

A PRELIMINARY ANALYSES OF THE PHYLOGENY
OF THE ETHMIINAE MOTHS (LEPIDOPTERA: GELECHIOIDEA)
WITH SPECIAL REFERENCE TO THE EVOLUTIONARY
PATTERNS OF HOST USE

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The subfamily Ethmiinae is a microlepidopteran group comprising more than 350 species in seven genera worldwide. The core genus *Ethmia* comprises 47 species-groups and many species unassigned to species groups. Their hostplant associations involve at least seven angiosperm families, of which Boraginaceae is utilized by the majority of the species. We attempted to reconstruct the phylogeny of the Ethmiinae to elucidate if the high diversity of *Ethmia* correlates with colonization on Boraginaceae. We first selected 52 *Ethmia* species having host-plant records to represent 21 of the 47 species-groups and used *Orophia*, *Depressaria*, *Agonopterix*, *Chrysethmia* and *Agrioceros* as the outgroups. Seventy six adult morphological characters were identified and were partitioned into two subsets, non-colour patterns versus colour pattern, to detect the impact of colour pattern characters on the phylogenetic structure. We employed maximum parsimony method to reconstruct the phylogenetic relationships of the Ethmiinae and found that neither the genus *Ethmia* nor most species-groups proposed by previous authors are monophyletic. The characters relevant to colour patterns produced significant effects on the tree topology, although the wing patterns may not be involved in mimicry. Optimization of host associations reveals that the clades using Hydrophyllaceae, Rosaceae, Phytolaccaceae, Scrophulariaceae, Ranunculaceae, and Malvaceae have evolved independently from the clade using Boraginaceae.

Keywords: Ethmiinae, phylogeny, hostplant, wing pattern

INTRODUCTION

The Ethmiinae – great diversity with chaotic taxonomic histories

The Ethmiinae (Elachistidae) is a large group of Gelechioidea of worldwide distribution, comprising of more than 350 species (SATTLER 1967, 2002, POWELL 1973, 1983, 1985). Compared with most microlepidopteran genera, the adult colour patterns, sizes wingspan (10–12 mm in *Ethmia alba* versus 40–50 mm in *E. lineatonotella*), genitalic structures, and androconial organs of Ethmiinae exhibit remarkable diversity in shapes and forms. Historically the higher classification of the

Ethmiinae is not consistent (POWELL 1973). It was considered as either a good family (SATTLER 1967, 2002, POWELL 1973, KUZNEZOV & STEKOLNIKOV 1978, COMMON 1990, ROBINSON *et al.* 1994), listed in Yponomeutidae (MEYRICK 1914, 1928), or associated with Oecophoridae (SCOBLE 1992). In recent decades it was a subfamily in Oecophoridae, and since MINET (1990) and HODGES (1999)'s discussions on Gelechioidea phylogeny based on adult and immature morphology, it has gradually been accepted that Ethmiinae should be placed in Elachistidae. Recently KAILA (2004) investigated the phylogeny of Gelechioidea using morphological and ecological characters and recovered the relationship of Ethmiinae (based on *Orophila* + *Ethmia*) as the sister group of the clade (Aeolonthinae + (Parametriotinae + (Agonoxeninae + Elachistinae))). BUCHELI and WENZEL (2005) reconstructed the phylogeny of the Gelechioidea based on molecular (COI + COII sequence data) and morphological data. The current concept of Elachistidae is not monophyletic and the Depressarinae is shown to be the sister group of Ethmiinae. These studies have greatly improved our knowledge of the phylogeny and character evolution of Gelechioidea, but the systematic problems of Ethmiinae itself remain unsolved due to the very limited taxon sampling in these works.

According to the opinion integrated from previous authors (CLARKE 1965, SATTLER 1967, DANILEVSKY 1969, POWELL 1973, KAILA 2004), the following seven genera are associated with the Ethmiinae: *Ethmia* HÜBNER, 1819, *Pyramidobela* BRAUN, 1923, *Orophia* HÜBNER, 1825, *Agrioceros* MEYRICK, 1928, *Pseudethmia* CLARKE, 1950, *Chrysethmia* DIAKONOFF, 1966, and *Dasyethmia* DANILEVSKY, 1969. The genera *Agrioceros* and *Chrysethmia* comprise only a few species with bright colouration distributed in the Indo-Australian and Pacific regions (DIAKONOFF 1966, 1969, CLARKE 1965). The genera *Pseudethmia*, *Pyramidobela* and *Dasyethmia* are putatively included in this subfamily because of their superficial similarity with some dull coloured *Ethmia* species. The genus *Orophia* was previously included Oecophorinae (Oecophoridae), but KAILA's (2004) phylogenetic analysis suggests its affinity with Ethmiinae. Although the taxonomic contents of the Ethmiinae seem to be debatable, most authors agree that the genus *Ethmia* harbours the greatest diversity of the subfamily.

As revealed by its generic name "ethmos" – a sieve (EMMET 1991), the genus *Ethmia* is usually characterized by its wing patterns composed of numerous dots, stripes or lines with various combinations on the forewing (see Figs 2–5). Previous studies on the Ethmiinae (mainly based on *Ethmia*) are mainly taxonomic works of regional faunas. SATTLER (1967) summarised the fauna of the Palaearctic region, and many following works, e.g. AMSEL (1969*a, b*) (Afghanistan), GANEV (1984) and KOÇAK (1986) (Turkey), KOSTYUK (1980), DANILEVSKY (1975) and DUBATOLOV & USTJUZHANIN (1998) (Central Asia), KARSHOLT & KUN (2003) and DO-

MINGO *et al.* (2003) (Europe), have increased the species number in the fauna up to 29. The Oriental fauna was first assessed in SATTLER's (1967) work and subsequently studied by DIAKONOFF (1969), YANG (1977), LIU (1980), and WANG and ZHENG (1997), KUN and SZABÓKY (2000), KUN (2001, 2002, 2004) and WANG and LI (2004). The New World fauna comprises about 140 species in 3 genera, about a half of the world fauna (POWELL 1973, CAPUSE 1981, HEPPNER 1988, 1991). In Australia the Ethmiinae only represented by 14 species (POWELL 1985). In the Afrotropical region 35 species are known (GHESQUIÈRE 1940, MADLER 1980, PINHEY 1975), but the records are only accumulated from few former European colonial countries (e.g. Tanzania, Kenya, and South Africa) and the fauna of Central Africa is yet to be investigated. The fauna of Madagascar is represented by 17 species after VIETTE's extensive works (VIETTE 1952, 1954, 1956, 1958*a, b, c*, 1963, 1976, 1990) and no recent revision is available.

Although the external and internal morphological characters of *Ethmia* and other genera associated with Ethmiinae exhibit a great diversity and heterogeneity, the monophyly of either the subfamily or the genus *Ethmia* has surprisingly never been doubted. All the previous authors (e.g. GOZMÁNY 1956, SATTLER 1967, POWELL 1973) recognized the Ethmiinae (or Ethmiidae) as a natural group, but no character has been proven to be the synapomorphy of this subfamily (or the genus *Ethmia*) using modern technology and a reasonable taxon sampling.

Infrageneric systematics of Ethmia

Due to the significant variations of wing patterns and genitalic structures, *Ethmia* has been separated into many species-groups or "sections". SATTLER (1967) and POWELL (1973) first attempted to establish an infrageneric classification of the genus for the Palaearctic fauna using genitalia characters, wing patterns, and other external morphological characters (e.g. androconial organs). POWELL (1973) recognized 24 species groups for the New World fauna and conducted a phenetic analysis to investigate the relationships and validity of the species groups. Subsequently, POWELL (1985) used almost the same array of morphological characters of adult to define the species groups in Australia and five of them are partly overlap with some characters defined by SATTLER (1967) and KUN (2004). LIU and XU (1982) re-analysed the phenetics of the Palaearctic species by following SATTLER's (1967) discussion on morphological characters and adding eight Chinese species. They compared the morphological similarity between species groups and considered that the 23 Palaearctic species groups defined by SATTLER should be

lumped to 15. To date 51 species groups in total are proposed for this genus, and many more species discovered in recent decades, and from Africa, have not been assigned to any species group.

The questions to be answered in the present study

In the present study, we attempt to reconstruct a preliminary phylogenetic tree of the Ethmiinae using selected species representing different species groups, using cladistic methods. This phylogeny is not only used to test the monophyly of the subfamily and the genus *Ethmia*, but also to infer the evolution of their hostplant uses. About 80% of the *Ethmia* species with hostplant records known to utilize Boraginaceae (including Ehretiaceae) (Palearctic, Oriental and Australian regions) and Hydrophyllaceae (Nearctic region) (SATTLER 1967, POWELL 1973, 1985). Other major hostplant records include Ranunculaceae, Rosaceae, Scrophulariaceae, Phytolaccaceae, and Malvaceae, and these occur in North America. POWELL (1973) considered that different host associations of the *Ethmia* moths may have evolved independently because there is no significant correlation between host plant uses and species groups in the New World. This pattern is very intriguing because it can be used to address, if the Boraginaceae-feeding behaviour, which is rare in the Lepidoptera (EHRlich & RAVEN 1964), represents an ancestral state originated from the Old World, or if the non-Boraginaceae-feeding behaviour is more ancestral and originated from the New World.

MATERIAL AND METHODS

Taxon sampling and material acquisition

Ideally, we hoped to use a dense taxon sampling representing all the lineages and species groups of the Ethmiinae to reach a global parsimony in the phylogenetic analysis. Many species, however, were not available for morphological study during the study and do not have hostplant records. We only selected 52 *Ethmia* species (20.8% of all the known species) that have hostplant records and represent 22 of the 51 species groups for the phylogenetic analysis (Table 1). Outgroup selecting conferred all the previous taxonomic opinions and phylogenetic assumptions involving Ethmiinae. *Orophia ferrugella* was placed in Oecophoridae in most literature, but KAILA (2004) suggested including it in the Ethmiinae. *Chrysethmia hypomelas* DIAKONOFF, 1966 and *Agrioceros magnificella* (SAUBER, 1902) were chosen to represent two non-*Ethmia* genera of Ethmiinae. Two species of Depressarinae, *Agonopterix heracliana* (LINNAEUS, 1758) and *Depressaria depressana* (FABRICIUS, 1775), were included because Depressarinae is recovered to be the sister group of Ethmiinae in previous phylogenetic studies. Many hundreds of adult specimens, both collected and borrowed from many institutions, were examined. The depositories of the material include: NSYSU (National Sun Yat-Sen University, Kaohsiung, Taiwan), TAI (Department of Entomology, National

Taiwan University, Taipei, Taiwan), USNM (National Museum of Natural History, Smithsonian Institution, Washington D.C., USA), NHM (The Natural History Museum, London), and HNHM (Hungarian Natural History Museum, Budapest, Hungary). The studied taxa are listed in Table 3, together with their geographical regions, hostplant records and literature sources. We also reared larvae to study immature morphology, and extensive collecting of larvae has carried out by S. H. YEN in various countries, e.g. Australia, China, Corsica, England, Indonesia, Japan, Kenya, United States, and Taiwan since 2004.

Table 1. An enumeration of the species-groups proposed by previous authors and separated by biogeographical regions (Palaeartic – SATTLER (1967), American – POWELL (1973), Australian – POWELL (1985), Oriental – KUN (2004)). The asterisk signs refer to the species groups that were established by SATTLER's (1967) work based on the Palaeartic fauna. According the current grouping system only one species group is shared by America and Eurasia. Many Eurasian and all the African species (Table 2) have not been assigned to any species group and this can not be determined before a comprehensive phylogenetic study becomes available

Palaeartic	American	Australian	Oriental
<i>amasina</i>	<i>albitogata</i> (Sectio I)	<i>crocosoma</i> *	<i>acontias</i>
<i>assamensis</i>	<i>bipunctella</i> *	<i>lapidella</i> *	<i>lineatonotella</i>
<i>aurifluella</i>	<i>charybdis</i>	<i>nigroapicella</i> *	<i>penesella</i>
<i>bipunctella</i>	<i>cypraeella</i>	<i>postica</i>	
<i>chrysopterygia</i>	<i>exornata</i>	<i>sporadica</i>	
<i>crocosoma</i>	<i>hagenella</i>		
<i>dehiscens</i>	<i>kirbyi</i>		
<i>discrepitella</i>	<i>macelhosiella</i>		
<i>distigmatella</i>	<i>mulleri</i>		
<i>ditreta</i>	<i>papiella</i>		
<i>dodecea</i>	<i>piperella</i>		
<i>haemorhoidella</i>	<i>semilugens</i>		
<i>lapidella</i>	<i>notatella</i> (Section II)		
<i>libyella</i>	<i>balsiostola</i>		
<i>nigripedella</i>	<i>confusella</i>		
<i>nigroapicella</i>	<i>conglobata</i>		
<i>rothschildi</i>	<i>cyanea</i>		
<i>suspecta</i>	<i>gigantea</i>		
<i>terminella</i>	<i>hamella</i>		
<i>tripunctella</i>	<i>joviella</i>		
<i>ultima</i>	<i>longimaculella</i>		
<i>vitalbella</i>	<i>prattiella</i>		
<i>wursteri</i>	<i>punctessa</i>		
	<i>trifurcella</i>		

Analysis of morphological characters and terminology

Although the immature morphology is considered to be very informative in defining species groups (POWELL 1973, 1985), we only included the adult characters in the present study as the immature stages of most species is still unknown. All the previous authors suggest that the colour patterns of Ethmiinae are important in defining species groups and distinguishing similar species, although

Table 2. The *Ethmia* species that have not been assigned to any species group proposed by previous authors

