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Molecular and morphological phylogeny of European *Udea* moths (Insecta: Lepidoptera: Pyraloidea)

Richard Mally & Matthias Nuss

Senckenberg Natural History Collections, Museum of Zoology
Königsbrücker Landstraße 159, 01109 Dresden, Germany
[richard.mally@senckenberg.de]
[matthias.nuss@senckenberg.de]

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> Abstract

Udea Guenée, 1845, comprising more than 200 species, predominantly occurs in temperate Eurasia and the New World, with few representatives on the southern continents of the Old World. We present a first phylogenetic analysis for the genus, mainly based on European species. We applied Bayesian and Maximum Parsimony approaches to a combined dataset of *coxI* (1,415 bp) and *wingless* (363 bp) sequences as well as morphological characters. The analysis of the concatenated dataset partitions with Bayesian inference yielded a hypothetical tree with 26 well supported (posterior probability ≥ 0.95) monophyla. A clade including the genera *Deana*, *Mnesictena* and *Udeoides* from the southern continents of the Old World is found as sister group to *Udea*. European *Udea* species do not form a monophyletic group in itself. There are four monophyla found within European *Udea*, the *ferrugalis*, *itysalis*, *alpinalis*, and *numeralis* species groups. These are well supported by molecular and morphological data. According to morphology, all four species groups have representatives also in other parts of the Holarctic region. Our data support the hypothesis that all *Udea* species endemic to oceanic islands in the Atlantic and Pacific belong to the *ferrugalis* group and all those endemic to the European Alps to the *alpinalis* group. Our data imply that the ancestors of two island species (*Udea azorensis*, *U. delineatalis*) have colonised the respective islands via ocean surface currents. Altogether, we are able to place 54 of the 213 described *Udea* species into species groups.

> Key words

Pyraloidea, Spilomelinae, *Udea*, Europe, species groups, phylogeny, morphology, *coxI*, *wingless*.

1. Introduction

Pyraloidea (snout moths) form one of the larger family groups of Lepidoptera, comprising nearly 16,000 described species. They are ditrysian moths and within this lineage well supported as a monophyletic group by the presence of a characteristic abdominal tympanal organ (Munroe & Solis 1998). Molecular-based phylogenetic analyses support the monophyly of Pyraloidea as well as their sister group relationship to Macrolepidoptera (Regier et al. 2009; Mutanen et al. 2010). Within the diverse group of snout moths, morphology-based phylogenetic analyses are available at subfamily level (Solis & Mitter 1992; Solis & Maes 2003), at genus level (Landry 1995; Sutrisno 2002a; Hayden 2009; Mally & Nuss 2010) and at species level (Clavijo 1990; Sutrisno 2002b). Otherwise, the current classification is still dominated by traditional typological concepts that lead to oversplitting into more than 2,000 genera.

Among the pyraloid genera, *Udea* Guenée, 1845 is one of the most speciose. It contains more than 200 species, which predominantly occur in temperate Eurasia and in the New World. In addition, there are less than 10 Afrotropical species and one species known from Australia. A remarkable number of endemic species occurs on islands in the Pacific and Atlantic Oceans, with 41 species on the Hawaiian Islands, two endemic species on Juan Fernandez Islands and one endemic species each on the Azores, Madeira, the Ca-

nary Islands, St. Helena, and Tristan da Cunha (NUSS et al. 2011).

Five species from Africa south of the Sahara formerly treated in *Udea* were placed in the separate genus *Udeoides* by MAES (2006). The monotypic *Deana* Butler, 1879 and *Mnesictena* Meyrick, 1884 with seven species, all occurring in New Zealand, are supposedly closely related to *Udea*. *Mnesictena* was regarded as a synonym of *Udea* by MUNROE (1983), a decision which was not followed by DUGDALE (1988).

Adults of all these genera are medium sized moths. Their fore wing length ranges from 9 mm (e.g., *U. numeralis*) to 14 mm (e.g., *U. maderensis*). The larval food plants are unknown for many species, but the larvae of those with a better known life cycle are usually polyphagous or at least oligophagous, mainly feeding on Apiaceae, Asteraceae, Lamiaceae, Plantaginaceae and Rosaceae (HANNEMANN 1964).

Adult morphology is fairly uniform and there is currently no available hypothesis on phylogenetic relationships, neither among the genera *Deana*, *Mnesictena*, *Udea* and *Udeoides* nor among species of the genus *Udea*. This group of genera is usually assigned to the subfamily Spilomelinae of Crambidae (MUNROE 1995; SOLIS & MAES 2003) based on several characters such as absence of chaetosemata, bilobed praecinctorium, fornix tympani projecting and absence of a gnathos (MINET 1982). None of the characters assigned to Spilomelinae is unique, but shared with other pyraloid taxa, and there is no phylogenetic study to confirm this placement. Important taxonomic contributions on *Udea* were published by MUNROE (1950, 1966, 1989, 1995), ZIMMERMAN (1958), HASENFUSS (1960), HANNEMANN (1964), INOUE (1982), YAMANAKA (1988), and INOUE et al. (2008). Few attempts to classify *Udea* resulted in the recognition of the *U. itysalis*, *U. lugubralis* and *U. orbicentralis* species groups, altogether containing 17 species (MUNROE 1966; YAMANAKA 1988; INOUE et al. 2008).

In this paper we present the results from the first phylogenetic analysis on *Udea*. We use both molecular and morphological data, the latter mainly being derived from male and female terminalia and wing pattern elements. In the first step of the work here documented, our sampling has strongly focussed on Eurasian *Udea* species.

2. Material and methods

2.1. Taxon sample and character systems

The main source of material for this study is pinned and dried museum specimens. This source has the advantage to contain a large number of taxa of interest, but the disadvantage that DNA is more degraded the older the specimens are. Due to the fact that numerous species are only known from old material, molecular investigations are of poor or no success at all. Moreover, targeted search for *Udea* species in the field has proven to be difficult because information on biology and ecology is very limited. As a result, we were able to obtain only a restricted number of *Udea* species for this study.

In total 33 *Udea* species (one represented by 2 subspecies) and 7 pyraloids from other genera have been investigated. Our *Udea* sample includes 27 (out of 35 known) European species and 6 from outside Europe: *U. delineatalis* (St. Helena), *U. itysalis* (Nearctic, East Palaearctic), *U. lugubralis* (East Palaearctic) as well as the Hawaiian *U. heterodoxa*, *U. liopis*, and *U. pyranthes*. One species each from *Deana*, *Mnesictena*, and *Udeoides*, all supposedly closely related to *Udea*, were investigated. We comprise these three taxa plus *Udea* as "*Udea* s.l.". The pyralid *Synaphe punctalis* (Pyralidae: Pyralinae), as well as the crambids *Haritalodes derogata*, *Agrotera nemoralis*, and *Mecyna lutealis* (Crambidae: Spilomelinae) were included as species distantly related to *Udea*; among these, *Synaphe* is most distantly related and therefore defined as outgroup taxon (see also 2.4.). An overview of the investigated material is given in Tab. 1.

We have investigated morphological and molecular characters of the same specimen using the method of KNÖLKE et al. (2005). Their protocol suggests digesting the abdomen using proteinase K. After digestion, the solution is taken for DNA isolation and the cleared exoskeleton, including terminalia, for morphological studies. Morphological features of the wings and the genitalia as well as nucleotide sequences of the mitochondrial, protein-coding *cytochrome oxidase subunit I* (*coxI*) gene and the nuclear, protein-coding *wingless* (*wg*) gene were obtained.

2.2. DNA methods

Total DNA was isolated from the specimens' abdomen from the solution yielded by proteinase K treatment of the abdomen using the NucleoSpin Tissue kit by Macherey-Nagel according to the manufacturer's protocol.

