialised on certain families. The study of aquatic Lepidoptera has always been a subject of lepidopterists alone, who on the other side, however, rarely have a limnological background.

Today, the accumulated knowledge on aquatic species has a focus on adults and is scattered in the

vast Lepidoptera literature, which is not easily accessible for limnologists. Data on larvae is limited. The larvae are caterpillars with a small degree of intrageneric morphological differentiation, which makes the identification at the species level very difficult or impossible. The genera and species of the Holarctic Region are rather well known. But Holarctic species make up only a minority of the world fauna in contrast to the overwhelming diversity of taxa present in the tropics. Many species were only provisionally assigned to a genus and remained there up to now. Several aquatic species are exceptional cases within their systematic groups. However, there is a group of Lepidoptera, whose larvae are almost exclusively aquatic; these are the so-called China-Mark-Moths (Pyraloidea: Acentropinae). The larval stages of most tropical species are undescribed, but might be expected as aquatic. Information on the biology of immatures is very poor. At this stage, available data on the distribution, phylogeny and taxonomy of aquatic moths are much too incomplete to embark seriously into a deeper analysis of the group concerning historical biogeography, faunal changes, centres of endemicity, etc. However, a summary of the currently recognised taxa and their distribution on the planet can be provided. The present account concentrates on families, which have true aquatic species, i.e., with submerged living larvae. These are the families Crambidae (Pyraloidea) and Arctiidae. Some further families contain semi-aquatic species. They are not considered here.

Species and generic diversity

Family Arctiidae: Arctiinae

The subfamily includes about 3,600 species (Heppner, 1991). One species is well-known for its aquatic caterpillars: *Paracles laboulbeni* (Bar, 1873). It was formerly placed in the genus *Palustra*. The species is widely distributed in the Neotropical Region. The caterpillars feed on submerged plants in stagnant or slow flowing waters (Adis, 1983). They lack tracheal gills. Respiration is mediated by air-holding hairs forming a plastron on the dorsal side. The genus *Paracles* is very speciose. It is unclear, whether *P. laboulbeni* is the only aquatic species or whether further congeners have aquatic immatures.

Family Crambidae: Pyraustinae

The subfamily is a mega-diverse group with over 7,000 species word-wide (Heppner, 1991), also sometimes retained in a larger concept of Pyralidae. A few species are reported to have aquatic larvae (Buckingham, 1994):

Samea multiplicalis Guenée, 1854—Neotropical Region,

Niphograpta albiguttalis Warren, 1889—Neotropical Region.

Both species have been used in biological control programme to suppress mass developments of aquatic weeds in stagnant and running waters. In South–East Asia there are several, hitherto unidentified species, which were collected only close to running waters. They form aggregations of adults on the underside of boulders and overhanging rocks, a behaviour known for aquatic moths. The larvae of these species are supposed to be aquatic, but have not been traced yet.

Family Crambidae: Acentropinae

The group is well known under its synonymous name Nymphulinae. Heppner (1991) has compiled species totals for each of the over 300 subfamilies and families of the Lepidoptera of the world. They were tabulated according to major faunal regions whose delimitations are essentially based on Darlington (1957). According to his figures the Acentropinae comprise 716 described species. During recent years a number of new checklists, catalogues and taxonomic changes were published, which provide current figures for Acentropinae of nearly all faunal regions or continents: Henning (2003), Li et al. (2003), Munroe (1983, 1995), Shaffer et al. (1996), Speidel (2005), Speidel & Mey (1999), Yen (2004), You et al. (2002). In addition, a large number of new species have been described especially from the Oriental Region in the last decade (Li et al., 2003; Mey, 2006; Mey & Speidel, 2005; Speidel, 2003; Yoshiyasu, 1987; You & Li, 2005; You et al., 2003, etc.). Based on these publications and our own studies a new synthesis was undertaken at the generic level. We have used Heppner's scheme with slight changes: the northern Mexican border line is the border of the Neotropical Region and the Australian Region is divided into a Newguinean-Polynesian and proper

Australian–New Zealand Region. The new figures are summarised in Table 2. Up to date, the Acentropinae encompass 737 species in 50 genera. Interestingly, the counts are similar to Heppner's ones. In the past, many more genera were included, mainly because of superficial resemblance of wing patterns of the adults. They has been subsequently excluded, but this process is not complete. Exclusion of misplaced taxa and synonymies have not equalled the number of new species descriptions since 1991 (Figs. 1, 2).