Palearctic and Oriental	Ethiopian	
<i>antennipilosa</i> WANG et LI, 2004	<i>ampanella</i> VIETTE, 1976	<i>iphicrates</i> MEYRICK, 1922
<i>baihua</i> YANG, 1977	<i>andranella</i> VIETTE, 1976	<i>judicialis</i> MEYRICK, 1921
<i>cribravia</i> WANG et LI, 2004	<i>argomicta</i> MEYRICK, 1920	<i>leucocirrho</i> MEYRICK, 1926
<i>defreinai</i> GANEV, 1984	<i>atriflorella</i> VIETTE, 1958	<i>linosella</i> VIETTE, 1976
<i>elimatella</i> DANILEVSKY, 1975	<i>ballistis</i> MEYRICK, 1908	<i>livida</i> (ZELLER, 1852)
<i>gonimodes</i> MEYRICK, 1925	<i>baronella</i> VIETTE, 1976	<i>melanocrates</i> MEYRICK, 1923
<i>hakkarica</i> KOCAK, 1986	<i>befasiella</i> VIETTE, 1958	<i>mixtella</i> (CHRÉTIEN, 1915)
<i>hunanensis</i> LIU, 1980	<i>bicolorella</i> (GUENÉE, 1879)	<i>novoryella</i> VIETTE, 1976
<i>jingdongensis</i> WANG et ZHENG, 1997	<i>bradleyi</i> VIETTE, 1952	<i>oberthurella</i> VIETTE, 1958
<i>kabulica</i> AMSEL, 1969	<i>cassiopeia</i> MEYRICK, 1927	<i>oculigera</i> (MÖSCHLER, 1883)
<i>menyuanensis</i> LIU, 1980	<i>circumdetella</i> (WALKER, 1863)	<i>oculimarginata</i> DIAKONOFF, 1948
<i>shensicola</i> AMSEL, 1969	<i>cirrhosoma</i> MEYRICK, 1920	<i>ovogenesis</i> STRAND, 1913
<i>sibirica</i> DANILEVSKY, 1975	<i>comoriensis</i> VIETTE, 1963	<i>pericentrota</i> MEYRICK, 1926
<i>soljanikovi</i> DANILEVSKY et ZAGULAJEV, 1975	<i>coscineutis</i> MEYRICK, 1912	<i>phricotype</i> BRADLEY, 1965
<i>turkmeniella</i> DUBATOLOV et USTJUZHANIN, 1998	<i>dactylia</i> MEYRICK, 1912	<i>pylonotella</i> VIETTE, 1956
<i>ubsensis</i> ZAGULAJEV, 1975	<i>decaryanum</i> (VIETTE, 1954)	<i>pylorella</i> VIETTE, 1956
<i>zaguljajevi</i> KOSTJUK, 1980	<i>deconfiturella</i> VIETTE, 1962	<i>rhomboidella</i> WALSINGHAM, 1897
	<i>ditreta</i> MEYRICK, 1920	<i>saalmullerella</i> VIETTE, 1958
	<i>arabica</i> AMSEL, 1961	<i>sabiella</i> FELDER, 1875
	<i>epiloxa</i> MEYRICK, 1915	<i>sotsaella</i> VIETTE, 1976
	<i>glabra</i> MEYRICK, 1920	<i>spyrathodes</i> MEYRICK, 1922
	<i>glandifera</i> MEYRICK, 1918	<i>taxiaca</i> MEYRICK, 1920
	<i>hamaxastra</i> MEYRICK, 1930	<i>tyranthes</i> MEYRICK, 1934
	<i>hemicosma</i> MEYRICK, 1920	<i>vulcanica</i> KUN, 2004
	<i>humiliella</i> (CHRÉTIEN, 1916)	

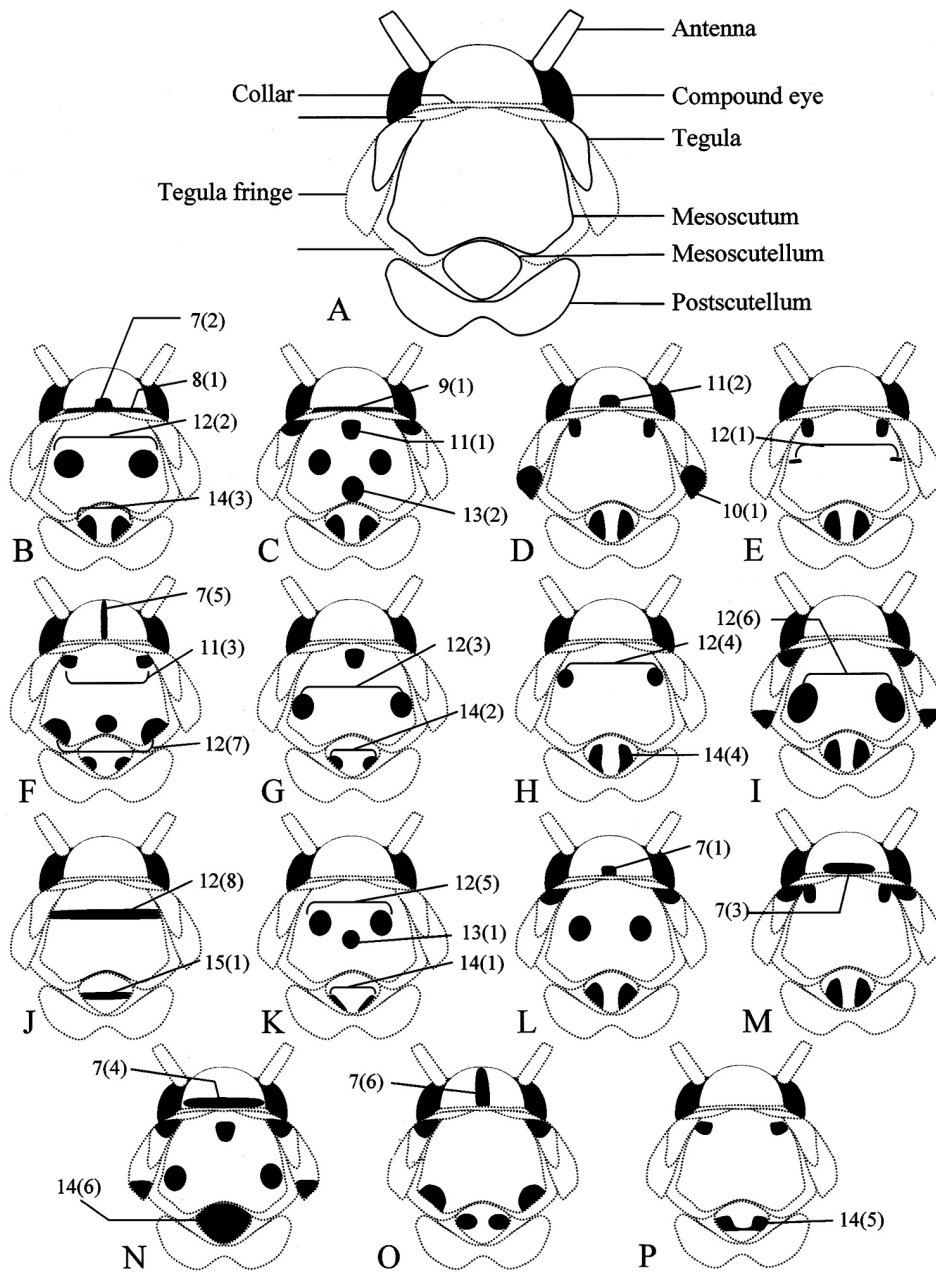


Fig. 1. Selected character states of head and thorax patterns: A = dorsal view of *Ethmia* thorax, B = *E. nigroapicella*, C = *E. assamensis*, D = *E. lapidella*, E = *E. subsimilis*, F = *E. confusella*, G = *E. c. candidella*, H = *E. bipunctella*, I = *E. sporadica*, J = *E. delliella*, K = *E. aobicostella*, L = *E. dentata*, M = *E. maculifera*, N = *E. funerella*, O = *E. pseudozygospila*, P = *E. zelleriella*

some species with polymorphism or “intermediate patterns” may not fit in any “well-defined” group. To investigate the phylogenetic significance of the colour patterns, we separated all the characters into two subsets: colour pattern and non-colour pattern characters. The colour-linked characters are often used in phylogenetic reconstruction of the Lepidoptera, but many authors suspect that colour patterns are more likely to be the source of homoplasy so that many colour-linked characters are excluded from the analyses. By analysing more than 40 phylogenetic datasets of different organisms AREKUL and QUICKE (2006) find that the colour-linked character which do not involve aposematism or mimicry may still provide evidence to support a lineage while morphological characters are similar between sister taxa. POWELL (1973) assigned the forewing patterns of the New World *Ethmia* into 6 types: (1) dark grey ground with black markings, (2) dark grey costal and white dorsal areas, (3) dark brown costal and pale dorsal areas, (4) white ground with linearly arranged black markings, (5) white ground with essentially transverse metallic blue markings, and (6) white ground with dorsal blotch and terminal band of metallic colour. However, as already stated by POWELL (1973), there are many more types of wing patterns and the “defined” ones are not necessarily applicable for the species of other zoogeographical regions. We analysed, therefore, the spots/stripes on the vertex, dorsal thorax, and wings in detail, and assessed the homology of these spots/stripes according to their relative positions to the cranial and thoracic sclerites (Fig. 1) and wing venation and wing areas (Figs 2–5). Homology of wing colour patterns has been extensively studied in various butterfly species (BRAKEFIELD & FRENCH 1999, NIJHOUT 1991, 2001a, b), but very few in smaller moths except for some Pyraloidea (YOSHIYASU 1985) and Tortricidae (BAIXERAS 2002) groups. Our strategy to code the wing patterns of Ethmiinae was first to assume that all the spots/stripes of the same wing zone are homologous. Then we surveyed the arrangements and combinations of spots/stripes within the wing zone and with those of other wing zones to determine how many characters and character states can be recognized. The terminology used for genitalic structures of the Ethmiinae varies according to authors. In this study, the terminology was chosen from different reference sources based on whether the terms were widely accepted and indicating homologous structures in different taxa. We finally obtained 36 non-colour pattern and 41 colour pattern characters for the phylogenetic analysis. Several morphological characters that were not available from the specimens examined were extracted

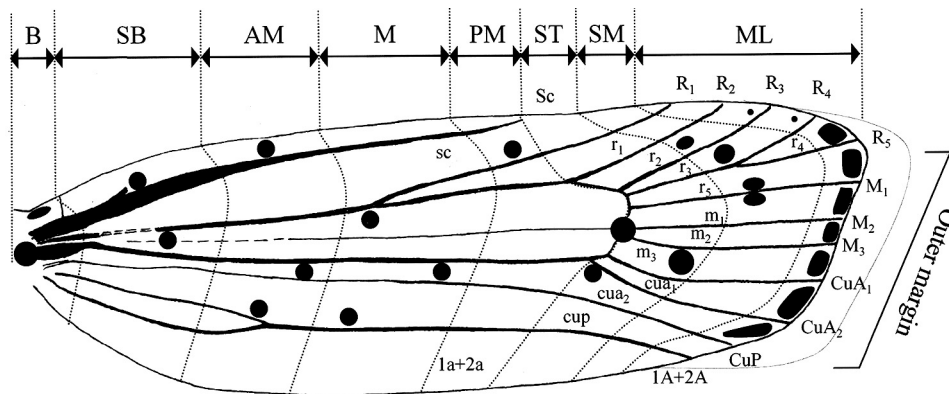


Fig. 2. The distribution of spots/stripes and wing area for wing pattern analysis: ML = marginal line, SM = sub-marginal zone, ST = sub-terminal zone, PM = post-medial zone, M = medial zone, AM = ante-medial zone, SB = sub-basal zone, B = basal zone

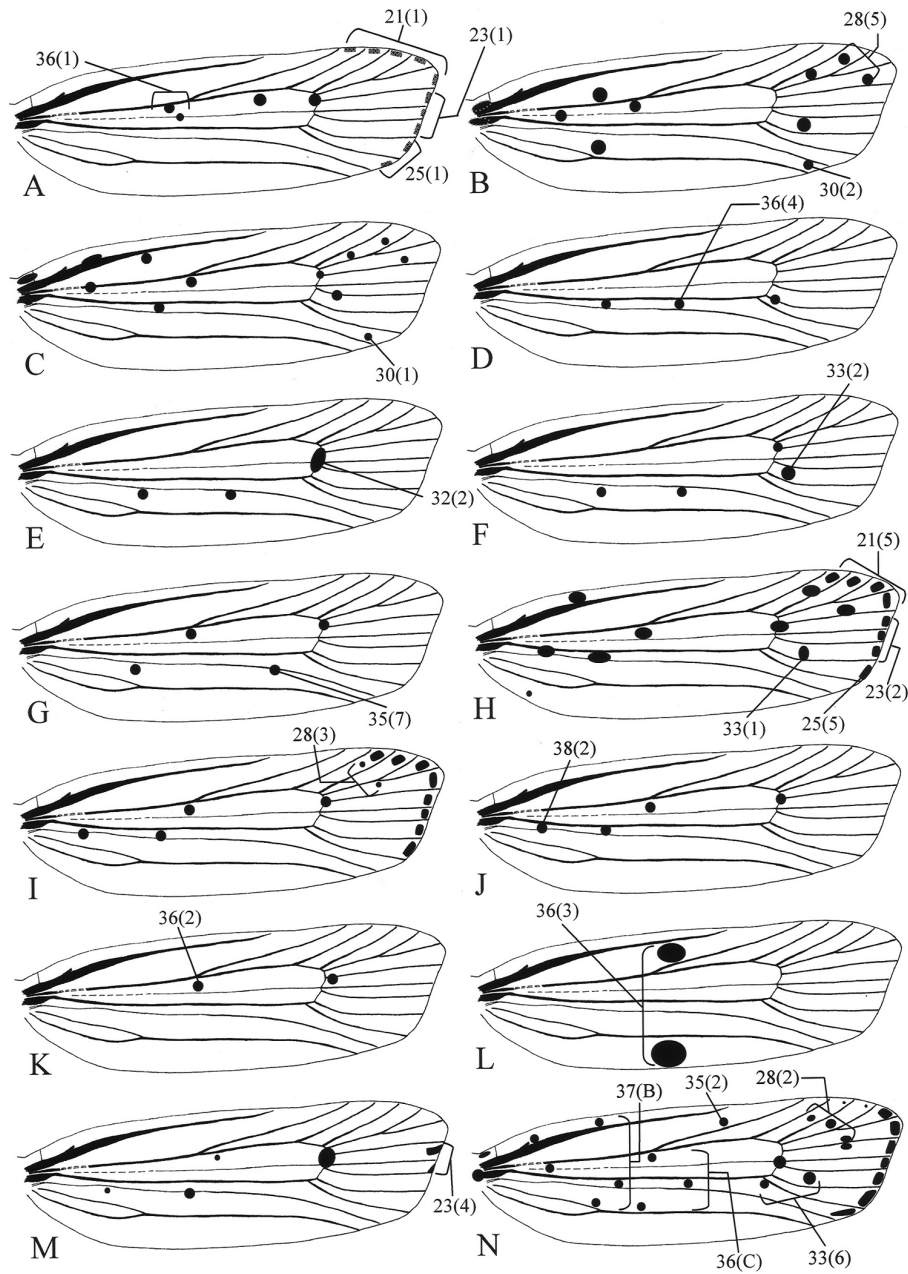


Fig. 3. Selected characters states of wing patterns: A = *A. heracliana*, B = *A. magnificella*, C = *C. hypomelas*, D = *E. plagiobothrae*, E = *E. chrysopygella*, F = *E. flavianella*, G = *E. aurifluella*, H = *E. lapidella*, I = *E. ocranoma*, J = *E. coquilletella*, K = *E. heliomela*, L = *E. b. brevistriga*, M = *E. q. quadrinotella*, N = *E. nigroapicella*