PCR was performed in either of two ways: **(1)** Use of SAWADY Taq DNA polymerase (PeqLab), initial denaturation for 5 min at 95°C, 40 cycles with denaturation for 30 sec at 94°C, annealing for 30 sec at 48°C (*coxI*) or 51°C (*wingless*) and extension for 90 sec at 72°C and a final extension period of 10 min at 72°C. **(2)** Use of BIO-X-ACT Short DNA polymerase

(Bioline) according to the manufacturer's recommendations and with the respective annealing temperature for the used primer pair.

All primers used in this study were chosen according to Wahlberg & Wheat (2008). The *coxI* gene was amplified using the primer pairs LCO/HCO or LCO/Nancy and Jerry/Pat. In the case of fragmentation of the *coxI* gene the PCR was performed with additional intermediary primers to amplify shorter DNA fragments: LCO/K699, Ron/Nancy, Jerry/Mila and Brian/Pat. The nuclear *wingless* gene was amplified using the LepWg1/LepWg2 primer pair.

Amplification success of the PCR was controlled using Agarose gel electrophoresis, subsequent gel dyeing with ethidium bromide and final analysis of DNA bands by visualisation under ultraviolet light.

Clean-up of the PCR products was done using ExoSAP-IT (USB Corporation) according to the manufacturer's recommendations. The sequence PCR was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). After the final clean-up of the samples, the sequences were obtained from the sample analysis on a 3130 Genetic Analyzer (Applied Biosystems).

For both the initial PCR amplification and the sequence PCR as well as for the ExoSAP-IT product clean-up either a Mastercycler ep gradient S (Eppendorf) or a PCR System 9700 (GeneAmp) was used.

DNA sequences were proofread by eye and aligned manually using PhyDE0995 (Müller et al. 2008). In total, 41 *coxI* sequences (1,415 bp) and 35 *wingless* sequences (363 bp) have been acquired. For most of the taxa, the *coxI* sequence comprises an internal sequence gap because of insufficient overlap of the two sequenced *coxI* fragments. Due to this gap, a fragment of 44 bp (basepairs 636–679 from 5' end) was consequently cut out from all sequences for the phylogenetic analyses. No indels were found in any sequence. All sequences have been submitted to GenBank (see Tab. 1 for accession numbers). In all sequences comprising the internal gap, this gap was filled with 'N' (stands for 'nucleotide' in IUPAC ambiguity code), which led to a maximum length of 1,459 bp for the submitted *coxI* sequences. For phylogenetic analysis the aligned sequence dataset was arranged in a NEXUS file.

2.3. Morphological methods

Dissection of genitalia was performed according to Robinson (1976). Morphological structures were investigated using a stereomicroscope. Photographic documentation of genitalia was done using a Nikon Eclipse E600 Microscope in combination with a Zeiss AxioCam MRc5 camera and AxioVision programme (Version 4.4) on a Windows PC. Characters were coded and their states scored in form of a character matrix (see section 4. and Tab. 2).

The female genitalia consist of an anterior corpus bursae (a saccate widening of the ductus bursae), followed posteriad by the ductus bursae. Its posterior part is composed of the junction with the ductus seminalis, followed by the colliculum and most posteriorly by the antrum.

The male genitalia consist of a dorsal tegumen (modified tergite IX) and a ventral vinculum (modified sternite IX). One valva per side is attached to the vinculum. *In situ*, the valvae have a posteriad orientation, but are opened for embedding on a dissection slide. Often, the valvae comprise an anteriodorsally attached, claw-shaped fibula (also called clasper) on their proximal side. The tegumen bears a dorsal uncus, which shows an apical bulbous thickening with ventrally orientated setae in the genus *Udea*. A juxta is attached mediodorsally to the vinculum, serving as foothold for the phallus. The vesica is everted from the phallus posteriorly during copulation. During dissection the phallus is detached from the juxta and it is separately embedded on the same slide.

The terminology of genitalia follows Kristensen (2003).

2.4. Phylogenetic analyses

The acquired data were arranged in three NEXUS files: (1) a molecular dataset with two partitions, i.e. sequence data for the genes *coxI* and *wingless*; (2) a morphological dataset, comprising the morphomatrix; and (3) a combined dataset with the two sequence data partitions and the morphological data as a third partition.

Phylogenetic analyses were performed via Bayesian inference using the programme MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Settings for analysis of the molecular data were chosen to fulfil the parameters of the GTR+G+I model: number of states ("nst") = 6; among site rate variation ("rates") = gamma-shaped rate variation with a proportion of invariable sites ("invgamma"). For the morphological data partition, parameters were set to fulfil gamma shaped rate variation. Model parameters for substitution rates, stationary nucleotide frequencies, shape parameter of the gamma distribution and proportion of invariable sites were unlinked in order to allow each partition to have its own set of parameters. In each dataset, overall rate was allowed to vary across the different partitions. The number of generations was set to 2 million for the molecular and the morphological dataset and to 7 million for the combined dataset, with sampling of every 100th generation. This lead to 20,001 saved

Tab. 1. Investigated material.