The counts for the faunal regions are not by type localities. Thus, the problem of double counting of species which are distributed in several faunal regions has to be considered. The problem is notoriously evident in the East Palaearctic and Oriental Faunal Regions, which have a broad, common transition zone. Widespread species were indicated for all faunal regions in which they occur, but recorded only once in the "total" column of Table 2.

Phylogeny and historical processes

Lepidoptera are essentially terrestrial insects. Only a tiny fraction of the 165,000 described species can be termed aquatic, which means that they have immature stages that live under water. The adults are terrestrial as in the majority of water insects. The conquest of the aquatic environment by lepidopteran larvae is not that astonishing as it may appear at first glance. Larvae of Lepidoptera—the caterpillars—have an enormous adaptive potential (Scoble, 1992). Primitive species like Micropterigidae or ancestral Pyraloidea are detritivorous and moss feeders sometimes are associated

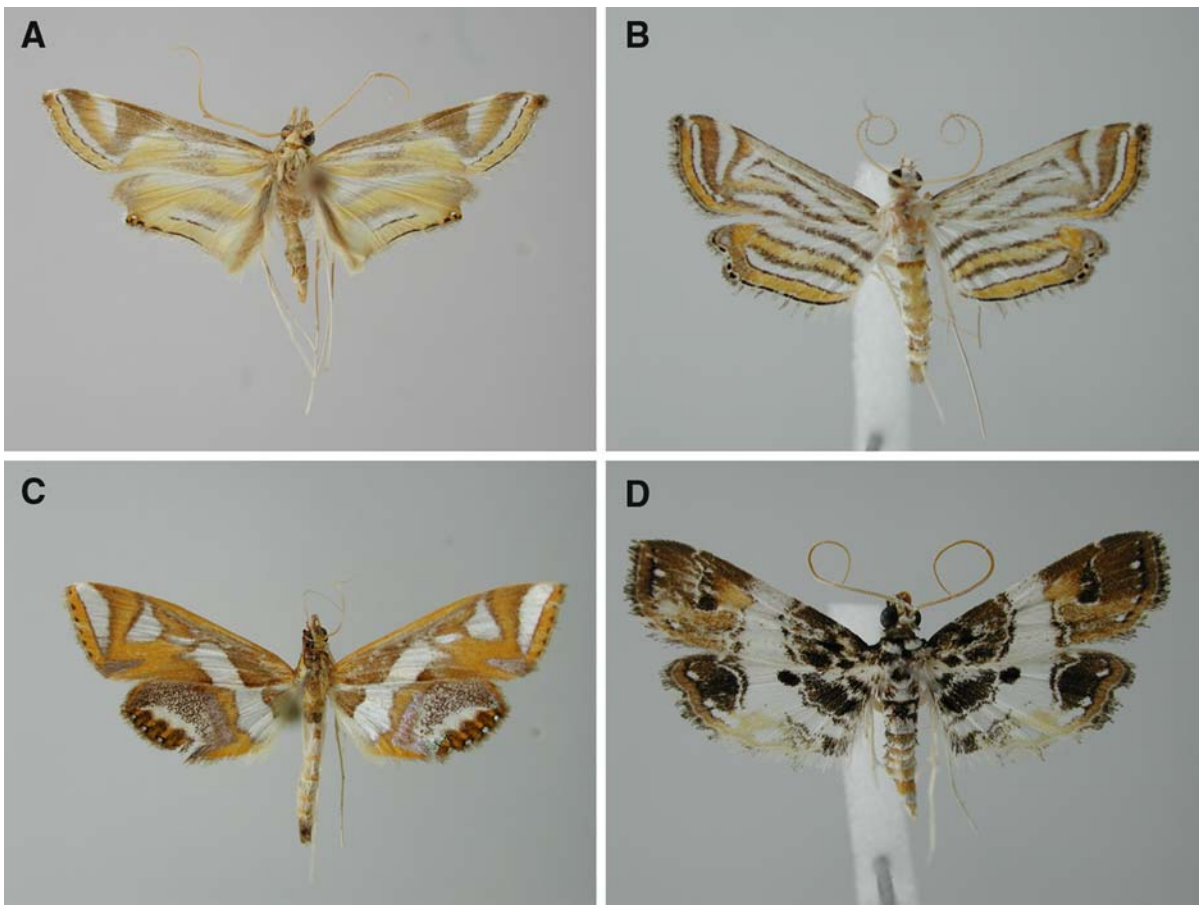