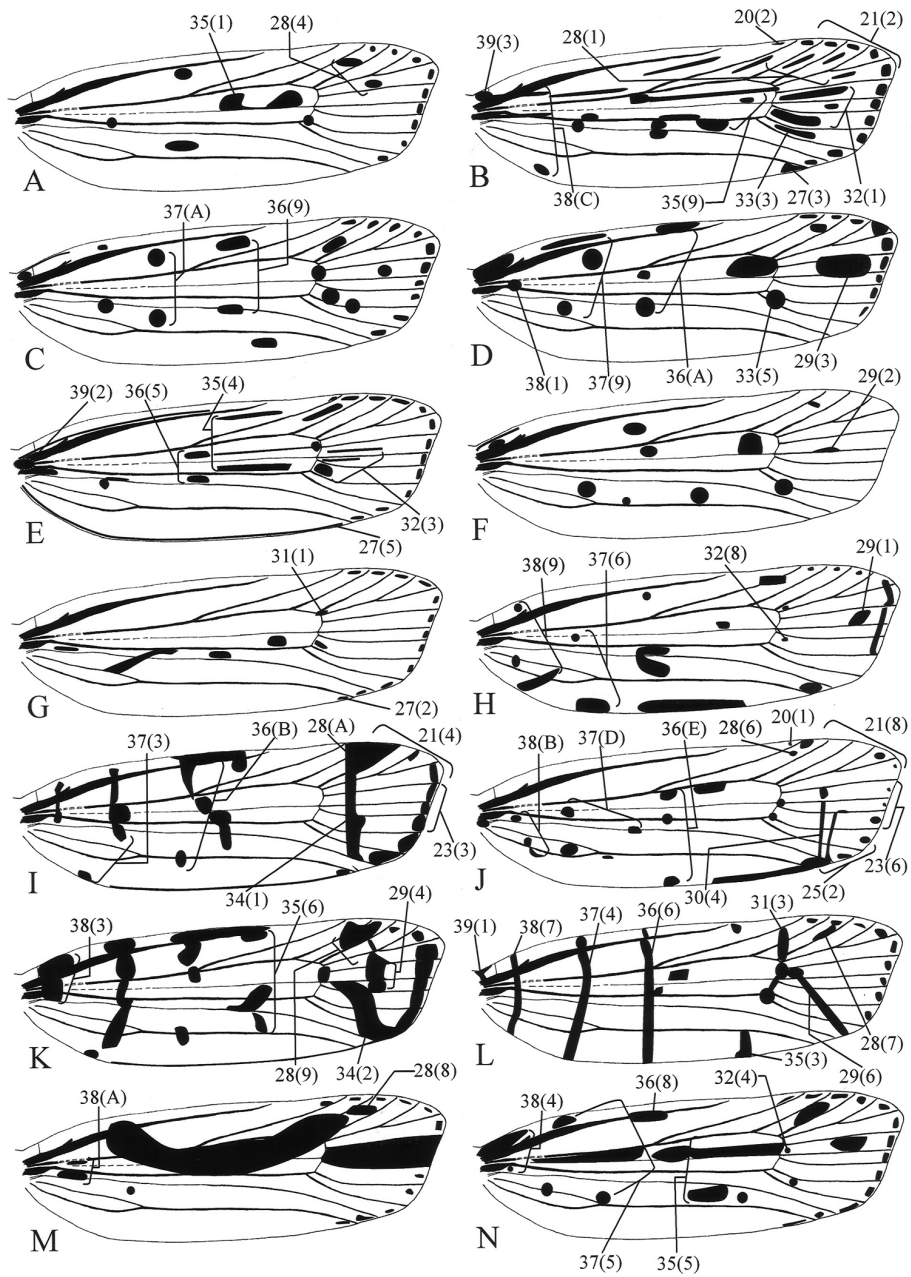


Fig. 4. Selected characters states of wing patterns: A = *E. maculifera*, B = *E. assamensis*, C = *E. sporadica*, D = *E. sphaerosticha*, E = *E. m. monticola*, F = *E. dodecea*, G = *E. d. discostrigella*, H = *E. bitteneilla*, I = *E. hemadelpha*, J = *E. subsmilis*, K = *E. eupostica*, L = *E. delliella*, M = *E. pseudozygospila*, N = *E. zelleriella*

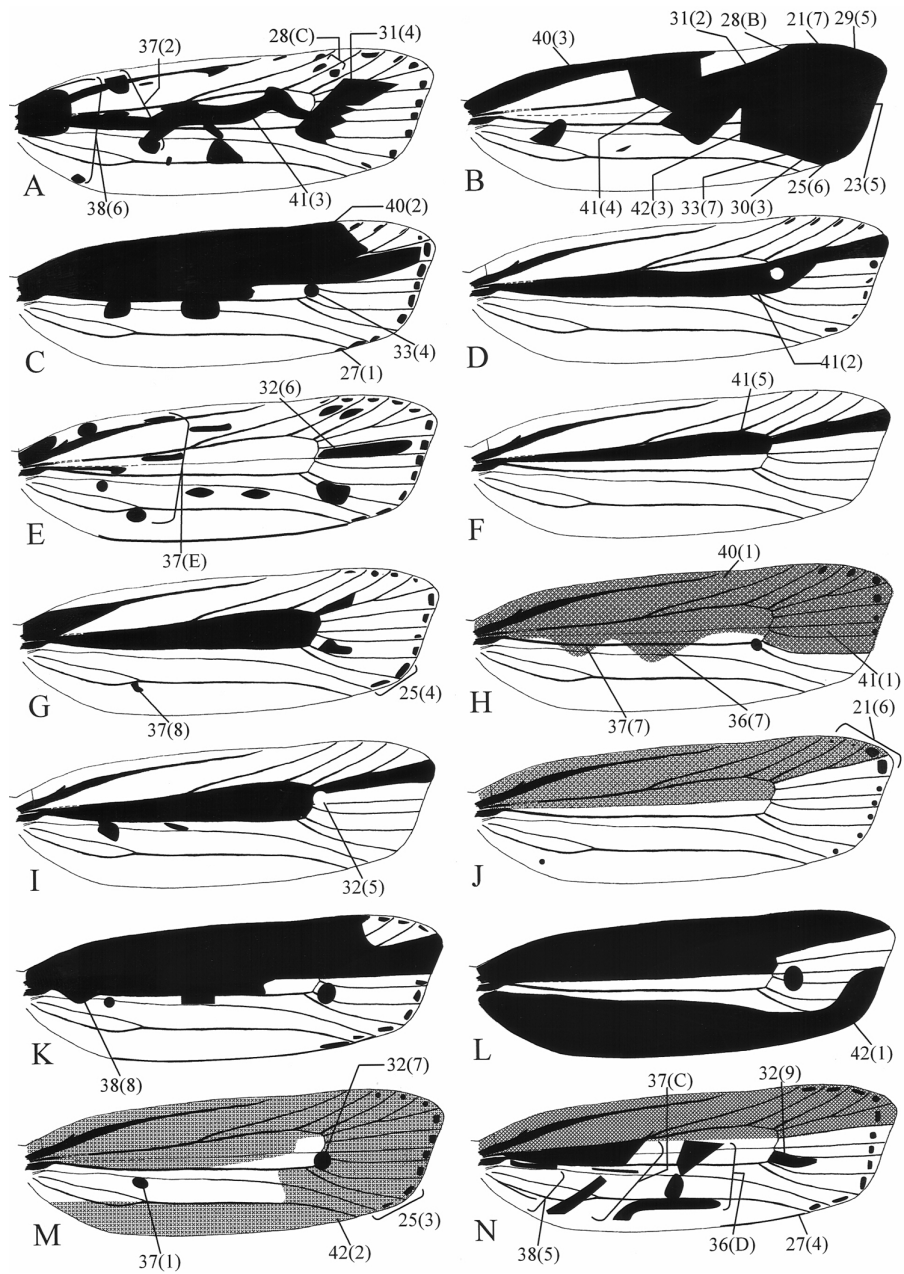


Fig. 5. Selected characters states of wing patterns: A = *E. p. pusiella*, B = *E. f. funerella*, C = *E. bipunctella*, D = *E. maceliosiella*, E = *E. confusella*, F = *E. timberlakei*, G = *E. albicostella*, H = *E. semiobra*, I = *E. geranella*, J = *E. osterosella*, K = *E. semilugen*, L = *E. minuta*, M = *E. nadia*, N = *E. semitenebrella*

from DIAKONOFF (1967), SATTLER (1967), POWELL (1973, 1985), KUN (2000), EMMET *et al.* (2002), and KAILA (2004). The characters included, and their recognized states and descriptions are enumerated in Appendix 1. The data matrix was compiled using MacClade 4.0 (MADDISON & MADDISON 1992) (Appendix 2).

Hostplant records

Our knowledge on the biology and immature stages of the Ethmiinae is very limited and fragmented. In a recently published work (DOMINGO *et al.* 2003), 29 species are listed in Europe, but only for half of them have hostplant records. We obtained the hostplant information of *Ethmia* and the outgroups from various references, especially SATTLER (1967), POWELL (1973, 1985), and ROBINSON *et al.* (2001) (and the online version at the Natural History Museum, London website) (see Table 3 for more records). In total, seven plant families were confirmed and coded as follows for inferring evolution of host uses: Campanulaceae (0), Phytolaccaceae (1), Scrophulariaceae (2), Boraginaceae (3), Hydrophyllaceae (4), Malvaceae (5), Rosaceae (6), and Apiaceae (= Umbelliferae) (7). The transformation series was arranged according to the host association of the outgroups (see Table 3) and the most current phylogenetic hypothesis of angiosperms (SOLTIS *et al.* 2005). Recent studies (e.g. FERGUSON 1998, OLMSTEAD & FERGUSON 2001) have shown that both Boraginaceae and Hydrophyllaceae, as traditionally circumscribed, are not monophyletic and the latter should be treated as a subfamily of the former. In the present study, we still treated "Hydrophyllaceae" as a different "character state" from Boraginaceae to correspond to the hostplant records in lepidopterological literature and to emphasize the unique association of *Ethmia* with the Hydrophyllaceae in North America, which harbours the highest diversity of this plant group. Several *Ethmia* species are reported to be polyphagous (see Table 3), but these non-Boraginaceae records seem to be doubtful, so they were excluded from our analysis.

Phylogenetic analysis

In the present study, maximum parsimony tree building for all 57 taxa and 76 characters (24 binary, 53 multistate) assigned equal weights (EW) was carried out using PAUP* 4.0b 10 (SWOFFORD 1998). Multistate characters were interpreted as being polymorphic rather than as uncertain. We excluded four uninformative characters when reconstructed Maximum Parsimomious Trees (MPT) to avoid overestimating the Consistency Index (CI) and Retention Index (RI). Missing data was coded as "?". Heuristic search was performed in searching MPTs. The initial parameters were set to 10000 random additions and used Tree Bisection Reconnection (TBR) branch swapping. Each swapping was set "no more than one tree held during swapping". Successive approximations weighting (SAW) (FARRIS 1969, 1989) was adopted and the maximum retention index (RI) was assigned for character weights. The difference between EW and SAW consensus trees (Figs 6–7) was compared. The support of cladogram was measured using bootstrap method. To calculate bootstrap values, we set 100 replicates of 100 random additions (Maxtree = 100). In order to understand the influence of different combinations of data subsets on the phylogeny of Ethmiinae, we implemented the incongruence length difference (ILD) test as described in FARRIS *et al.* (1994). We partitioned the data matrix into two subsets: colour-pattern related and non-colour pattern related characters. We constructed MPTs based on the colour pattern characters deactivated and then compared them with the initial MPTs based on the whole data set, to check whether the topological structure was greatly influenced by this exclusion. We also carried out SAW for the MPTs recovered from the dataset with colour pattern characters excluded. The ILD test was carried out using 100 replicates with 100 random addi-

Table 3. The taxa included in the phylogenetic analysis and the material depositories, hostplant associations, geographical regions and literature sources. The geographical origin refers to the locality depicted from the collection data, but not the distribution range. The symbol “*” denotes the hostplant record in question. Hostplant records of a species are extracted from all the information available and do not necessarily correspond the collection data of the material examined.