Taxon	Collection	Genitalia prep. ♂	Genitalia prep. ♀	*coxI* GenBank accession no.	*wg* GenBank accession no.
Synaphe punctalis (Fabricius, 1775)	MTD	186, 326	327	JF497027	JF497068
Agrotera nemoralis (Scopoli, 1763)	MTD	242	174	JF497028	JF497069
Deana hybreasalis (Walker, 1859)	NZAC	075	076	JF497029	JF497070
Haritalodes derogata (Fabricius, 1775)	MTD	413	415	JF497030	JF497071
Mecyna lutealis (Duponchel, 1833)	MTD	237	162	JF497031	JF497072
Mnesictena marmarina Meyrick, 1884	NZAC	077	078	JF497032	JF497073
Udeoides muscosalis (Hampson, 1913)	MTD	007, 187	(MAES 2006: 131–132, fig. 3B)	JF497033	JF497074
Udea accolalis (Zeller, 1867)	MTD, TLMF	141, 143	066, 145	JF497034	JF497075
Udea alpinalis (Denis & Schiffermüller, 1775)	AW, MTD	003, 046, 081	004, 113, 221	JF497035	JF497076
Udea austriacalis (Herrich-Schäffer, 1851)	MTD, TLMF	009, 069	010, 050, 114	JF497036	JF497077
Udea azorensis Meyer, Nuss & Speidel, 1997	MM	182	159	JF497037	–
Udea bourgognealis Leraut, 1996	ZMUC	160, 161	196	JF497038	JF497078
Udea carniolica Huemer & Tarmann, 1989	SG, MTD, TLMF	034, 146, 147, 148	88I194 (PT, TLMF)	JF497039	JF497079
Udea costalis costalis (Eversmann, 1852)	MTD	194	193	JF497040	–
Udea costalis maurinalis (W.P. Curtis, 1934)	TLMF, ZMUC	151	103, 150, 152	JF497041	JF497080
Udea decrepitalis (Herrich-Schäffer, 1848)	MTD, TLMF	031, 061, 222	032	JF497042	JF497081
Udea delineatalis (Walker in Meliss, 1875)	MTD	–	074, 170	JF497043	–
Udea ferrugalis (Hübner, 1796)	MTD	017, 062, 105, 220, 282	018, 219	JF497044	JF497082
Udea fimbriatralis (Duponchel, 1833)	JDA, ZMHB	190, 191, 198	188	JF497045	JF497083
Udea fulvalis (Hübner, 1809)	AS, MTD	019, 132, 216	020, 022, 129, 208, 215	JF497046	JF497084
Udea hamalis (Thunberg, 1792)	MTD, ZIS	025, 157	026, 158	JF497047	JF497085
Udea heterodoxa (Meyrick, 1899)	UHIM	176	(ZIMMERMAN 1958: fig. 163)	JF497048	JF497086
Udea inquinatalis (Lienig & Zeller, 1846)	MTD, TLMF	029, 048, 055	030	JF497049	JF497087
Udea institalis (Hübner, 1819)	AS, AW, MTD	040, 079, 080	045	JF497050	JF497088
Udea itysalis (Walker, 1859)	JDO	243	244, 245	JF497051	JF497089
Udea languidalis (Eversmann, 1842)	TLMF, ZMHB	092, 095, 163, 199	93, 104, 133	JF497052	JF497090
Udea liopis (Meyrick, 1899)	UHIM	178	177	JF497053	JF497091
Udea lugubralis (Leech, 1889)	NKUM	172	171	JF497054	JF497092
Udea lutealis (Hübner, 1809)	MTD	015, 049, 057, 115	016	JF497055	JF497093
Udea maderensis (Bethune-Baker, 1894)	MTD, ZMUC	044, 070, 127	043, 065	JF497056	–
Udea murinalis (Fischer von Röslerstamm, 1842)	MTD, TLMF	023, 149	024	JF497057	JF497094
Udea nebulalis (Hübner, 1796)	MTD	033, 054, 067, 082, 109, 111	008, 110	JF497058	JF497095
Udea nordmani (Rebel, 1935)	FMNH	NLW 4011 (HT, FMNH), 126, 173	125	JF497059	–
Udea numeralis (Hübner, 1796)	MTD, ZMUC	085, 153, 192	035, 036, 156	JF497060	JF497096
Udea cf. *numeralis*	FMNH	200	189, 201	JF497061	–
Udea olivalis (Denis & Schiffermüller, 1775)	MTD, TLMF	013, 168	014, 072	JF497062	JF497097
Udea prunalis (Denis & Schiffermüller, 1775)	MTD	011, 108, 372, 373	012, 068, 107	JF497063	JF497098
Udea pyranthes (Meyrick, 1899)	UHIM	181	179	JF497064	JF497099
Udea rhododendronalis (Duponchel, 1834)	MTD, TLMF	005, 047, 056	006	JF497065	JF497100
Udea rubigalis (Guenée, 1854)	GB	175	180	JF497066	JF497101
Udea uliginosalis (Stephens, 1834)	MTD, TLMF	001, 059, 112	002, 106, 166	JF497067	JF497102
Udea ardekanalis Amsel, 1961	SMNK	Amsel GU3582 (HT, SMNK)	–	–	–
Udea bipunctalis (Duponchel, 1832)	ZMHB	094	100	–	–
Udea catilualis (Hampson, 1900)	ZMHB	164, 360	–	–	–
Udea confinalis (Lederer, 1858)	ZMHB, ZMUC	089, 102	101	–	–
Udea cyanalis (La Harpe, 1855)	MTD, TLMF, ZMHB	116, 129	117, 119, 121	–	–
Udea praepetalis (Lederer, 1869)	ZMHB	405 (ST)	406	–	–
Udea sviridovi Bolshakov, 2002	ZMMU	197 (PT), 323 (HT)	–	–	–
Udea tachdirtalis (Zerny, 1935)	NMW	214	209	–	–
Udea tritalis (Christoph, 1881)	ZMHB	320 (ST)	321 (ST)	–	–
Udea zernyi (Klima in Zerny, 1940)	ZMUC	135, 136	134, 137	–	–

trees for the molecular and the morphological datasets and to 70,001 saved trees for the combined dataset in total after completion of the runs. Ten per cent of the saved trees, i.e. 2,000 of the 20,001 and 7,000 of the 70,001 acquired trees, were deleted as burn-in proportion for the datasets, which resulted in 18,001 trees for the molecular and the morphological datasets and 63,001 trees for the combined dataset remaining for analysis. A posterior probability (PP) of ≥ 0.95 is regarded as sufficient statistical support for a monophylum.

In addition, Maximum Parsimony (MP) analyses using PAUP* 4.0b10 (Swofford 2003) in combination with the PaupUp 1.0.3.1 Beta graphical interface for Microsoft Windows systems (Calendini & Martin 2005) were performed for the molecular and the morphological dataset. For each dataset a heuristic search was undertaken, setting the number of trees to be saved to auto-increase for the molecular dataset and to 5,000 without further increment for the morphological dataset. The following settings were identical for both datasets: starting trees for branch-swapping via stepwise addition; random addition sequence with 10 repetitions; Tree Bisection and Reconnection (TBR) swapping algorithm. For estimation of clade supports, resampling via Jackknife was performed. 1,000 replicates with deletion of 25% of characters per replicate were performed for each dataset. A Jackknife proportion (JK) of ≥ 75% is regarded as sufficient statistical support for a monophylum.

In all phylogenetic analyses, *Synaphe punctalis* was defined as outgroup taxon and the root of the trees placed accordingly. The spilomeline species *Agrotera nemoralis*, *Haritalodes derogata* and *Mecyna lutealis* served as control taxa in order to evaluate the plausibility especially of the morphological phylogeny. Therefore, they were not explicitly defined as outgroup taxa.

3. Abbreviations

Morphology

(x : y)	(character : character state)
ant	antrum
cb	corpus bursae
cl	colliculum
co	cornutus / -i
db	ductus bursae
de	opening of ductus ejaculatorius
dr	dextrally projecting short denticulate ridge of praephallus
ds	ductus seminalis
ea	anterior projection of ductus bursae
ep	posterior projection of ductus bursae
fi	fibula
fsd	colouration of fore wing stigmata darker than ground colour
fsi	colouration of fore wing stigmata identical with ground colour
ga	granulated area of praephallus
hp	ventrally projecting tooth- to hook-shaped process of praephallus
js	median apical split of juxta
ju	juxta
pl	postmedial line of fore wing with loop
pr	postmedial line of fore wing with rectangular or less angled bow
ps	longitudinal, twined split of praephallus
rs	transversal signum ridge
sa	accessory signum
scl	partial sclerotisation of ductus bursae
sp	posterior arm of signum
sv	dark spots at end of veins Sc and R_{1-4} of fore wing
un	uncus
va	valve
ve	vesica (endotheca) with cluster of small cornuti on its surface

Museums and Collections

AS	coll. Andreas Stübner (Germany)
AW	coll. Andreas Werno (Germany)
FMNH	Finnish Museum of Natural History, Helsinki (Finland)
GB	coll. George Balogh (U.S.A.)
JDA	coll. Jordi Dantart (Spain)
JDO	coll. Jason Dombroskie (Canada)
MM	coll. Marc Meyer (Germany)
MTD	Museum für Tierkunde Dresden (Germany)
NKUM	College of Life Sciences, Nankai University, Tianjin (China)
NMW	Naturhistorisches Museum Wien (Austria)
NZAC	New Zealand Arthropod Collection, Auckland (New Zealand)
SG	coll. Stanislav Gomboc (Slovenia)
SMNK	Staatliches Museum für Naturkunde, Karlsruhe (Germany)
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck (Austria)
UHIM	University of Hawaii Insect Museum, Mānoa (U.S.A.)
ZIS	Zoological Institute St. Petersburg (Russia)
ZMHB	Zoologisches Museum, Humboldt-University Berlin (Germany)
ZMMU	Zoological Museum, Moscow State University (Russia)
ZMUC	Zoological Museum, University of Copenhagen (Denmark)
ZSM	Zoologische Staatssammlung Munich (Germany)

Others

C-	Central-
E-	East-
HT	holotype
JK	jackknife
MP	Maximum Parsimony
Nea	Nearctic region
Neo	Neotropical region
NZ	New Zealand
Pal	Palaearctic region