Fig. 1 (**A**) *Eoophyla boernickei* Mey, 2006, male (Borneo), (**B**) *Parapoynx leucographa* Speidel, 2003, male (Borneo) (**C**) *Margarosticha* spec., male (Sulawesi), (**D**) *Paracymoriza* spec., male (Borneo)

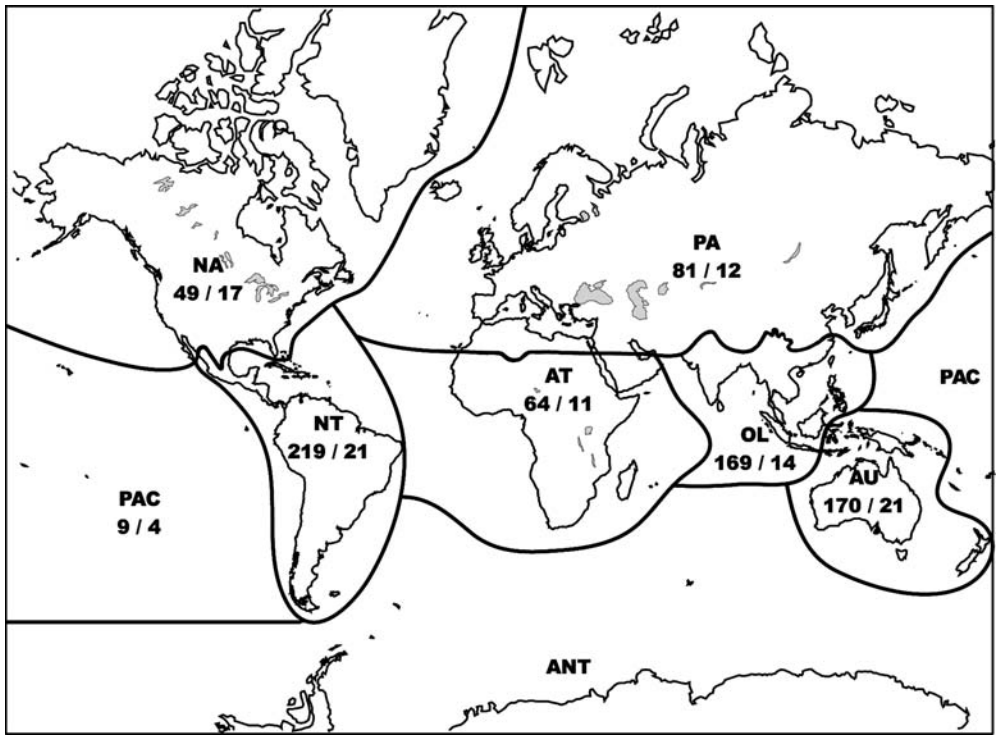

Fig. 2 Distribution of freshwater Lepidoptera species and genera by zoogeographical region (species number/genus number). PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands

with fungi or animal matter (Munroe & Solis, 1998: 235). The larvae often live in a humid environment on the ground. With the development and radiation of the angiosperms in the Cretaceous a new food resource became widely available. Caterpillars of early evolutionary lineages started to use green-plant tissue as a food source and became phytophagous. In a process of co-evolution and radiation together with the angiosperms, the Lepidoptera were able to adapt to all plant groups and developed a wide array of life histories, forms and strategies which allowed them to exploit all parts of a plant: leaves, stems, roots, bark, twigs, flowers, seeds, etc. Aquatic or semiaquatic plants, being no exceptions, are hosts of a number of lepidopteran species, too.