Species	Geographical origin	Depository	Hostplant	References
Outgroups				
<i>Orophia ferrugella</i> (DENIS & SCHIFFERMÜLLER, 1775)		NHM, HNHM	Campanulaceae	BRYNER (2007)
<i>Depressaria depressana</i> (FABRICIUS, 1775)	Surrey, England	NHM, HNHM	Umbelliferae	HARPER <i>et al.</i> (2002)
<i>Agonopterix heracliana</i> (LINNAEUS, 1758)	Surrey, England	NHM, HNHM	Umbelliferae	HARPER <i>et al.</i> (2002)
<i>Chryselthmia hypomelas</i> DIAKONOFF, 1966	Sulawesi, Indonesia	NHM, HNHM	Unknown	
<i>Agrioceros magnificella</i> (SAUBER, 1902)	Palawan, Philippines	NHM, HNHM	Unknown	DIAKONOFF (1967)
Ingroup				
<i>Eithmia albitogata</i> -group				
<i>coquilletella</i> BUSCK, 1907	California, USA	NMNH, NHM	<i>Phacelia</i> sp. (Hydrophyllaceae)	POWELL (1973)
<i>scylla</i> POWELL, 1973	California, USA	NMNH, NHM	<i>Collinsia heterophylla</i> (Scrophulariaceae)	POWELL (1973)
<i>brevistriga</i> CLARKE, 1950	California, USA	NMNH, NHM	<i>Phacelia distans</i> (Hydrophyllaceae)	POWELL (1973)
<i>albitogata</i> WALSINGHAM, 1907	California, USA	NMNH, NHM	<i>Amsinckia lunaris</i> (Boraginaceae)	POWELL (1973)
<i>plagiobothrae</i> POWELL, 1973	California, USA	NMNH, NHM		POWELL (1973)
<i>minuta</i> POWELL, 1973	California, USA	NMNH, NHM	<i>Cryptantha intermedia</i> (Boraginaceae)	POWELL (1973)
<i>Eithmia charybdis</i> -group				
<i>charybdis</i> POWELL, 1973	California, USA	NMNH, NHM	<i>Amsinckia menziesii</i> , <i>A. tessellata</i> (Boraginaceae)	POWELL (1973)
<i>Eithmia semilugens</i> -group				
<i>albitrigella</i> POWELL, 1973	Colorado, USA	NMNH, NHM	<i>Phacelia ramosissima</i> (Hydrophyllaceae)	POWELL (1973)
<i>nadia</i> CLARKE, 1950	California, USA	NMNH, NHM	<i>Phacelia ramosissima</i> (Hydrophyllaceae)	POWELL (1973)
<i>semilugens</i> (ZELLER, 1872)	Colorado, USA	NMNH, NHM	<i>Phacelia calthifolia</i> (Hydrophyllaceae)	POWELL (1973)
<i>arctostaphylella</i> (WALSINGHAM, 1880)	California, USA	NMNH, NHM	<i>Eriodictyon californicum</i> , <i>E. tomentosum</i> , <i>E. trichocalyx</i> (Hydrophyllaceae)	POWELL (1973)
<i>discostrigella</i> (CHAMBERS, 1877)	Colorado, USA	NMNH, NHM	<i>Cercocarpus ledifolius</i> (Rosaceae)	POWELL (1973)
<i>semitenebrella</i> DYAR, 1902	Arizona, USA	NMNH, NHM	<i>Cercocarpus ledifolius</i> (Rosaceae)	POWELL (1973)

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>Ethmia macelthosiella</i> -group				
<i>macelthosiella</i> BUSCK, 1907	Eastern USA	NMNH, NHM	<i>Phacelia</i> sp. (Hydrophyllaceae)	POWELL (1973)
<i>geranella</i> BARNES & BUSCK, 1920	California, USA	NMNH, NHM	<i>Phacelia</i> sp. (Hydrophyllaceae)	POWELL (1973)
<i>timberlakei</i> POWELL, 1973	California, USA	NMNH, NHM	<i>Phacelia ramosissima</i> var. <i>suffrutescens</i> (Hydrophyllaceae)	POWELL (1973)
<i>Ethmia bipunctella</i> -group				
<i>bipunctella</i> (Fabricius, 1775)	New Jersey, USA	NMNH, NHM	<i>Echium vulgare</i> (Boraginaceae)	POWELL (1973)
<i>monticola</i> (WALSINGHAM, 1880)	California, USA	NMNH, NHM	<i>Veronica</i> (Scrophulariaceae)	ALPHERAKY (1876)
<i>monticola fuscipede</i> (WALSINGHAM, 1880)	Kansas, USA	NMNH, NHM	<i>Phacelia heterophylla</i> , <i>P. leucophylla</i> (Hydrophyllaceae)	POWELL (1973)
<i>monticola hagenella</i> -group				
<i>zellertella</i> (CHAMBERS, 1878)	Ohio, USA	NMNH, NHM	<i>Lithospermum ruderale</i> (Boraginaceae)	POWELL (1973)
<i>Ethmia kirbyi</i> -group				
<i>delliella</i> (FERNALD, 1891)	Texas, USA	NMNH, NHM	<i>Phacelia dubia</i> and <i>P. bipinnatifida</i> (Hydrophyllaceae), <i>Ulmus racemosa</i> (Ulmaceae)*	POWELL (1973)
<i>subsimilis</i> WALSINGHAM, 1897	Jamaica	NMNH, NHM	<i>Ehretia elliptica</i> (Boraginaceae)	POWELL (1973)
<i>bitenella</i> (BUSCK, 1906)	Texas, USA	NMNH, NHM	<i>Trichilia hirta</i> (Meliaceae)	POWELL (1973)
<i>Ethmia confusella</i> -group				
<i>confusella</i> (WALKER, 1863)	Florida, USA	NMNH, NHM	<i>Ehretia anacua</i> (Boraginaceae)	POWELL (1973)
<i>Ethmia longimaculella</i> -group				
<i>longimaculella longimaculella</i> (CHAMBERS, 1872)	Ottawa, Canada	NMNH, NHM	<i>Bourreria ovata</i> (Boraginaceae)	POWELL (1973)
<i>Ethmia trifurcella</i> -group				
<i>semitombra semitombra</i> DYAR, 1902	Texas, USA	NMNH, NHM	<i>Lithospermum officinale</i> (Boraginaceae)	POWELL (1973)
<i>albicostella</i> (BEUTENMÜLLER, 1889)	Montana, USA	NMNH, NHM	<i>Ehretia elliptica</i> (Boraginaceae)	POWELL (1973)
<i>trifurcella</i> (CHAMBERS, 1873)	Florida, USA	NMNH, NHM	<i>Lithospermum</i> sp. (Boraginaceae)	POWELL (1973)
<i>oteroestella</i> BUSCK, 1934	Santiago, Cuba	NMNH, NHM	<i>Cynoglossum virginianum</i> (Boraginaceae)	POWELL (1973)
			<i>Stegnospermum halimifolia</i> , <i>Trichostigma octandrum</i> (Phytolaceae)	POWELL (1973)

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>Ethmia distigmatella</i> -group <i>quadrimotella</i> (MANN, 1861)	Algeria	NHM	<i>Heliotropium ramosissimum</i> (Boraginaceae)	CHRÉTIEN (1915)
<i>Ethmia dodecea</i> -group <i>dodecea</i> (HAWORTH, [1828])	Spain	NHM	<i>Lithospermum officinale</i> (Boraginaceae)	KALTENBACH (1862, 1874), JOURDHEUILLE (1870), MORRIS (1870), HARTMANN (1880), CURÓ & TURATI (1883), RÖSSLER (1882, 1866), SNELLEN(1882), SCHMID (1886), CROMBRUGGHE (1906), THOMANN (1908), MEESS (1910), MÜLLER- RUTZ (1914), MARTINI (1917), HÖFNER (1918), <i>Lithospermum officinale</i> (Boraginaceae) PROHASKA & HOFFMANN (1927), FORD (1949), LHOMME (1949), KLIMESCH (1961) GIANELLI (1911), HRUBÝ (1964) MARIANI (1943) KOCH (1856), DISQUÉ (1908), LHOMME (1949) MILLIÈRE (1868), CURÓ & TURATI (1883)
	Italy	NHM	<i>Symphytum officinale</i> (Boraginaceae) <i>Erythraea</i> (Gentianaceae) <i>Cynoglossum</i> sp., <i>Lithospermum</i> <i>arvense</i> (Boraginaceae) <i>Echium vulgare</i> (Boraginaceae) <i>Asperugo procumbens</i> (Boraginaceae) <i>Borago officinalis</i> (Boraginaceae) <i>Cerinthe major</i> (Boraginaceae)	WILTSHIRE (1957) MILLIÈRE (1868 & 1875), MILLIÈRE (1868 & 1875), HARTMANN (1880), CURÓ & TURATI (1883), SOK- HAGEN (1886), DISQUÉ (1908), GIANELLI (1911),

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>candidella</i> (ALPHERAKY, 1908)			<i>Cerithe major</i> (Boraginaceae)	LHOMME (1949), WÖRZ (1954)
<i>pusiella</i> (LINNAEUS, 1758)	France	NHM	<i>Lithospermum purpurocaeruleum</i> (Boraginaceae) <i>Borago officinalis</i> (Boraginaceae)	KASY (1964) MILLIÈRE (1868 & 1875), HARTMANN (1880), CURÓ & TURATI (1883), SOR- HAGEN (1886), DISQUÉ (1908), GIANELLI (1911), LHOMME (1949), WÖRZ (1954) GALVAGNI (1955) DISQUÉ (1908) FETTIG (1882), RAPP (1936), WÖRZ (1954), BENANDER (1965) TREITSCHKE (1832), SORHAGEN (1886), DISQUÉ (1908), MITTERBERGER (1918), LHOMME (1949) TREITSCHKE (1832), COSTA (1832–1836), WOCKE (1849), KALTEN- BACH (1862 & 1874), HARTMANN (1880), FETTIG (1882), HAAR (1887), SORHAGEN (1886), DISQUÉ (1908), MEISS (1910), HAUDER (1912), SKALA (1913), FÜGER & TROEDER (1930), LHOMME (1949), WÖRZ (1954), KLIMESCH (1961)
			<i>Echium vulgare</i> (Boraginaceae) <i>Lithospermum arvense</i> (Boraginaceae) <i>Lithospermum officinale</i> (Boraginaceae)	
			<i>Lithospermum purpurocaeruleum</i> (Boraginaceae)	
			<i>Pulmonaria officinalis</i> (Boraginaceae)	

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>pustiella</i> (LINNAEUS, 1758)			<i>Pulmonaria striata</i> (Boraginaceae)	PROHASKA & HOFFMANN (1927), KLIMESCH (1961)
			<i>Quercus</i> sp. (<i>Fagaceae</i>) *	MARIANI (1943)
			<i>Salix</i> sp. (<i>Salicaceae</i>) *	KÜHN (1777)
			<i>Silene</i> sp. (<i>Caryophyllaceae</i>) *	SKALA (1913), MARIANI (1943), SCHÜTZE (1931)
			<i>Silene armeria</i> (<i>Caryophyllaceae</i>) *	HARTMANN (1880), HÖFNER (1918), SORHAGEN (1886), LHOMME (1949)
			<i>Silene viscosa</i> (<i>Caryophyllaceae</i>) *	SCHÜTZE (1931), WÖRZ (1954)
			<i>Viscaria</i> (<i>Caryophyllaceae</i>) *	SCHÜTZE (1931), WÖRZ (1954)
<i>funerella</i> (FABRICIUS, 1787)	England	NHM	<i>Urtica</i> (<i>Urticaceae</i>) *	HÜBNER (1786), TREITSCHKE (1832), KALTENBACH (1974), SORHAGEN (1886), SKALA (1913), HÖFNER (1918), SCHÜTZE (1931), MARIANI (1943), WÖRZ (1954)
			<i>Lithospermum officinal</i> (Boraginaceae)	KALTENBACH (1862, 1869, 1874), JOUR- DHEUILLE (1870), MORRIS (1870), RÖSSLER (1882), SORHAGEN (1886), FÜGER & TROEDER (1930), WÖRZ (1954)
			<i>Lithospermum purpureoceruleum</i> (Boraginaceae)	MILLIÈRE (1875), RAPP (1936), LHOMME (1949), WÖRZ (1954)

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>funerella funerella</i> (FABRICIUS, 1787)			<i>Pulmonaria officinalis</i> (Boraginaceae)	RÖSSLER (1866, 1882), KALTENBACH (1869), HARTMANN (1880), SORHAGEN (1886), DISQUÉ (1908), LHOMME (1951), WÖRZ (1954), HEINEMANN (1870), MORIS (1870), HARTMANN (1880), CURÓ & TURATI (1882), STERDEL & HOFMANN (1882), SCHMID (1886), SORHAGEN (1886), GIANELLI (1911), LHOMME (1951), WÖRZ (1954), SULCS (1964) FORD (1949)
			<i>Pulmonaria officinalis</i> (Boraginaceae)	
			<i>Symphytum officinale</i> (Boraginaceae)	
			<i>Symphytum tuberosum</i> (Boraginaceae)	
<i>Ethmia aurifluella</i> -group <i>aurifluella</i> (HÜBNER, [1810])	Spain	NHM	<i>Anchusa</i> sp. (Boraginaceae)	THOMANN (1923)
<i>Ethmia discrepitiella</i> -group <i>pyrausta</i> (PALLAS, 1771)	Finland	NHM	<i>Thalictrum aquilegifolium</i> (Ranunculaceae)	NOLCKEN (1871), HARTMANN (1880), MEESS (1910), MARIANI (1943)
<i>Ethmia nigripedella</i> -group <i>chrysopygella</i> (KOLENATI, 1846) MÜLLER-RUTZ (1914)	S. France	NHM	<i>Thalictrum flavum</i> (Ranunculaceae)	MEESS (1910),
<i>flavianella</i> (TREITSCHKE, 1832) (1925)	S Italy	NHM	<i>Thalictrum foetidum</i> (Ranunculaceae) <i>Thalictrum minus</i> (Ranunculaceae) <i>Thalictrum foetidum</i> (Ranunculaceae)	LHOMME (1949) THOMANN (1923) LHOMME (1949), CLEU
			<i>Pistacia terebinthus</i> (Anacardiaceae)*	KRONE (1913)