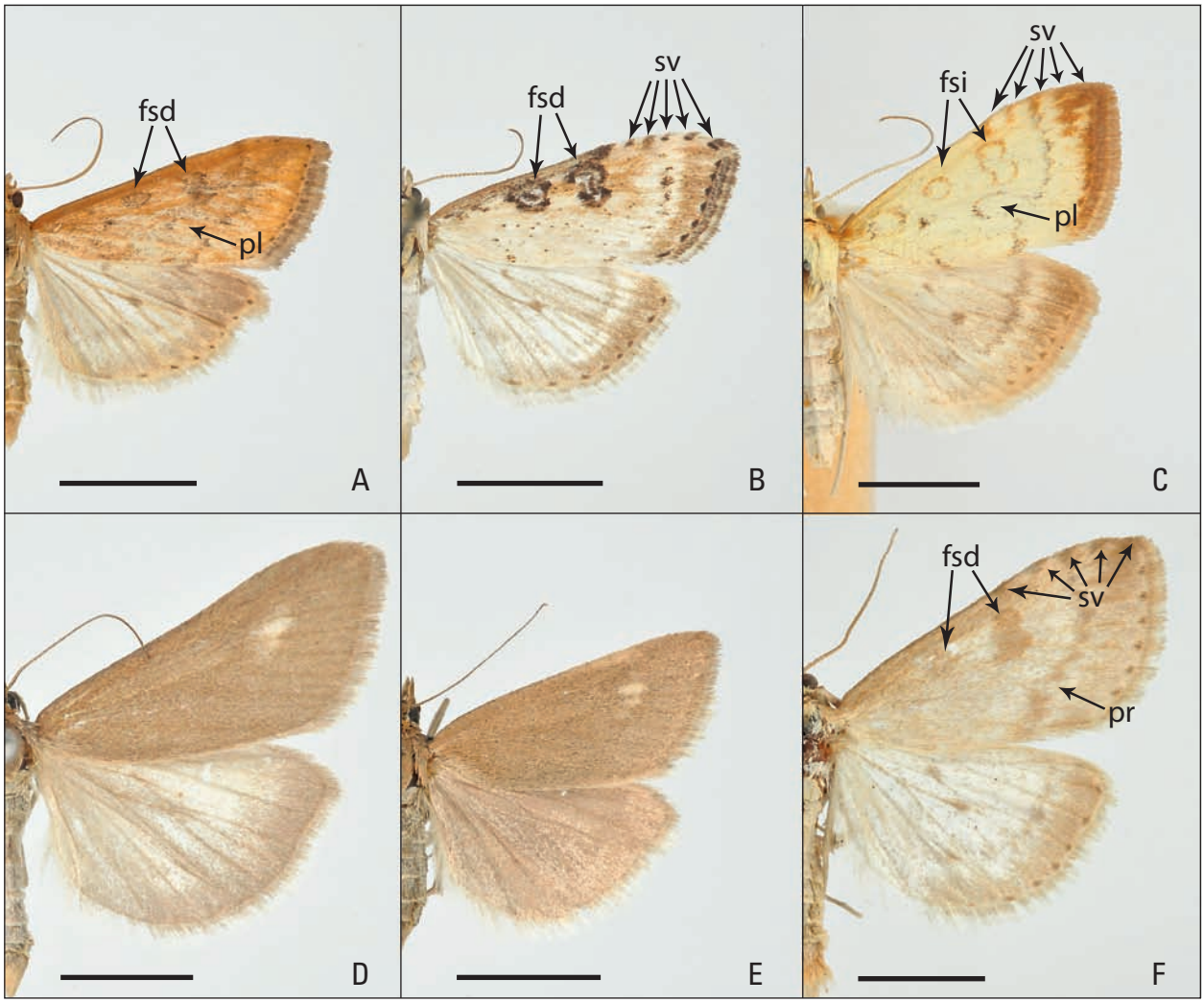

Fig. 1. Characters of wings (dorsal view). **A**: *Udea ferrugalis*; **B**: *U. costalis*; **C**: *U. institalis*; **D–E**: *U. uliginosalis*, D: male, E: female; **F**: *U. decrepitalis*. (Scale bars: 5 mm)

PP	posterior probability of Bayesian inference
PT	paratype
S-	South-
SE-	Southeast-
ST	syntype
SW-	Southwest-
W-	West-

4. Results

4.1. Analysis of molecular dataset

The MP and Bayesian analyses both resulted in a largely resolved tree, with only few polytomies. The two are fully congruent, though some nodes are present in one analysis but not in the other. Fig. 4 shows the tree resulting from both analyses, the nodes only supported in one analysis being additionally included (with "–" above or below branches as indication for absence of the respective support value). This tree altogether includes 35 monophyletic groups, 22 of which have PP support of ≥ 0.95 and 25 have JK support of ≥ 75%. In Fig. 4, polytomies are found at node 4 (3 branches) and at node 7 (4 branches).

Monophyly of *Udea* s.l. (1.00 PP, 98% JK; node 1 in Fig. 4) and *Udea* s.str. (0.99 PP, 75% JK; node 3) is well supported. A clade including *Udeoides muscosalis* from Africa as well as *Deana hybreasalis* and *Mnesictena marmarina* from New Zealand is weakly supported as monophyletic (0.71 PP; node 2), being the sister group to *Udea* s.str.

Within *Udea*, there is a basal dichotomy into the *U. ferrugalis* group (1.00 PP, 99% JK; node 4) and a monophylum containing three well-supported species groups (1.00 PP, 61% JK; node 5) and a few other species. The latter clade splits into the *U. itysalis* group (1.00 PP, 100% JK; node 6) and a polytomic group (1.00 PP, 99% JK; node 7) containing the *U. numeralis* group (1.00 PP, 59% JK; node 8), the *U. alpinalis* group (1.00 PP, 95% JK; node 9), a monophy-

lum comprising *U. decrepitalis*, *U. inquinatalis*, *U. hamalis*, *U. prunalis*, and *U. rhododendronalis* (0.54 PP, 53% JK), as well as the species pair *U. lutealis* and *U. olivalis* (62% JK).

4.2. Analysis of morphological dataset

Twenty-four morphological characters of adults were investigated, of which five refer to the wing pattern (characters 1–5), twelve to the male genitalia (characters 6–17) and seven to the female genitalia (characters 18–24). All characters have a binary coding. The character matrix is shown in Tab. 2.

Characters of the wings

01. Fore wing – postmedial line: with loop (0) (pl in Fig. 1A,C); with rectangular or less angled bow (1) (pr in Fig. 1).
02. Fore wing – colouration of discoidal stigmata: identical with ground colour of wing (0) (fsi in Fig. 1C); darker than ground colour of wing (1) (fsd in Fig. 1A,B,F).
03. Fore wing – apical dark spots at end of veins Sc and R_{1-4}: absent (0) (Fig. 1A,D,E); present (1) (sv in Fig. 1B,C,F).
04. Wings – intersexual size difference: in female wing length and shape of fore wing apex as in male (0); in female wing length reduced and fore wing apex more pointed as compared to male (1) (Fig. 1D,E).
05. Hind wing – intersexual colouration difference: equally dark in female and in male (0); darker in female than in male (1) (Fig. 1D,E).