The caterpillars usually feed on green leaves or on the periphyton in rocky habitats. The cuticule of caterpillars has morphological preadaptions to some kind of plastron respiration. With these larval preadaptions it was only a small step in the evolution from a wet terrestrial to a semiaquatic life history. It is, therefore, not surprising that a transition to aquatic or semiaquatic life occurred several times and independently in different, unrelated taxa of Lepidoptera. Aquatic larvae are known to occur in the mega-diverse families Crambidae and Arctiidae (Table 1). There are probably more families with aquatic representatives. The poor exploration and knowledge of tropical Lepidoptera, especially of rain forest areas with their huge variety of aquatic habitats

Table 1 Generic and species diversity of currently known Lepidoptera taxa with aquatic larvae

Superfamily/Family	Subfamily	Number of genera	Number of species
Pyraloidea			
Crambidae	Acentropinae	50	737
	Pyraustinae	2	2
Noctuidoidea			
Arctiidae	Arctiinae	1	1

Table 2 The genera of Acentropinae—their distribution and diversity in the major Biogeographical Regions of the world (PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic Islands (Micronesia-Polynesia))

Genus	PA	NA	NT	AT	OL	AU	PAc	Total
Acentria Stephens, 1829	1	1						1
Agassiziella Yoshiyasu, 1989				2	10			12
Ambia Walker, 1859*						7*		7
Anydraula Meyrick, 1885						2	3*	5
Araeomorpha Turner, 1908						2		2
Argyractis Hampson, 1897		1	12	8*				21
Argyractoides Lange, 1956			12					12
Argyrophorodes Marion, 1957*				7*				7
Aulacodes Guenée, 1854			35				3	38
Callilitha Munroe, 1959						2		2
Cataclysta Hübner, [1825]	1			9*		9*	2*	21
Chrysendeton Grote, 1881		3	16					19
Cryptocosma Lederer, 1863			1					1
Contiger Lange, 1956		1						1
Elophila Hübner, 1822	13	4	2	2	7*	6		31
Eoophyla Swinhoe, 1900	11			12*	54	73		142
Eoparargyractis Lange, 1956		3						3
Ephormotris Meyrick, 1933				2*	2			4
Eristena Warren, 1896	12				26	3*		41
Giorgia Clarke, 1965			1					1
Hemiloba Swinhoe, 1901					1			1
Hygraula Meyrick, 1885						2		2
Hylebatis Turner, 1908						1		1
Kasania Krulikowsky, 1910	1							1
Langessa Munroe 1972		1						1
Lathroteles Clarke, 1971*							1*	1
Margarosticha Lederer, 1863					2	13		15
Neargyractis Lange, 1956		1	7					8
Neocataclysta Lange, 1956		1						1
Neoschoenobia Hampson, 1900	1					1		2
Nyctiplanes Turner, 1937						1		1
Nymphicula Snellen, 1880	7			10*	22	7		46
Nymphula Schrank, 1802	4	1			2	2*		9
Nymphuliella Lange, 1956		1						1
Nymphulodes Hampson, 1919			1					1
Oligostigma Guenée, 1854			7	2*		2*		11
Oligostigmoides Lange, 1956		1	5					6
Oxyelophila Forbes, 1922		1	7					8
Paracataclysta Yoshiyasu, 1983				1*	1	1		3
Paracymoriza Warren, 1890	11*				22*	4*		37
Parapoynx Hübner, [1825]	17	8	13	9*	16	22		76
Petrophila Guilding, 1830		15	82					97
Potamomusa Yoshiyasu, 1985	2							2

Table 2 continued

Genus	PA	NA	NT	AT	OL	AU	PAc	Total
Pseudolithosia Hampson, 1907			1					1
Strepsinoma Meyrick, 1897					2	9		11
Synclita Lederer, 1863		4	3					7
Synclitodes Munroe, 1974			1					1
Tetrernia Meyrick, 1890						1		1
Thysanoidma Hampson, 1891					2			2
Usingeriessa Lange, 1956		2	10					12
Number of genera	12	17	18	11	14	21	4	50
Number of species	81	49	216	64	169	170	9	737

Numbers with * denote unclear generic or subfamily associations

suggests that we can expect further families with aquatic members.