Table 3 (continued)

Species	Geographical origin	Depository	Hostplant	Sources of literature
<i>Ethmia assamensis</i> -group <i>assamensis</i> (BUTLER, 1879)	Assam, India	NHM	<i>Ehretia ovalifolia</i> (Boraginaceae) <i>Ehretia serrata</i> (Boraginaceae)	MORIUTI (1963) WALSINGHAM (1880), DURRANT (1906), FLETCHER (1920) FLETCHER (1920)
<i>Ethmia penesella</i> -group <i>maculifera</i> (MATSUMURA, 1931)	Kaohsiung, Taiwan	NSYSU	<i>Ehretia dicksonii</i> (Boraginaceae)	Present study
<i>Ethmia nigroapicella</i> -group <i>nigroapicella</i> (SAALMÜLLER, 1880)	Kaohsiung, Taiwan	NHM, NSYSU	<i>Cordia subcordata</i> (Boraginaceae) <i>Ehretia buxifolia</i> <i>E. dicksonii</i> var. <i>japonica</i> , <i>E. laevis</i> <i>E. resinosa</i> (Boraginaceae)	LEGRAND (1965) MORIUTI (1963) POWELL (1985) Present study
<i>thoraea</i> MEYRICK, 1910 <i>dentata</i> DIAKONOFF & SATTLER, 1966	Queensland, Australia Kaohsiung, Taiwan	NHM NHM	<i>Cynoglossum</i> sp. (Boraginaceae) <i>Ehretia</i> sp. (Boraginaceae)	POWELL (1985) MORIUTI (1963)
<i>Ethmia crocosoma</i> -group <i>sphaerosticha</i> (MEYRICK, 1887)	Queensland, Australia	NHM	<i>Ehretia acuminata</i> (Boraginaceae)	POWELL (1985)
<i>Ethmia lapidella</i> -group <i>lapidella</i> (WALSINGHAM, 1880) <i>octanoma</i> MEYRICK, 1914 <i>heptasema</i> TURNER, 1898 <i>heliomela</i> LOWER, 1923	Kaohsiung, Taiwan Kaohsiung, Taiwan Queensland, Australia Queensland, Australia	NHM, NSYSU NHM, NSYSU NHM NHM	<i>Ehretia resinosa</i> (Boraginaceae) <i>Ehretia resinosa</i> (Boraginaceae) <i>Ehretia acuminata</i> (Boraginaceae) <i>Ehretia acuminata</i> (Boraginaceae)	Present study Present study POWELL (1985) POWELL (1985)
<i>Ethmia sporadica</i> -group <i>pseudozygospila</i> KUN & SZABÓKY, 2000 <i>sporadica</i> TURNER, 1941	Kaohsiung, Taiwan Queensland, Australia	NHM, NSYSU NHM	<i>Ehretia dicksonii</i> (Boraginaceae) <i>Ehretia acuminata</i> (Boraginaceae)	Present study POWELL (1985)
<i>Ethmia postica</i> -group <i>postica</i> POWELL, 1985 <i>hemadelpha</i> (LOWER, 1903)	N. Territory, Australia SE Queensland, Australia	NHM NHM	<i>Halgania cyanea</i> (Boraginaceae) <i>Ehretia saligna</i> (Boraginaceae)	POWELL (1985) POWELL (1985)

tions and maxtrees set at 100. All tests were run with uninformative characters excluded. We adopted TEMPLETON'S (1983) test as implemented in PAUP* under parsimony tree scores, for testing the monophyly of Ethmiinae and the genus *Ethmia*. To trace the evolution of host uses we executed character trace and character optimisation using MacClade 4.0 to map the hostplant uses onto the consensus trees obtained from the MPTs.

RESULTS

Phylogenetic pattern

The initial heuristic search based on EW characters and the whole dataset produced 28 EW MPTs (TL = 696, CI = 0.45, RI = 0.576). The MPTs were used to obtain the shortest consensus tree shown in Fig. 6A. The consensus tree shows unresolved relationships of the *Ethmia* and the monophyly of Ethmiinae is not recovered. Three SAW trees (TL = 370.09005, CI = 0.478, RI = 0.628) were found and the consensus (Fig. 6B) shows much better resolution than the EW one, but neither the Ethmiinae nor the genus *Ethmia* is monophyletic because the clade (*Chrysethemia* + *Agrioceros*) inserts into *Ethmia*.

When the colour pattern characters were excluded, only one EW MPT (TL = 262, CI = 0.427, RI = 0.631) was found (Fig. 7A). Compared with the SAW consensus based on the whole dataset, resolution of this tree is not significantly different but the relationships between species groups recovered by this treatment are very different from those shown in Fig. 6. The genus *Chrysethemia* becomes the sister-group of (*lapidella* + *octonoma*), and more species groups were recovered to be monophyletic. The clade including *Ethmia*, *Chrysethemia* and *Agrioceros* is supported by 7 apomorphies: 32:4 (subterminal spot of m cell rounded at base of m1) (Fig. 4N), 52:E (uncus with paired long processes) (DIAKONOFF 1967: fig. 387), 61:6 (ventral margin of sacculus slightly emarginated and extruded to be arched) (SATTLER 1967: fig. 62–1), 63:1 (costal subdivision elongate) (POWELL 1973: fig. 51), 67:1 (a differentiated dorsal shield of juxta present, surrounding aedeagus), 68:1 (coecum penis present as a sac ventrad of basal opening of aedeagus), and 69:1 (aedeagus bended interiorly to 180°) (POWELL 1973: fig. 51). The consensus of the 96 SAW trees (TL = 158.41001, CI = 0.462, RI = 0.667) (Fig. 7B) is slightly different from the EW one only in the phylogenetic positions of *zelleriella*, *assamensis* and *charybdis* species groups. It is worth notice that neither the New World nor the Old World species form a monophyletic entity (Fig. 7A).

We also reconstructed the phylogenetic trees based on colour pattern characters. Either the consensus of the 74 EW MPTs (Fig. 8A) (TL = 370, CI = 0.543, RI = 0.66) or that of the more than 10000 SAW trees (Fig. 8B) (TL = 214.18973, CI = 0.575, RI = 0.721) show poor resolution and interestingly the species having simi-

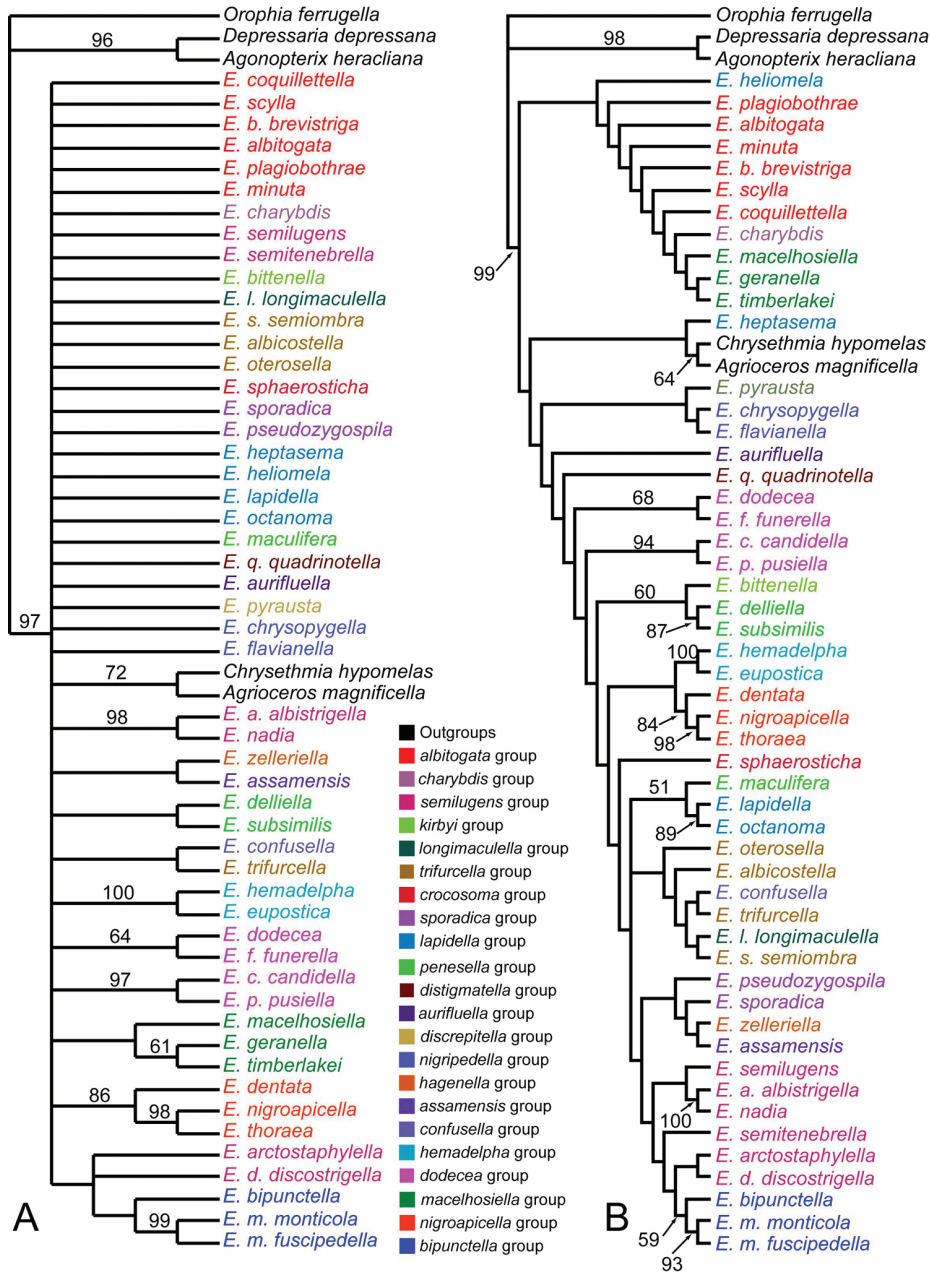


Fig. 6. Comparison of two strict consensus cladograms of 28 MPTs (TL = 696 = CI = 0.45 = RI = 0.576) under EW (A) and 3 MPTs (TL = 370.09005 = CI = 0.478 = RI = 0.628) under SAW (B) based on the whole dataset. Bootstrap values are labelled above the branches or indicated by arrows. Colours of taxa names refer to the species-groups which they are belonging to

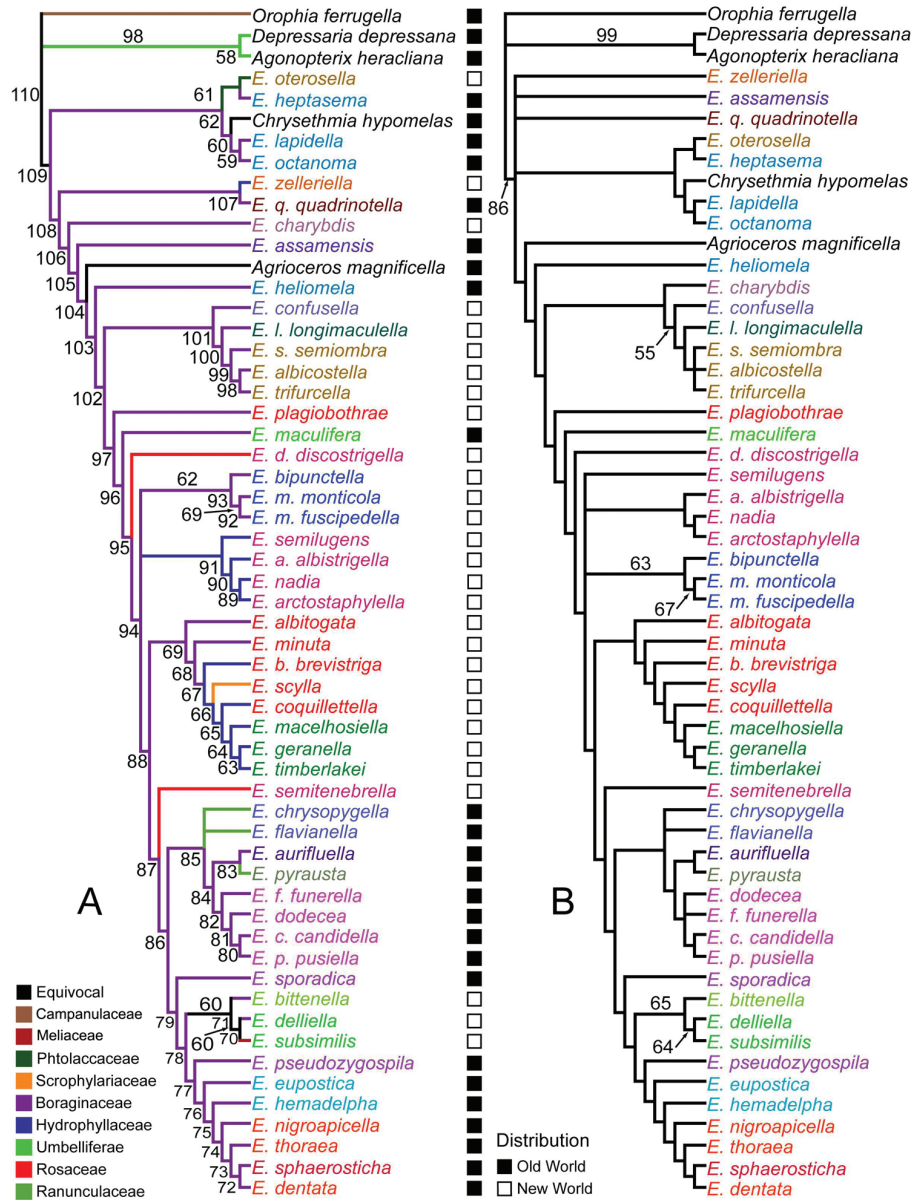


Fig. 7. Comparison of two strict consensus cladograms of 1 MPT (TL = 262 = CI = 0.427 = RI = 0.631) under EW (A) and 96 MPTs (TL = 158.41001 = CI = 0.462 = RI = 0.667) under SAW (B) with colour pattern characters inactivated. Bootstrap values are labelled above the branches or indicated by arrows. Numbers below the branches correspond to node numbers in Appendix 3. Colours of taxa names refer to the species-groups which they are belonging to (see Fig. 6). Colours of branches in A correspond to hostplant associations. Solid and hollow squares denote distribution of taxa