Characters of the male genitalia

06. Cornuti in phallus: absent (0) (Fig. 2K,L); present (1) (co in Fig. 2E,G–J).
07. Number of cornuti: 1–2 (0) (Fig. 2E,G); ≥ 4 (1) (Fig. 2H,J). (A condition with three cornuti was not found.)
08. Praephallus – sclerotised ridge: absent (0) (Fig. 2E–J); present (1) (Fig. 2K,L).
09. Praephallus – location and shape of sclerotised ridge: ventrally projecting tooth- to hook-shaped process (0) (Fig. 2L); dextrally projecting short denticulate ridge (1) (Fig. 2K).
10. Praephallus – sclerotised, granulated area: absent (0) (Fig. 2G,K,L); present (1) (ga in Fig. 2H,J).
11. Praephallus – location of sclerotised, granulated area: most posteriorly (0) (ga in Fig. 2H); distad from posterior end (due to posteriad elongation of the praephallus) (1) (ga in Fig. 2J).
12. Vesica (endotheca) – cluster of small cornuti at posterior end of uneverted vesica (close to the junction of vesica and praephallus): absent (0) (Fig. 2H–L); present (1) (ve in Fig. 2G).
13. Praephallus – ventrally with longitudinal, twined split: absent (0) (Fig. 2G,K,L); present (1) (ps in Fig. 2H,J).
14. Opening of ductus ejaculatorius in the phallus: anterior (0) (de in Fig. 2F); anterodorsal (1) (de in Fig. 2E).
15. Juxta – median apical split: absent (0) (Fig. 2A); present (1) (js in Fig. 2D).
16. Fibula: absent (0) (Fig. 2C); present (1) (fi in Fig. 2A,B).
17. Uncus – apex with bulbous thickening: absent (0) (Fig. 2B); present (1) (un in Fig. 2A,C).

Characters of the female genitalia

18. Posterior arm of signum: elongated towards a bodkin-shaped acute tip (0) (sg in Fig. 3A); convex sides, converging towards a rounded tip (1) (sg in Fig. 3B,C).
19. Transversal signum ridge: absent (0) (Fig. 3B); present (1) (rs in Fig. 3A,C).
20. Accessory signum anterior of ductus bursae: absent (0) (Fig. 3A,B); present (1) (sa in Fig. 3C).
21. Ductus bursae – projection at anterior end: absent (0) (Fig. 3A,C); present (1) (ea in Fig. 3B).
22. Ductus bursae – projection at posterior end: absent (0) (Fig. 3B,C); present (1) (ep in Fig. 3A).
23. Ductus bursae – length: as long as or longer than corpus bursae (0) (db in Fig. 3B,C); conspicuously shorter than corpus bursae (1) (db in Fig. 3A).
24. Ductus bursae – sclerotisation (excluding the colliculum): completely membranous (0) (Fig. 3A); partly sclerotised (1) (sc in Fig. 3B,C).

The phylogenetic analysis of the morphological data using MP resulted in a rather poorly resolved phylogeny with sufficient statistical support for few monophyla (Fig. 5B), while the Bayesian analysis yields better resolution in some parts of the tree (Fig. 5A). The Bayesian phylogeny contains 11 unique apomorphies supporting 10 monophyla. In contrast, the MP phylogeny comprises 7 unique apomorphies supporting 6 monophyla.

Neither *Udea* s.l. nor *Udea* s.str. is found to be monophyletic. Monophyly of the *U. ferrugalis* group is only found in the Bayesian analysis (0.64 PP, node 4), with the Hawaiian species arising separately from a basal polytomy, while the remaining species form a clade (0.56 PP). A highly congruent topology of the MP and Bayesian phylogenies is found only for the monophylum comprising the *U. itysalis* group, *U. numeralis* group, and *U. alpinalis* group as well as the species *U. prunalis*, *U. inquinatalis*, *U. decrepitalis*

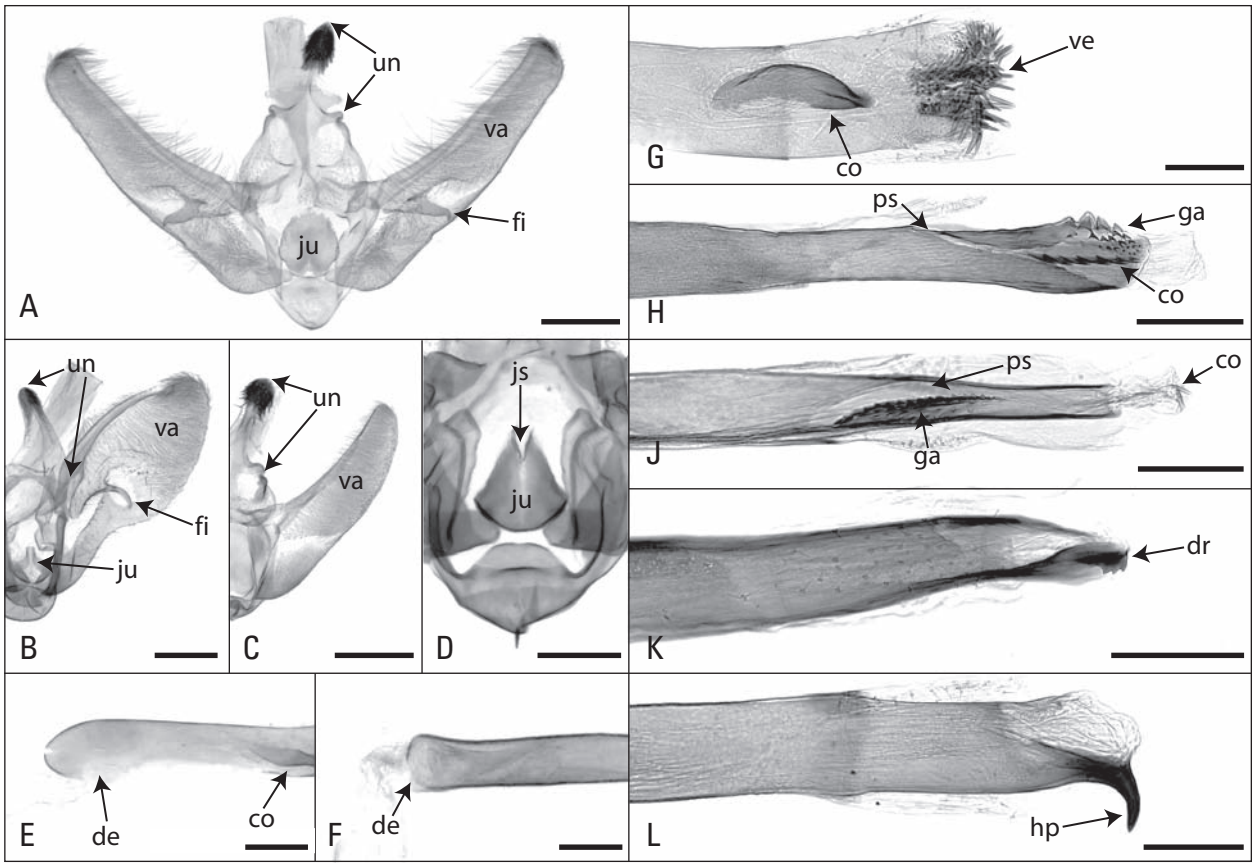

Fig. 2. Characters of male genitalia. **A–D:** Terminalia (caudal view), **A**: *Udea maderensis*, **B**: *Mecyna lutealis*, **C**: *Udea heterodoxa*, **D**: *U. nebulalis*. **E–F:** Anterior phallus (lateral view, left side: anterior, bottom: ventral), **E**: *U. ferrugalis*, **F**: *U. institalis*. **G–L:** Posterior phallus (G–J,L: lateral view, left side: anterior, bottom: ventral; K: ventral view, left side: anterior, bottom: dextral), **G**: *U. maderensis*, **H**: *U. fulvalis*, **J**: *U. languidalis*, **K**: *U. alpinalis*, **L**: *U. uliginosalis*. (Scale bars: A–D 500 μm; E–L 200 μm)

and *U. hamalis* (0.98 PP, 86% JK, node 5). In the MP phylogeny, the *U. itysalis* group is sister to the remaining *Udea* species included in this large clade, but monophyly of these "remaining taxa" is weakly supported (55% JK). In contrast, in the Bayesian phylogeny the *U. itysalis* group is one branch of a polytomy that otherwise gives rise to the *U. numeralis* group, the *U. alpinalis* group, *U. prunalis* and the clade *U. inquinatalis* + *U. decrepitalis* + *U. hamalis*. Monophyly of the *U. itysalis* group is moderately to well supported, respectively (0.79 PP, 81% JK, node 6), but the sister group relationship of *U. costalis costalis* and *U. c. maurinalis* is poorly supported (0.53 PP, 54% JK).