The most advanced adaptations to an aquatic existence can be found in the pyraloid subfamily Acentropinae (=Nymphulinae). The majority of aquatic species belong to this subfamily. Hasenfuss (1991) published a convincing scenario for the evolution of the aquatic habit of Acentropinae. According to the plant species or food resource, the caterpillars developed a wide spectrum of adaptations towards a semiaquatic and finally towards a fully aquatic life: species with plastron respiration and open tracheal system feed on floating or partly submerged leaves, whereas species with tracheal gills and closed spiracles are able to live on fully submerged plants or are rock-dwellers in streams. A comparative, taxonomic analysis of the genera on a world-wide scale was not attempted so far, and thus, makes the validity of some taxa questionable. Phylogenetic relationships among genera were studied only on a restricted geographical scale (cf. Speidel, 1984, 2005; Yoshiyasu, 1985). A subdivision of the subfamily into two tribes was proposed by Lange (1956). He included in Nymphulini the case-making shredders and green-plant tissue feeders, and in Argyractini the free living scrapers and web spinning algae feeders. The division, however, was not found to be an adequate reflection of phylogenetic relationships (Munroe & Solis, 1998) and, thus, is not followed here. Consequently, the genera are listed alphabetically in Table 2.

The sister group relationship of the Acentropinae is unresolved (Solis & Maes, 2002). Traditionally, Acentropinae and Schoenobiinae have been considered closely related (Speidel, 1984; Munroe & Solis, 1998). They have semiaquatic larvae, which usually feed as internal borers in the stems of water monocots. Species of both subfamilies often occur together in a wide range of aquatic habitats.

Present distribution and main areas of endemicity

As mentioned in the introduction, our inadequate knowledge only allows rough conclusions from the numbers in Table 2. The data show that tropical regions have many more species than other faunal regions. With approximately 40% of the world total of described species, the peak diversity is in Malesia, including the Pacific islands from Micronesia to Polynesia. This is mainly due to the radiation of the genus *Eoophyla* in maritime South East Asia and, even more pronounced, in New Guinea. More than 140 Acentropinae species are endemic to this islands and the Wallacea, which had to be included into the Australian Region here in Table 2. *Eoophyla* is the largest group in Acentropinae. It is rather homogeneous but includes some isolated forms that may necessitate the establishment of separate genera. A comparably large genus in the Neotropical Region is *Petrophila*, which also gets into the Nearctic. It makes up nearly 50% of all Neotropical species. In contrast to *Eoophyla*, the radiation of *Petrophila* developed in a continental setting. The poor figures for tropical Africa are in accordance with figures from other Lepidoptera groups. However, Africa south of the Sahara, including Madagascar, is a poorly sampled continent and should contain many more species. There are two genera which occur in all faunal regions:

Elophila and *Parapoynx*. Their species are mainly inhabitants of stagnant waters.

Most genera have ranges restricted to one continent or to a single faunal region. The high number of generic taxa in the New World and Australia appears to demonstrate a higher diversity of evolutionary lines on these continents. This can be genuine or is merely an artifact due to the poor systematic investigation of the Afrotropical and Oriental faunas.

Human related issues

In general, aquatic moths are of little economic importance. A few species are known to damage rice in Asian countries: *Parapoynx fluctuosalis* (Guenée, 1854), *P. vittalis* (Bremer, 1864) and *P. stagnalis* (Zeller, 1852). Sometimes the injury can be serious, but usually remains localised. The species are clearly of less importance than rice stem borers of the subfamily Schoenobiinae. The species from rice paddies have a wide distribution. Some tropical species were incidentally introduced together with aquatic plants to other continents. In temperate countries they are unable to adapt to the low winter temperatures, and remain minor pests in greenhouses. In warmer regions, some species have managed to establish permanent populations in the field. The phytophageous caterpillars have been regarded as a promising means for the biological control of aquatic weeds. They have been successfully used in the suppression of *Hydrillia* and *Elodea* in Florida (Buckingham, 1994).

Acentropine species from running waters are very susceptible to water pollution and water channel regulations. They are among the first organisms which would disappear when facing a drop in water quality.

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