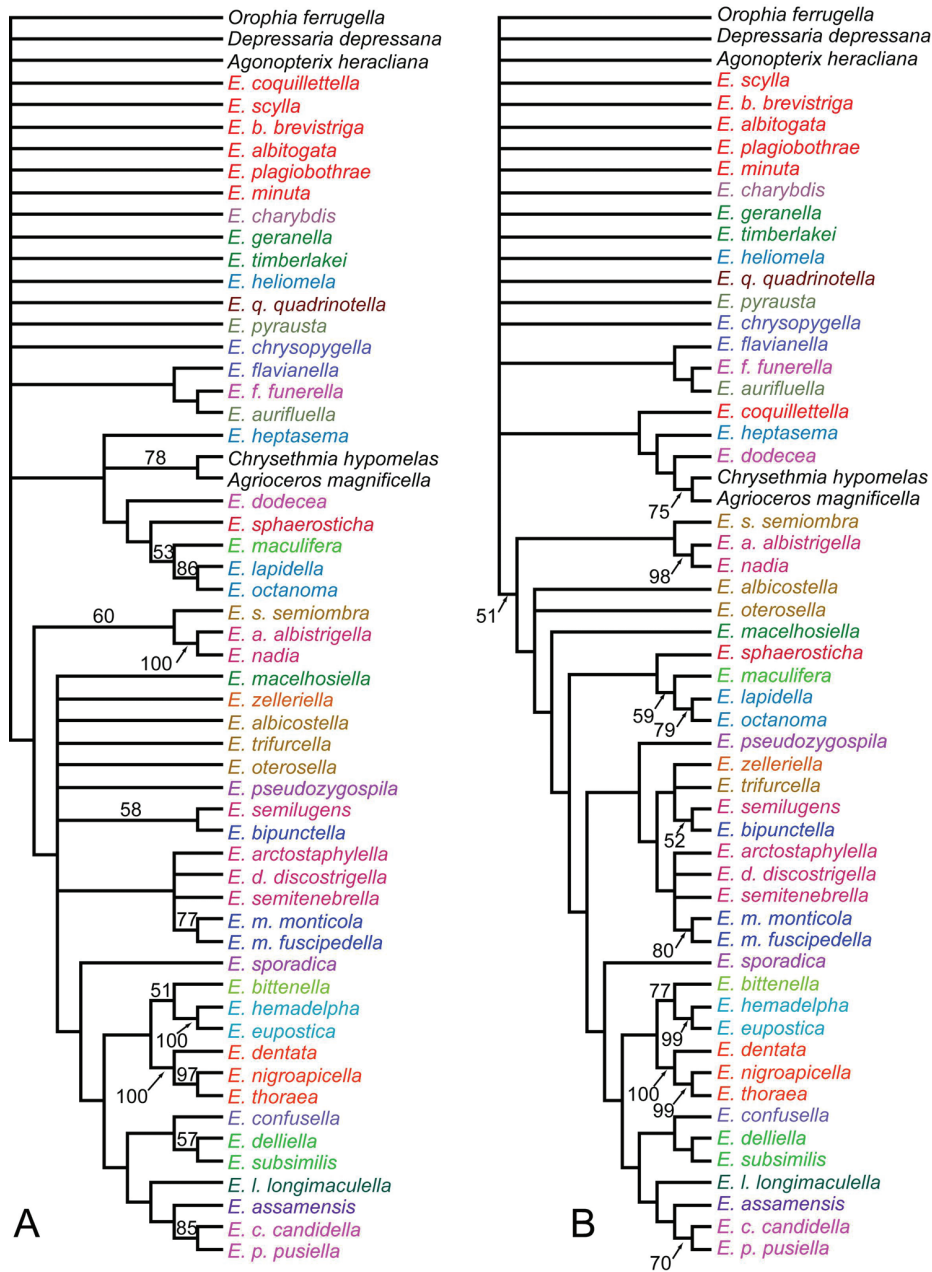


Fig. 8. Comparison of two strict consensus cladograms of 74 MPT (TL = 370 = CI = 0.543 = RI = 0.66) under EW (A) and more than 10000 MPTs (TL = 214.18973 = CI = 0.575 = RI = 0.721) under SAW (B) based on colour pattern characters. Bootstrap values are labelled above the branches or indicated by arrows

lar colour patterns (defined by POWELL 1973) do not necessarily form a monophyletic group under this treatment.

Result of the ILD test for comparing the MPTs colour pattern related and non-colour pattern related characters, respectively, shows that the phylogenies generated by these two character subsets are significantly incongruent ($P < 0.05$). Although all the phylogenies based on different character weighting schemes and treatments show that *Ethmia* is not monophyletic, result of the Templeton test did not reject the null hypothesis ($P > 0.05$) so the possibility that *Ethmia* is monophyletic cannot be ruled out.

Evolution of host associations

The hostplant family associations were mapped onto the phylogeny based on the dataset with colour pattern characters inactivated (Fig. 7A). The majority of the species (65.38%) included in the analysis utilize Boraginaceae and this association seems to be a more ancestral state than those of other plant families. The species utilizing Hydrophyllaceae (or Hydrophyloideae) occupy 19.23% of the included species and are confined to North America. This feeding behaviour has evolved independently from the Boraginaceae-association twice in the *semilugens*, *macelhsiella* and *albitogata* species groups (Fig. 7A). The non-Boraginaceae/Hydrophyllaceae hostplant associations are not shown as ancestral states, so these species may have evolved independently from the Boraginaceae-feeding ancestors.

The relationship between hostplant switching and species-group has no significant connection. The *semilugens*, *albitogata* and *bittenella* species-groups utilize various hostplants including Scrophulariaceae, Hydrophyllaceae, Boraginaceae, Malvaceae and Rosaceae, but these plant families are not related to each other but belong to a monophyletic group according the most recent phylogeny reconstructed by the APG group (SOLTIS *et al.* 2005). These hostplant associations also do not correlate with zoogeographical regions.

FUTURE CONTEXT

This is the first attempt to investigate the phylogenetic status of the Ethmiinae and the genus *Ethmia*. The purpose of the present study is to infer the evolution of host uses in the Ethmiinae moths. However, the present taxon sampling does not well represent all the lineages of the subfamily. Due to the limited information of hostplant records, many species-groups have only one representative included in present study (except the *charybdis* species group, which comprises only one spe-

cies). This may have weakened the phylogenetic information possessed by these taxa. In future studies, more species from Africa, many intriguing character states (e.g. the single and long uncus of the *lineatonotella* species group), and a large number of phylogenetically potential characters (e.g. forewing and antennal core-matal organs, and immature morphology) need to be included to produce a global parsimony phylogeny that a sound classification can be based on.

*

Acknowledgements – This paper is dedicated to the memory of Dr. L. GOZMÁNY, the former curator of Microlepidoptera collection of the HHNM. ANDRÁS KUN would like to thank for his continuous help and encouraging guidance in Lepidoptera taxonomy and systematics. We thank for KLAUS SATTLER, KEVIN TUCK and DAVID AGASSIZ (The Natural History Museum, London) and DONALD DAVIS (National Museum of Natural History, Smithsonian Institution, Washington D. C.) for allowing us to examine the collection and sharing the knowledge about this moth group. The studies of ANDRÁS KUN on Ethmiinae in Royal Museum for Central Africa, Tervuren, Belgium, and the Natural History Museum, Vienna, Austria received support from the SYNTHESYS Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area” Programme (applications AT-TAF-327, BE-TAF-332). The visits to Taiwan supported by Hungarian Academy of Sciences and the National Science Council (Taiwan). The study of the Taiwan team is supported by the grants provided by Council of Agriculture (Taiwan) and National Science Council (Taiwan).

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Revised version received May 3, 2007, accepted May 30, 2007, published July 30, 2007

APPENDIX 1

Characters used in the cladistic analysis. The CI and RI values were obtained from the analysis based on the whole dataset with equal weighting scheme (EW).

Adult head

1. Hair-like androconia in antenna: absent (0); present (1) (CI_{EW} = 0, RI_{EW} = 0)
2. Antennal dilation: not dilated (0); slightly dilated (1); dilated (2) (CI_{EW} = 0.08, RI_{EW} = 0.2)
3. Scales on front: smooth (0); appressed (1); rough (2) (CI_{EW} = 0.2, RI_{EW} = 0.06)
4. Scale of vertex: smooth (0); appressed (1); rough (2) (CI_{EW} = 0.43, RI_{EW} = 0.14)
5. Labial palpus: slightly upcurved (0); strong upcurved (1); porrect (2) (CI_{EW} = 0.18, RI_{EW} = 0.18)

6. Scale colour of proboscis base: white (0); white mixed with black (1); yellow (2); brown (3); grey (4); black (5) ($CI_{EW} = 0.63$, $RI_{EW} = 0.25$)
7. Spot(s)/strip(s) on postoccipt: absent (0); single, small rounded spot, 1/5 width of head (1) (Fig. 1L); single, rounded spot, 1/3 width of head (2) (Fig. 1B); single, bell-shaped, 1/2 width of head (3) (Fig. 1M); single, spot horizontally extended (4) (Fig. 1N); slender longitudinal stripe at middle (5) (Fig. 1F); broad longitudinal stripe at middle (6) (Fig. 1O) ($CI_{EW} = 0.55$, $RI_{EW} = 0.17$)
8. Black line at front margin of collar: absent (0); present (1) (Fig. 1B) ($CI_{EW} = 0.25$, $RI_{EW} = 0.25$)

Thorax

9. Black spot on tegula base: absent (0); present (1) (Fig. 1C) ($CI_{EW} = 0.05$, $RI_{EW} = 0.18$)
10. Black spot on tegula apex: absent (0); present (1) (Fig. 1D) ($CI_{EW} = 0.33$, $RI_{EW} = 0$)
11. Anterior black spots on mesoscutum: absent (0); single at middle (1) (Fig. 1C); two near middle (2) (Fig. 1D); two situated at frontolateral corners (3) (Fig. 1F) ($CI_{EW} = 0.23$, $RI_{EW} = 0.17$)
12. Black spots/stripes on mesoscutum: absent (0); two slender transverse bars near lateral margins of mesoscutum (1) (Fig. 1E); two small oblique spots laterally compressed (2) (Fig. 1B); two spots higher laterally (3) (Fig. 1G); two small circular spots near middle line (4) (Fig. 1H); two larger circular spots near middle line (5) (Fig. 1K); two larger circular spots extended to posterior portion of mesoscutum (6) (Fig. 1I); two large black areas extended from below tegula apex to hind margin of mesoscutum (7) (Fig. 1F); present as a transverse band (8) (Fig. 1J) ($CI_{EW} = 0.38$, $RI_{EW} = 0.32$)
13. Medial black spot on mesoscutum: absent (0); present prior to hind margin of mesoscutum (1) (Fig. 1K); present at hind margin of mesoscutum (2) (Fig. 1C) ($CI_{EW} = 0.5$, $RI_{EW} = 0$)
14. Black stripes on mesoscutellum: absent (0); two black lines along lateral margins (1) (Fig. 1K); two small laterally compressed spots along lateral margins (2) (Fig. 1G); two larger oblong spots along lateral margins (3) (Fig. 1B); two kidney-shaped spots along lateral margins (4) (Fig. 1H); two oblong spots along lateral margins, connected medially (5) (Fig. 1P); all black (6) (Fig. 1N) ($CI_{EW} = 0.2$, $RI_{EW} = 0.18$)
15. Black line at anterior margin of mesoscutellum: absent (0); present (1) (Fig. 1J) ($CI_{EW} = 0.5$, $RI_{EW} = 0.5$)
16. Shaggy hairs on ventral side of thorax: absent (0); present (1) ($CI_{EW} = 0.33$, $RI_{EW} = 0$)
17. Tibial hairs: absent (0); weakly develop (1); well develop (2) ($CI_{EW} = 0.17$, $RI_{EW} = 0.17$)
18. Mesothoracic spiracle (equivalent to the character 148 in KAILA 2004): same as other spiracles (0); with a protuberance (1) ($CI_{EW} = 1$, $RI_{EW} = 1$)

Forewing

19. Forewing fringes: developed at tornus (0); not developed at tornus (1) ($CI_{EW} = 1$, $RI_{EW} = 1$)
20. Marginal spot in sc cell: absent (0); present, slender (1) (Fig. 4J); present, elongated (2) (Fig. 4B) ($CI_{EW} = 0.29$, $RI_{EW} = 0.38$)
21. Marginal spots in male r cells: absent (0); obscure in r1-r5 (1) (Fig. 3A); slender in r1-r5 (2) (Fig. 4B); slender in r1-r5 and the r1 spot on R1 vein (3); slender in r1-r5 and r5 connect to m1 (4) (Fig. 4I); slender in r2-r5 (5) (Fig. 3H); small in r2 and r3, rounded in r4 and r5 circular (6) (Fig. 5J); indistinguishable (7) (Fig. 5B); rounded in r1 and r4, smaller in r5 (8) (Fig. 4J) ($CI_{EW} = 0.31$, $RI_{EW} = 0.38$)
22. Marginal spots in female r cells: absent (0); obscure in r1-r5 (1); slender in r1-r5 (2); slender in r1-r5 and the r1 spot on R1 vein (3); slender in r1-r5 and r5 connect to m1 (4); slender in r2-r5 (5);