The *U. alpinalis* group is well supported in both analyses (0.99 PP, 95% JK, node 9). In the Bayesian phylogeny, *U. alpinalis*, *U. nebulalis*, *U. uliginosalis*, *U. bourgognealis* and *U. rhododendronalis* form an additional, weakly supported suclade (0.56 PP) within the *U. alpinalis* group. In both topologies, a monophylum comprising the species pair *U. decrepitalis* and *U. hamalis* (0.55 PP, 64% JK) and their sister species *U. inquinatalis* (0.56 PP, 69% JK, congruent with node 10 in Fig. 4 with exception of *U. prunalis*) is sister to the *U. alpinalis* group.

In the Bayesian phylogeny, the *U. numeralis* group forms a weakly supported monophylum (0.54 PP, node 8) with the species pair *U. numeralis* and *U.* cf. *numeralis* (0.83 PP) being sister to the moderately supported polytomic monophylum (0.84 PP) comprising *U. fulvalis*, *U. olivalis* and the species pairs *U. fimbriatralis* and *U. languidalis* (0.52 PP) as well as *U. institalis* and *U. lutealis* (0.75 PP). In the MP phylogeny, the *U. numeralis* group is represented by two clades arising separately from a polytomy, one including *U. numeralis* and *U.* cf. *numeralis* (77% JK), and the other one the remaining taxa of the species group. Together with *U. olivalis*, the *U. fimbriatralis* – *U. languidalis* (69% JK) and *U. institalis* – *U. lutealis* (77% JK) species pairs form a polytomic group (62% JK), which is the well supported sister (81% JK) to *U. fulvalis*.

4.3. Analysis of combined dataset

The combined analysis (Fig. 6) resulted in a similar topology as the molecular analysis (Fig. 4), with only minor differences in statistical support values.

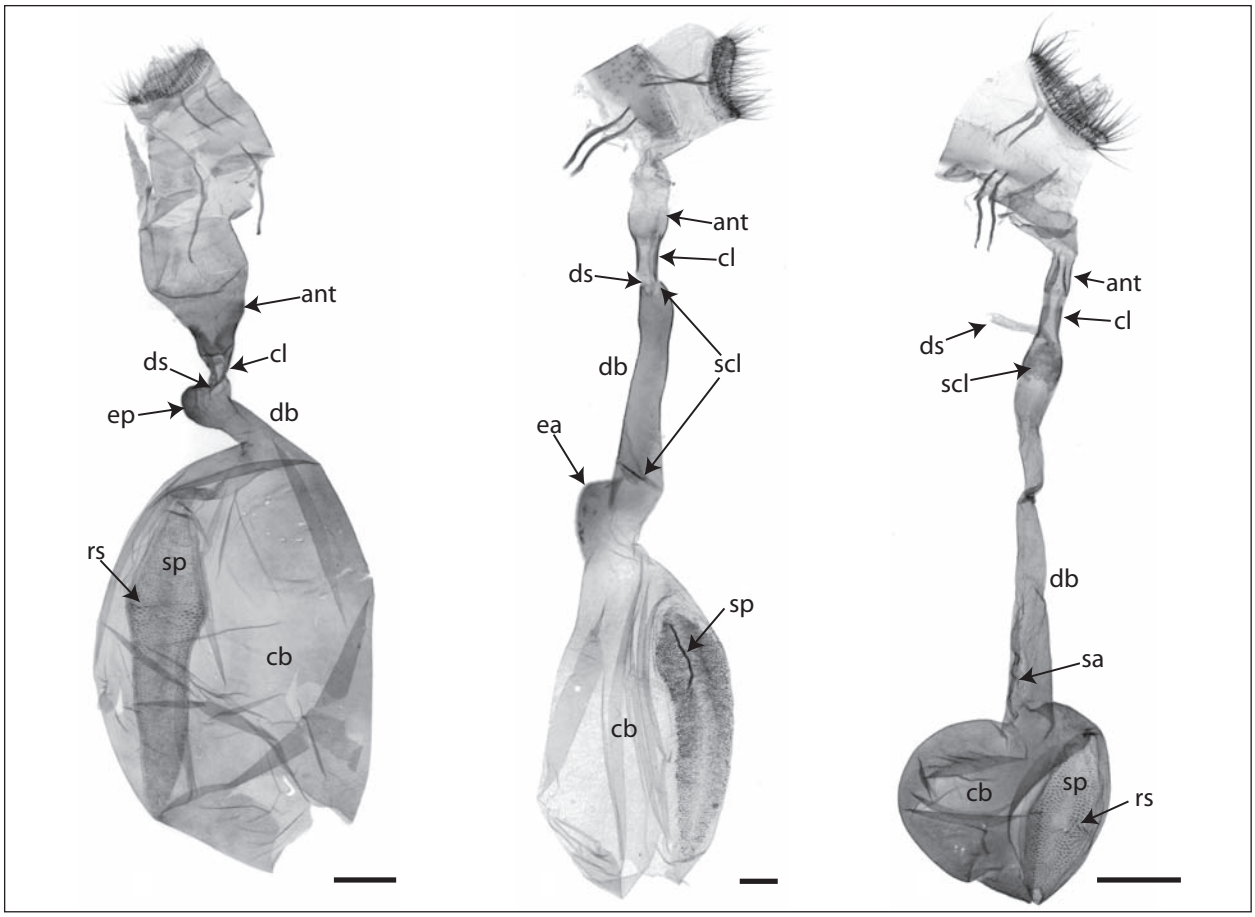

Fig. 3. Characters of female genitalia (bottom: anterior). **A**: *Udea maderensis*; **B**: *U. costalis*; **C**: *U. institalis*. (Scale bars: 500 µm)

Thirty-six monophyletic groups were found, of which 26 have a PP support value of ≥ 0.95. One polytomy each was found within the *U. ferrugalis* group (3 branches) and within the *U. alpinalis* group (3 branches).

Morphological character transformations are plotted onto the tree of this combined analysis, showing 13 unique apomorphies, which support 9 monophyla (Tab. 3) (while some apomorphies undergo reversals in subclades). In addition, there are many apomorphies that have originated more than once and therefore are homoplastic.

Together with the monophylum composed of *Deana hybreasalis*, *Mnesictena marmarina* and *Udeoides muscosalis* (0.69 PP; node 2 in Fig. 6), *Udea* (s.str.) forms the well supported monophylum *Udea* s.l. (1.00 PP; node 1). *Udea* s.l. is supported by one unique apomorphy: a bulbous thickening at the apex of the uncus (17 : 1). For this character, no reversals but one case of inapplicability has been observed within *Udea* s.l.

Udea s.str. (0.98 PP; node 3) is supported by the unique apomorphy that in the fore wing the discoidal stigmata are darker than the ground colour (2:1), but within *Udea* there are three reversals and five cases of inapplicability (due to absence of stigmata).

The basal dichotomy within *Udea* separates the *U. ferrugalis* group (node 4) from a clade comprising all other *Udea* species (node 5); both clades are well supported (both 1.00 PP) and for each, two unique apomorphies are recognised. In the large clade of node 5, the subgroups correspond with those found in the molecular analysis with few changes: The *U. alpinalis* group now also comprises *Udea rhododendronalis* (0.99 PP; node 9), and *Udea olivalis* as well as *Udea lutealis* are part of the *U. numeralis* group (0.99 PP; node 8). Sister to the *U. numeralis* group is a monophylum (0.99 PP) comprising *U. decrepitalis*, *U. inquinatalis*, *U. hamalis* and *U. prunalis*. However, this monophylum has no unique apomorphies and is therefore not explicitly recognised as a species group.