- smaller in r2 and r3, rounded in r4 and r5 circular (6); indistinguishable (7); smaller in r2 and r3, rounded in r4 and r5 circular (8) ($CI_{EW} = 0.31$, $RI_{EW} = 0.38$)
23. Marginal spots in male m cells: absent (0); obscure in m1-m3 (1) (Fig. 3A); slender in m1-m3 (2) (Fig. 3H); connected in m1 to m3 (3) (Fig. 4I); connected in m2-m3 (4) (Fig. 3M); indistinguishable (5) (Fig. 5B); small in m1 and m2, slightly elongated in m3 (6) (Fig. 4J) ($CI_{EW} = 0.26$, $RI_{EW} = 0.19$)
 24. Marginal spots in female m cells: absent (0); obscure in m1-m3 (1); obscure in m1-m3 (2); connected in m1 to m3 (3); connected in m1 to m3 (4); indistinguishable (5); connected in m1 to m3 (6) ($CI_{EW} = 0.29$, $RI_{EW} = 0.19$)
 25. Marginal spots in male cu cells: absent (0); obscure in cua1-cua2 (1) (Fig. 3A); slender in cua1-cup (2) (Fig. 4J); connected in cua1-cup (3) (Fig. 5M); slender in cua1 and cua2 (4) (Fig. 5G); slender in cua1 (5) (Fig. 3H); connected in cua1 and cua2 (6) (Fig. 5B) ($CI_{EW} = 0.23$, $RI_{EW} = 0.33$)
 26. Marginal spots in female Cu cells: absent (0); obscure in cua1-cua2 (1); obscure in cua1-cua2 (2); obscure in cua1-cua2 (3); obscure in cua1-cua2 (4); obscure in cua1-cua2 (5); indistinguishable (6) ($CI_{EW} = 0.24$, $RI_{EW} = 0.35$)
 27. Marginal spot in 1a+2a cell: absent (0); little (1) (Fig. 5C); slender (2) (Fig. 4G); larger (3) (Fig. 4B); straight (4) (Fig. 5N); elongated (5) (Fig. 4E) ($CI_{EW} = 0.42$, $RI_{EW} = 0.3$)
 28. Sub-marginal spots in r cells: absent (0); slender in r1, r2, r3 and r5 (1) (Fig. 4B); slender in r2, r3 and r5 (2) (Fig. 3N); rounded and smaller in r2 and r5 (3) (Fig. 3I); rounded and larger in r2 and r5 (4) (Fig. 4A); smaller in r3 and r5 (5) (Fig. 3B); slender in r1 (6) (Fig. 4J); slender in r2 (7) (Fig. 4L); rounded and larger in r2 (8) (Fig. 4M); connected in r1 to m1 (9) (Fig. 4K); connected in r1 and r2 (A) (Fig. 4I); indistinguishable (B) (Fig. 5B); slender in r1 and r2 (C) (Fig. 5A) ($CI_{EW} = 0.6$, $RI_{EW} = 0.33$)
 29. Submarginal spots in m cells: absent (0); rounded in m1 (1) (Fig. 4H); slender in m1 (2) (Fig. 4F); rounded and larger in m1 (3) (Fig. 4D); connected in m1 and m2 (4) (Fig. 4K); indistinguishable (5) (Fig. 5B); slender in m1, connected in m2 and m3 (6) (Fig. 4L) ($CI_{EW} = 0.75$, $RI_{EW} = 0.33$)
 30. Submarginal spot(s)/stripe in cu cells: absent (0); slender in cua2 (1) (Fig. 3C); slender in cup (2) (Fig. 3B); connected in cua1 & cua2 (3) (Fig. 5B); longitudinal in m3 to cua2 (4) (Fig. 4J) ($CI_{EW} = 0.8$, $RI_{EW} = 0$)
 31. Subterminal spot(s)/stripe in r cells: absent (0); slender in r3 (1) (Fig. 4G); indistinguishable (2) (Fig. 5B); longitudinal from r1 to r2 (3) (Fig. 4L); connected in r5-cua2 (4) (Fig. 5A) ($CI_{EW} = 0.67$, $RI_{EW} = 0.5$)
 32. Subterminal spot(s) in m cells: absent (0); larger and elongated in m1 & m3, slender in m2 (1) (Fig. 4B); connected in m1-m3 (2) (Fig. 3E); slender in m1 and m2, larger in m3 (3) (Fig. 4E); rounded at base of m1 (4) (Fig. 4N); rounded and white in m1 (5) (Fig. 5I); larger and elongated in m1 (6) (Fig. 5E); larger and rounded in m3 (7) (Fig. 5M); rounded in m3 (8) (Fig. 4H); larger and elongated in m3 (9) (Fig. 5N); indistinguishable (A) ($CI_{EW} = 0.39$, $RI_{EW} = 0.27$)
 33. Subterminal spots at cu cell: absent (0); rounded on cua1 (1) (Fig. 3H); rounded at base of cua1 (2) (Fig. 3F); larger and elongated in cua1 (3) (Fig. 4B); smaller and rounded on CuA2 (4) (Fig. 5C); larger and rounded on CuA2 (5) (Fig. 4D); rounded in cua2 (6) (Fig. 3N); connected cua1-cua2 (7) (Fig. 5B) ($CI_{EW} = 0.39$, $RI_{EW} = 0.21$)
 34. Longitudinal line on Sub-terminal: absent (0); from anterior to CuP (1) (Fig. 4I); from M2 to CuP (2) (Fig. 4K) ($CI_{EW} = 0.67$, $RI_{EW} = 0.5$)
 35. Spot(s)/Stripe on submedial zone: absent (0); in medial cell (1) (Fig. 4A); in sc (2) (Fig. 3N); in 1a+2a (3) (Fig. 4L); elongated to medial zone, one in sc and two in medial cell (4) (Fig. 4E); in medial cell elongate into medial zone and two spots in cu (5) (Fig. 4N); in sc and one from medial to cu (6) (Fig. 4K); rounded in cu (7) (Fig. 3G); in sc and medial cell (8); in medial cell and cu (9) (Fig. 4B) ($CI_{EW} = 0.47$, $RI_{EW} = 0.27$)

36. Spots(s)/stripe on medial zone: absent (0); two in medial cell (1) (Fig. 3A); in medial cell (2) (Fig. 3K); two in sc & 1a+2a (3) (Fig. 3L); single spot/stripe in cu (4) (Fig. 3D); two spots in medial and cu (5) (Fig. 4E); longitudinal line from anterior to posterior margin (6) (Fig. 4L); elongated from background in cu (7) (Fig. 5H); in sc (8) (Fig. 4N); rounded in sc and cu (9) (Fig. 4C); rounded in c, medial cell and cu (A) (Fig. 4D); rounded in sc, medial cell and cu (B) (Fig. 4I); in sc, two in cu (C) (Fig. 3N); elongated to ante-medial zone in cu and 1a+2a (D) (Fig. 5N); variable (E) (Fig. 4J) ($CI_{EW} = 0.39$, $RI_{EW} = 0.21$)
37. Spot(s)/stripe on ante-medial zone: absent (0); circular or elongated in cu (1) (Fig. 5M); circular in sc, medial cell and cu (2) (Fig. 5A); connected as a line from anterior margin to 1a+2a and a distinguishable spot at posterior margin (3) (Fig. 4I); a longitudinal line from anterior to posterior margin (4) (Fig. 4L); a spot in c, a stripe in medial cell and two in cu (5) (Fig. 4N); in medial cell and 1a+2a (6) (Fig. 4H); a stripe elongate from background in cu (7) (Fig. 5H); slender in 1a+2a (8) (Fig. 5G); slender in c, sc and cu (9) (Fig. 4D); slender in sc and cu (A) (Fig. 4C); slender in c, cu and 1a (B) (Fig. 3N); connected in medial cell and cu (C) (Fig. 5N); variable (D) (Fig. 4J); slender in c, medial cell and 1a+2a (E) (Fig. 5E); slender in medial cell, cu and 1a+2a (F) ($CI_{EW} = 0.47$, $RI_{EW} = 0.29$)
38. Spot(s)/stripe on sub-basal zone: absent (0); slender in medial cell (1) (Fig. 4D); slender or elongated in cu (2) (Fig. 3J); slender in c and medial cell (3) (Fig. 4K); slender in c and cu cells (4) (Fig. 4N); slender in cu and 1a+2a (5) (Fig. 5N); slender in sc, medial cell and 1a+2a (6) (Fig. 5A); longitudinal from anterior to posterior margin (7) (Fig. 4L); elongated from background in cu (8) (Fig. 5K); slender in c, cu and 1a+2a (9) (Fig. 4H); slender in medial cell and cu (A) (Fig. 4M); slender in c, medial cell and cu (B) (Fig. 4J); slender in sc and medial cell (C) (Fig. 4B) ($CI_{EW} = 0.48$, $RI_{EW} = 0.24$)
39. Spot(s)/stripe on basal zone: absent (0); circular or slender at base of Sc (1) (Fig. 4L); circular or slender at base of medial cell (2) (Fig. 4E); circular or slender at base of Sc and medial cell (3) (Fig. 4B) ($CI_{EW} = 0.23$, $RI_{EW} = 0.33$)
40. Colour filled from base of c to r4: absent (0); c to r4 filled (1) (Fig. 5H); base of c to half of R4+5 filled (2) (Fig. 5C); c, half of sc and r1 to r4 filled (3) (Fig. 5B) ($CI_{EW} = 0.43$, $RI_{EW} = 0.2$)
41. Colour filled in medial cell to m3: absent (0); medial cell to m3 filled (1) (Fig. 5H); medial cell to r5 filled (2) (Fig. 5D); cross line in medial cell (3) (Fig. 5A); half of medial cell to m3 filled (4) (Fig. 5B); medial cell filled (5) (Fig. 5F) ($CI_{EW} = 0.5$, $RI_{EW} = 0.44$)
42. Colour filled from base of cu to cua1: absent (0); cup and a1+a2 filled, elongated from cua2 to m2 at sub-margin and margin (1) (Fig. 5L); 1a+2a and posterior half of cua1+cup filled (2) (Fig. 5M); cua1 and posterior half of cua2 filled (3) (Fig. 5B) ($CI_{EW} = 1$, $RI_{EW} = 1$)

Hindwing

43. Hindwing Rs (equivalent to the character 54 in KAILA 2004): separated from Sc+R1 (0); R1 running into Sc, Rs laterally free (1) ($CI_{EW} = 0.5$, $RI_{EW} = 0.5$)
44. Cross-vein between Sc and R: absent (0); present (1) ($CI_{EW} = 0.5$, $RI_{EW} = 0$)
45. Range of apical dark patch: concolourous with other wing regions (0); margin upperside (1); margin (2); to middle (3) ($CI_{EW} = 0.2$, $RI_{EW} = 0.25$)
46. Ground colour: grey (0); white (1); yellow (2); brown (3) ($CI_{EW} = 0.11$, $RI_{EW} = 0.19$)

Abdomen

47. A2 spot: absent (0); present, round (1) ($CI_{EW} = 1, RI_{EW} = 0$)
 48. A3 spot: absent (0); present, round (1) ($CI_{EW} = 1, RI_{EW} = 1$)
 49. A4 spot: absent (0); present, round (1) ($CI_{EW} = 1, RI_{EW} = 1$)
 50. A5 spot: absent (0); present, round (1) ($CI_{EW} = 1, RI_{EW} = 1$)
 51. A6 spot: absent (0); present, round (1) ($CI_{EW} = 1, RI_{EW} = 0$)