5. Discussion

5.1. Genus-level relationships

The analyses of the molecular (Fig. 4) and of the combined (Fig. 6) datasets lead to highly congruent phylo-

Tab. 2. Data matrix of 24 adult morphological characters and 41 taxa. The first two lines read vertically provide the character number.

Character number	**0000000001 1234567890**	**1111111112 1234567890**	**2222 1234**
Synaphe punctalis	1?01010?0	?001000??0	0000
Agrotera nemoralis	1?00010?0	?0011?0200	0010
Deana hybreasalis	1?0?0??0?0	?001111000	0010
Haritalodes derogata	1000010?0	?00??10200	0000
Mecyna lutealis	1000011?0	?001010?00	0011
Mnesictena marmarina	0?1?0110?0	?001011010	0011
Udeoides muscosalis	101??110?0	?001011??0	000?
Udea accolalis	0100010?0	?101011010	0110
Udea alpinalis	??0110?110	?000111101	0011
Udea austriacalis	0?0100?0?0	?000111101	0011
Udea azorensis	010??10?0	?101111000	0111
Udea bourgognealis	1?0?10?110	?000011101	0001
Udea carniolica	0101002110	?000111101	0001
Udea costalis costalis	?110011?0	?000111100	1001
Udea costalis maurinalis	0110011?0	?000111100	1001
Udea decrepitalis	111000?0?0	?010111101	0010
Udea delineatalis	110???????	??????1010	0110
Udea ferrugalis	0100010?0	?101?11010	0110
Udea fimbriatralis	0110011?1	1010111111	0001
Udea fulvalis	1110011?1	0010111111	0011
Udea hamalis	11?000?0?0	?000111101	0010
Udea heterodoxa	110??100?0	?101001000	0010
Udea inquinatalis	011000?0?0	?000111101	0010
Udea institalis	0010011?1	0010111111	0001
Udea itysalis	?110011?0	?000111100	1001
Udea languidalis	0110011?1	1010111111	0001
Udea liopis	0110010?0	?101001000	0010
Udea lugubralis	0110?100?0	?101011010	0110
Udea lutealis	0010011?1	0010111111	0001
Udea maderensis	0110010?0	?101011010	0110
Udea murinalis	0101002?0	?000111101	0011
Udea nebulalis	010110?100	?000111101	0011
Udea nordmani	0110010?0	?101011000	0110
Udea numeralis	0110010?0	?010111101	0011
Udea cf. *numeralis*	0110010?0	?010111101	0011
Udea olivalis	0110011?1	0010111111	0001
Udea prunalis	0110011?0	?000111111	0011
Udea pyranthes	1100?100?0	?101101000	0010
Udea rhododendronalis	??01111110	?000111101	001?
Udea rubigalis	0010010?0	?101111010	0111
Udea uliginosalis	??0110?100	?000111101	0011

genies, while the morphology-based analysis (Fig. 5) yielded little resolution and no information on genus-level relationships.

Deana hybreasalis and *Mnesictena marmarina*, both restricted to New Zealand, are well-supported sister taxa in the molecular and combined phylogenies. Both phylogenies also indicate *Udeoides* from Africa to be sister to the New Zealand clade, all these taxa together forming a monophyletic group of the Old World southern hemisphere with moderate support of 0.71 PP (molecular) or 0.69 PP (combined).

For *Udea* s.str., the phylogenetic analyses of the molecular and the combined datasets show high support values of 0.99 PP and 75% JK as well as 0.98 PP, respectively. The combined analysis results in one unique apomorphy for this monophylum, the darkened fore wing stigmata (2:1). However, several of the investigated *Udea* taxa lack fore wing maculation, so this character is not fully applicable to all *Udea* species.

The clades *Deana* + *Mnesictena* + *Udeoides* and *Udea* s.str. are strongly supported to be sister groups (1.00 PP), and support includes the presence of a bulbous thickening of the uncus apex (17:1) as a unique apomorphy.

In future studies an enlarged taxon sampling should be analysed in order to investigate the phylogenetic relationships in greater detail and to verify whether the status of all these genera is justified. This taxon sampling should include representatives of all genera considered by MUNROE (1995) to belong to the *Udea* genus group.

5.2. *Udea ferrugalis* group

(node 4 in Figs. 4–6)

The *U. ferrugalis* species group is morphologically characterised by two unique apomorphies: presence of a cluster of small cornuti on posterior surface of uneverted vesica (12:1, Fig. 2G) and presence of a projection at the posterior end of the ductus bursae (22:1, Fig. 3A). The latter structure is reduced in the three investigated Hawaiian *Udea* species, but it is present in other Hawaiian *Udea* species which we regard as belonging to the *ferrugalis* group due to the presence of small teeth on the surface of the vesica. Similarly, a valval fibula is absent (16:0) in the three Hawaiian *Udea* species (homoplastic transition in our analysis, since it is also absent in the outgroup taxon *Synaphe punctalis*), but the fibula is present in several other Hawaiian *Udea* species (see ZIMMERMAN 1958).

Since the morphological character states 14:1 (anterodorsal opening of ductus ejaculatorius in the phallus), 18:0 (posterior arm of signum elongated towards bodkin-shaped acute tip) and 20:0 (absence of accessory signum anterior of ductus bursae) present in the *U. ferrugalis* species group also occur in the *Udeoides* + *Deana* + *Mnesictena* clade, which is sister to *Udea*, as well as in the included pyraloid taxa that are less closely related to *Udea*, they are likely plesiomorphic for *Udea*.

The *U. ferrugalis* group is most remarkable due to the occurrence of many endemic species on remote islands in the Pacific and Atlantic oceans, suggesting considerable long-distance dispersal abilities in this species group. For *U. ferrugalis*, a widespread species in the Afrotropical and Palaearctic regions, a swarm of adults has been observed migrating off land (WOLFF 1971).

Tab. 3. Monophyla found in the Bayesian inference phylogeny of combined dataset and supported by unique morphological apomorphies.

Udea s.l. (1.00 PP)
17 : 1 – uncus – apex with bulbous thickening: present.
Udea s.str. (0.98 PP)
2 : 1 – fore wing - colouration of discoidal stigmata: darker than ground colour of wing.
U. ferrugalis group (1.00 PP)
12 : 1 – vesica (endotheca) with cluster of small cornuti on its posterior (uneverted) surface: present;
22 : 1 – ductus bursae – projection at posterior end: present.
Node 5 (1.00 PP)
14 : 0 – opening for ductus ejaculatorius in the phallus: frontal;
18 : 1 – posterior arm of signum: convex sides, converging towards a rounded tip.
U. itysalis group (1.00 PP)
21:1 – ductus bursae – projection at anterior end: present.
Node 7 (1.00 PP)
20 : 1 – accessory signum anterior of ductus bursae: present.
U. numeralis group (0.99 PP)
10 : 1 – praephallus – sclerotised, granulated area: present (1);
13 : 1 – praephallus – ventrally with longitudinal, twined split: present.
U. fimbriatralis + *U. languidalis* (1.00 PP)
11 : 1 – praephallus with sclerotised, granulated area: present distad from posterior end (due to posteriad elongation of the praephallus).
U. alpinalis group (0.99 PP)
5 : 1 – hind wing – intersexual colouration difference: darker in female than in male;
8 : 1 – praephallus – sclerotised ridge: present.