Male genitalia

52. Uncus: present, sclerotized (0); present, membranous (1); absent (2) ($CI_{EW} = 0.29, RI_{EW} = 0.17$)
 53. Uncus shape: oblong (0); rounded (1) (POWELL 1973: fig. 51); rounded with a slightly concave top (2) (SATTLER 1967: fig. 3–1); rounded with a notch at apex (3) (POWELL 1973: fig. 58); two protuberances at apex (4) (POWELL 1973: fig. 67); rounded, separated and sclerotized (5) (POWELL 1973: fig. 88); protuberances slightly separated (6) (POWELL 1973: fig. 61); protuberances widely separated (7) (POWELL 1973: fig. 56); protuberances widely separated with apices tubular (8) (POWELL 1985: fig. 34); apical bifurcation extended to base with apices rounded (9) (HARPER *et al* 2002: fig. 13d); apical bifurcation extended to base with apices obtuse (A) (SATTLER 1967: fig. 19); apical bifurcation extended to base with apices sharp (B) (POWELL 1985: fig. 38); trifurcate (C) (POWELL 1973: fig. 82); ?? (D) (SATTLER 1967: fig. 62–1); paired with long processes (E) (DIAKONOFF 1967: fig. 387); paired, tongue-shaped (F) (KUN 2000: fig. 10) ($CI_{EW} = 0.48, RI_{EW} = 0.33$)
 54. Gnathos: present (0); absent (1) ($CI_{EW} = 0.13, RI_{EW} = 0.13$)
 55. Anterior gnathos: absent (0); present, single with little spine (1) (POWELL 1973: fig. 54); present, single with larger spine (2) (POWELL 1973: fig. 51); present, triangle with larger spine (3) (SATTLER 1964: fig. 23–1); paired (4) (SATTLER 1967: fig. 3–1) ($CI_{EW} = 0.19, RI_{EW} = 0.29$)
 56. Posterior part of gnathos: smooth (0); slight protruded with minute scobination (1) (SATTLER 1964: fig. 3–1); spherical, smooth (2) (HARPER *et al.* 2002: fig. 13d); variably differentiated posteriorly, minutely dentate anteriorly (3) (POWELL 1985: fig. 38); oblong with a row of sharp spines (4) (POWELL 1973: fig. 83); oblong with a row of stout spines (5) (SATTLER 1967: fig. 64–1); rounded with short scattered spines (6) (POWELL 1973: fig. 51); oblong with a row of long and sharp spines (7) (POWELL 1985: fig. 34); sharp with long arcuate spines (8) (SATTLER 1967: fig. 65–1); fan-like with small teeth caudally (9) (POWELL 1985: fig. 37); blade-like with a row of spines (A) (POWELL 1973: fig. 59) ($CI_{EW} = 0.33, RI_{EW} = 0.22$)
 57. Shape of basal process: absent (0); short, membranous (1) (POWELL 1973: fig. 58); short and stout, membranous (2) (POWELL 1973: fig. 54); triangular (3) (POWELL 1973: fig. 60); blade-like (4) (POWELL 1973: fig. 56); broad blade-like (5) (POWELL 1973: fig. 51); compressed triangular with a prominent caudal end (6) (POWELL 1985: fig. 45); oblong with basal part broad and caudal end slimmer (7) (SATTLER 1967: fig. 23–1); narrow and linear (8) (SATTLER 1967: fig. 68–1); linear and long (9) (KUN 2000: fig. 10); linear with a curved end (A) (POWELL 1985: fig. 42); linear, slightly “S”-shaped (B) (POWELL 1973: fig. 123); S-shaped with a long beak-like caudal end (C) (POWELL 1973: fig. 148); S-shaped, with very long and narrow caudal end (D) (POWELL 1973: fig. 75) ($CI_{EW} = 0.35, RI_{EW} = 0.2$)
 58. Cucullus: Angulate at apex (0) (POWELL 1985: fig. 33); protruded at apex and slightly curved downwards (1) (POWELL 1985: fig. 34); hooked, robust (2) (SATTLER 1967: fig. 30–1); spine-like, pointed downwards (3) (POWELL 1973: fig. 83); hooked, slender (4) (POWELL 1985: fig. 44); extending dorsally with irregular margin (5) (SATTLER 1967: fig. 68–1); extending dorsally, slender and slightly zigzag (6) (POWELL 1973: fig. 136); extending upwards with undulate mar-

- gin (7) (POWELL 1973: fig. 148); digital process extending posteriorly (8) (SATTLE 1967: fig. 3–1); slightly triangular extending upwards (9) (SATTLE 1967: fig. 62–1); compressed triangular, extending posteriorly (A) (DIAKONOFF 1967: fig. 387); digital, extending upwards and curved anteriorly (B) (POWELL 1985: fig. 45); broad triangular, curved upwards and anteriorly (C) (POWELL 1973: fig. 82); thick digital process, extending upwards and curved downwards (D) (POWELL 1973: fig. 51); triangular with a sharp apex (E) (POWELL 1973: fig. 58) ($CI_{EW} = 0.41$, $RI_{EW} = 0.26$)
59. Relative position of cucullus and sacculus apices: both almost equally distant from valval base (0) (POWELL 1973: fig. 51); cucullus more protruded than sacculus (1) (POWELL 1973: fig. 76); cucullus less protruded than sacculus (2) (DIAKONOFF 1967: fig. 387) ($CI_{EW} = 0.09$, $RI_{EW} = 0.19$)
60. Incision between cucullus and sacculus: deeply incised (0) (SATTLE 1967: fig. 30–1); slightly incised (1) (POWELL 1985: fig. 33); not incised (2) (POWELL 1973: fig. 51) ($CI_{EW} = 0.15$, $RI_{EW} = 0.35$)
61. Sacculus: attenuate toward caudal end (0) (SATTLE 1967: fig. 64–1); caudal end with a small angular process, ventral margin extruded (1) (POWELL 1985: fig. 33); caudal process short, ventral part broad (2) (POWELL 1973: fig. 83); caudal end rounded, ventral margin smooth (3) (SATTLE 1967: fig. 65–1); caudal end thick, ventral part fan-like (4) (POWELL 1973: fig. 164); caudal end absent, ventral part extruded and extended posteriorly (5) (POWELL 1973: fig. 148); caudal end absent, ventral part extruded and extended downwards (6) (SATTLE 1967: fig. 62–1); caudal end absent, ventral part triangular, extending downwards (7) (POWELL 1985: fig. 34); caudal end absent, ventral part quadrate, extended posteriorly (8) (POWELL 1973: fig. 123); semi-rounded (9) (POWELL 1985: fig. 44); orbicular (A); caudal end and ventral protuberance absent (B) (POWELL 1973: fig. 52); caudal end and ventral protuberance absent, oblong (C) (POWELL 1973: fig. 82); oblong, extending towards apex of cucullus (D) (DIAKONOFF 1967: fig. 397) ($CI_{EW} = 0.42$, $RI_{EW} = 0.28$)
62. Basal process of sacculus: absent (0); present (1) ($CI_{EW} = 1$, $RI_{EW} = 1$)
63. Costal subdivision: not prominent (0); elongate (1) (POWELL 1973: fig. 51); semi-triangular (2) (POWELL 1973: fig. 70) ($CI_{EW} = 0.5$, $RI_{EW} = 0.67$)
64. Saccus: absent (0); present (1) ($CI_{EW} = 0.2$, $RI_{EW} = 0$)
65. Setae on valva: only present on cucullus (0); present on both valva and cocullus (1); absent (2) ($CI_{EW} = 1$, $RI_{EW} = 0$)
66. Apical “claw-like” structure: absent (0) (POWELL 1973: fig. 87); present (1) (POWELL 1973: fig. 136) ($CI_{EW} = 0.25$, $RI_{EW} = 0.25$)
67. A differentiated dorsal shield of juxta (equivalent to the character 108 in KAILA 2004): absent (0); present, surrounding aedeagus (1) ($CI_{EW} = 1$, $RI_{EW} = 1$)
68. Coecum penis (equivalent to the character 111 in KAILA 2004): absent (0); present as a sac ventrad of basal opening of aedeagus (1) ($CI_{EW} = 1$, $RI_{EW} = 1$)
69. Curvature of aedeagus: straight (0); bended interiorly to 180° (1) (POWELL 1973: fig. 51); bended to be a circle (2) (POWELL 1973: fig. 70); bended to be a straight angle (3) (POWELL 1973: fig. 83) ($CI_{EW} = 0.21$, $RI_{EW} = 27$)

Female genitalia

70. Sterigma: not sclerotized (0) (POWELL 1973: fig. 186); sclerotized (1) (POWELL 1973: fig. 178) ($CI_{EW} = 0.13$, $RI_{EW} = 0.13$)
71. Apophysis anteriores: absent (0) (POWELL 1973: fig. 185); short (1) (POWELL 1973: fig. 183); long (2) (POWELL 1973: fig. 190) ($CI_{EW} = 0.13$, $RI_{EW} = 0.33$)

72. Ductus bursae: coil absent (0) (DIAKONOFF 1967: fig. 388); loosely coiled (1) (POWELL 1973: fig. 177); tightly coiled (2) (POWELL 1973: fig. 185) ($CI_{EW} = 0.11$, $RI_{EW} = 0.2$)
73. Distance between antrum and the coiled ductus bursae: short (0) (POWELL 1973: fig. 185); long (1) (POWELL 1973: fig. 184) ($CI_{EW} = 0.1$, $RI_{EW} = 0.25$)
74. Signum: present, single (0) (POWELL 1973: fig. 177); present, paired and symmetrical (1) (POWELL 1985: fig. 58); absent (2) (POWELL 1985: fig. 59) ($CI_{EW} = 0.29$, $RI_{EW} = 0$)
75. Ornamentation of signum: small, margin dentate (0) (POWELL 1973: Fig. 187); small, with little dentate (1) (POWELL 1973: fig. 177); larger, dentate inner (2) (POWELL 1985: fig. 52); larger, dentation absent (3) (POWELL 1973: fig. 184) ($CI_{EW} = 0.18$, $RI_{EW} = 0.26$)
76. Appendix bursae: absent (0); present (1) ($CI_{EW} = 0.33$, $RI_{EW} = 0.67$)

APPENDIX 3

Character change lists of the strict consensus tree obtained from EW analysis with colour pattern character inactivated. Node number correspond to those in Fig. 7A; each is followed by a list of character numbers and unambiguous state changes. Changes are listed only for the main clades. Single-width arrows indicate an ambiguous change and double-width arrows indicate a change that is unambiguous.

node_110 → node_58	57 0 ⇒ 3	71 2 ⇒ 1	
8 0 ⇒ 1	node_110 → node_109	7 0 ⇒ 4	
18 0 ⇒ 1	32 0 → 4	14 0 ⇒ 4	
19 1 ⇒ 0	53 0 → E	25 2 → 0	
53 0 → 9	61 0 → 6	28 0 ⇒ 5	
61 0 → D	63 0 ⇒ 1	30 0 ⇒ 2	
62 0 ⇒ 1	67 0 ⇒ 1	31 0 ⇒ 1	
6 2 → 4	68 0 ⇒ 1	32 0 → 7	
10 0 ⇒ 1	69 0 → 1	36 B ⇒ 2	
14 0 ⇒ 3	32 4 → 0	38 0 ⇒ 1	
21 0 ⇒ 5	58 C ⇒ E	58 E ⇒ A	
22 0 ⇒ 5	node_106 → node_105	61 6 ⇒ D	
23 0 ⇒ 2	9 0 → 1	64 1 ⇒ 0	
24 0 ⇒ 2	25 0 → 2	71 2 ⇒ 1	
25 0 ⇒ 5	36 0 → B	node_60 → <i>Chrysethmia</i>	
26 0 ⇒ 5	37 0 → A	<i>hypomelas</i>	
53 E ⇒ F	39 0 → 3	2 0 ⇒ 2	
57 0 ⇒ 9	59 0 ⇒ 2	28 3 → 5	
node_58 → <i>Depressaria</i>	node_109 → node_62	30 0 ⇒ 1	
<i>depressana</i>	6 1 → 2	31 0 ⇒ 1	
52 0 ⇒ 2	11 0 → 2	33 0 ⇒ 4	
58 C ⇒ 9	28 0 → 3	38 2 → A	
node_58 → <i>Agonopterix</i>	36 0 → 2	39 0 ⇒ 3	
<i>heracliana</i>	38 0 → 2	46 0 ⇒ 3	
21 0 ⇒ 1	58 C ⇒ 4	59 0 ⇒ 2	
22 0 ⇒ 1	61 6 → 9	61 9 ⇒ A	
23 0 ⇒ 1	69 1 → 3	65 1 ⇒ 2	
24 0 ⇒ 1	72 0 ⇒ 1	node_104 → node_103	
25 0 ⇒ 1	node_105 → node_104	9 1 → 0	
26 0 ⇒ 1	2 0 ⇒ 1	37 A → 0	
35 0 ⇒ 1	43 0 → 1	39 3 → 0	
36 0 ⇒ 1	46 0 → 2	72 0 ⇒ 2	
56 0 ⇒ 2	57 3 ⇒ 9	node_60 → node_59	
node_62 → node_61	node_104 → <i>Agrioceros</i>	5 0 → 1	
52 0 ⇒ 2	<i>magnificella</i>	21 0 → 2	
54 0 ⇒ 1	node_62 → node_60	22 0 → 2	
73 0 → 1	5 0 → 1	23 0 → 2	
77 1 → 3	7 0 → 2	24 0 → 2	
node_109 → node_108	37 0 ⇒ A	26 0 → 2	

37 0 → 1	32 0 → 4	36 B ⇒ C
46 2 → 0	36 0 → 4	37 3 ⇒ B
59 2 → 0	46 1 → 0	39 0 ⇒ 3
36 B → 4	72 2 ⇒ 1	46 1 ⇒ 2
57 9 ⇒ 2	node_87 → node_86	48 0 → 1
61 6 ⇒ B	57 2 ⇒ 3	49 0 → 1
node_96 → node_95	58 D → 0	50 0 → 1
node_108 → node_106	59 0 ⇒ 1	61 7 ⇒ 3
35 1 → 0	12 0 → 1	70 1 ⇒ 0
36 4 → 0	25 0 → 4	71 1 → 2
38 2 → 0	26 0 → 4	73 1 ⇒ 0
46 0 → 1	28 0 → 8	75 0 ⇒ 3
73 0 ⇒ 1	36 4 → 9	55 0 ⇒ 1
node_94 → node_88	38 0 → 3	58 5 → D
5 1 ⇒ 0	53 7 ⇒ 8	node_95 → node_94
6 1 → 0	56 9 ⇒ 4	9 1 ⇒ 0
25 2 → 0	58 0 → 1	21 2 ⇒ 0
26 2 → 0	61 B ⇒ 7	22 2 ⇒ 0
53 1 ⇒ 7	node_103 → node_102	23 2 ⇒ 0
71 2 ⇒ 1	node_102 → node_97	24 2 ⇒ 0
node_88 → node_69	7 0 → 2	72 1 ⇒ 0
2 1 ⇒ 2	12 5 → 2	node_84 → node_82
9 1 → 0	21 4 ⇒ 6	9 0 ⇒ 1
14 3 → 0	22 4 ⇒ 6	11 0 ⇒ 1
21 2 ⇒ 0	23 3 → 2	14 3 → 6
22 2 ⇒ 0	24 3 → 2	15 0 → 1
23 2 ⇒ 0	25 3 → 4	28 0 → 7
24 2 ⇒ 0	26 3 → 4	32 4 → 0
37 1 ⇒ 0	27 5 → 0	33 0 → 5
56 9 ⇒ 4	29 4 → 0	53 7 ⇒ 6
75 0 → 1	33 0 ⇒ 6	60 2 ⇒ 1
node_88 → node_87	35 6 ⇒ 2	node_86 → node_79