Our results support sister group relationships (all with 1.00 PP) between *U. ferrugalis* (Afrotropic, Palaearctic) and *U. delineatalis* (St. Helena), between *U. maderensis* (Madeira) and *U. nordmani* (Canary Is.), and between *U. azorensis* (Azores) and *U. rubigalis* (New World). The sister group relationship of *U. azorensis* and *U. rubigalis* implies the colonisation of the Azores by the ancestor of *U. azorensis* to have taken place from the New World over a distance of about 4000 km. (In contrast, the European continent is much closer with a distance of 1400 km.) This hypothesis is also more plausible, because it is more likely that the long distance dispersal has taken place with the Gulf Stream and not against it. Similarly, the colonisation of St. Helena by the ancestor of *U. delineatalis* might have started from Africa. Corresponding scenarios have been already suggested for the colonisation of the Azores via the Gulf Stream as well as of St. Helena via the Benguela current by Scopariinae (Pyraloidea) (Nuss et al. 1998; Nuss 1999).

Our data do not bear evidence on the origins of the island clade *U. maderensis* + *U. nordmani* and of the Hawaiian *Udea* species. For the latter, it would be of special interest to investigate whether the 41 endemic species have a common Hawaiian ancestor or not, and what is/are the respective area(s) of origin. To solve this question, special attention should be paid to East Asian and New World species, which are sparsely represented in our study. For the moment, we consider the three investigated Hawaiian *Udea* species to be members of the *U. ferrugalis* group, whereas the remaining 38 *Udea* species of Hawaii should be the focus of future research.

U. hageni Viette, 1952, a species with brachypterous males from the Atlantic island of Tristan da Cunha, represents another *Udea* species endemic to a remote oceanic island. Characters of the male genitalia as figured by Viette (1952) indicate that *U. hageni* belongs to the *U. ferrugalis* group.

With the Palaearctic *U. accolalis, U. rubigalis* and the East Asian *U. lugubralis*, the *U. ferrugalis* group contains three continental species. With the inclusion of *U. lugubralis*, three additional species of the *U. lugubralis* group sensu Yamanaka (1988) – *U. montensis* Mutuura, 1854, *U. exigualis* (Wileman, 1911) and *U. stationalis* Yamanaka, 1988 – are consequently included in the *U. ferrugalis* group. The taxonomic treatment of Nearctic *Udea* by Munroe (1966) shows that the synapomorphy of the cluster of small cornuti on the surface of the vesica is also present in *U. profundalis* (Packard, 1873) and *U. rusticalis* (Barnes & McDunnough, 1914). However, the presence of a projection at the posterior end of the ductus bursae in these two species is not clear from the figures given by Munroe (1966).

5.3. *Udea itysalis* group + (*Udea alpinalis* group + (*Udea numeralis* group + species around *Udea decrepitalis*))

(node 5 in Figs. 4–6)

Sister to the *U. ferrugalis* species group is a large, well supported monophylum that can be found in all phylogenies. It comprises the *U. itysalis* group, the

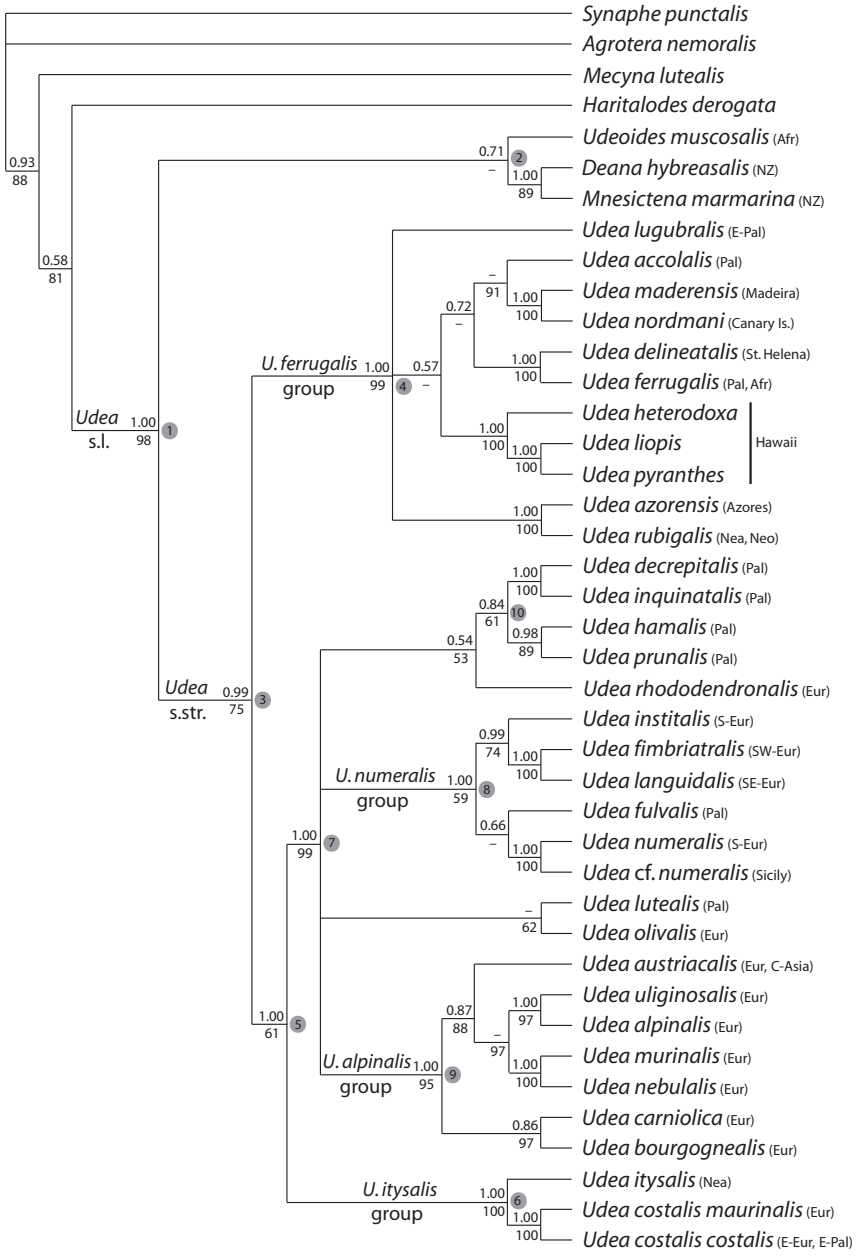

Fig. 4. Phylogeny derived from molecular dataset; combined from results of Bayesian inference and MP heuristic search, which are fully congruent but each with a few nodes missing. PP values from Bayesian inference are above branches, JK values from MP analysis are below branches; nodes missing in Bayesian or MP topology indicated by "–" in the respective position; nodes of importance for discussion are numbered 1–10 for reference in the text.

U. alpinalis group, the *U. numerali*s group, the species around *U. decrepitalis* (and, depending on the resolution of the phylogeny, a few unplaced species). In both morphological and combined analyses two unique apomorphies can be recognised for this taxon: frontal opening of ductus ejaculatorius in the phallus (14:0), and the posterior arm of signum having convex sides, which converge towards a rounded tip (18:1). In contrast to the *U. ferrugalis* group, which shows several plesiomorphic character states (see 5.2.), the monophylum of node 5 represents the more "modern" clade of *Udea*.

5.4. *Udea itysalis* group

(node 6 in Figs. 4–6)

The *U. itysalis* group has been already recognised by MUNROE (1966), who included the following North American species: *U. abstrusa* Munroe, 1966, *U. brevipalpis* Munroe, 1966, *U. cacuminicola* Munroe, 1966, *U. derasa* Munroe, 1966, *U. itysalis* (Walker, 1859), *U. livida* Munroe, 1966, *U. radiosalis* (Möschler, 1883), and *U. turmalis* (Grote, 1881). He discussed a possible relationship of *U. itysalis* with the

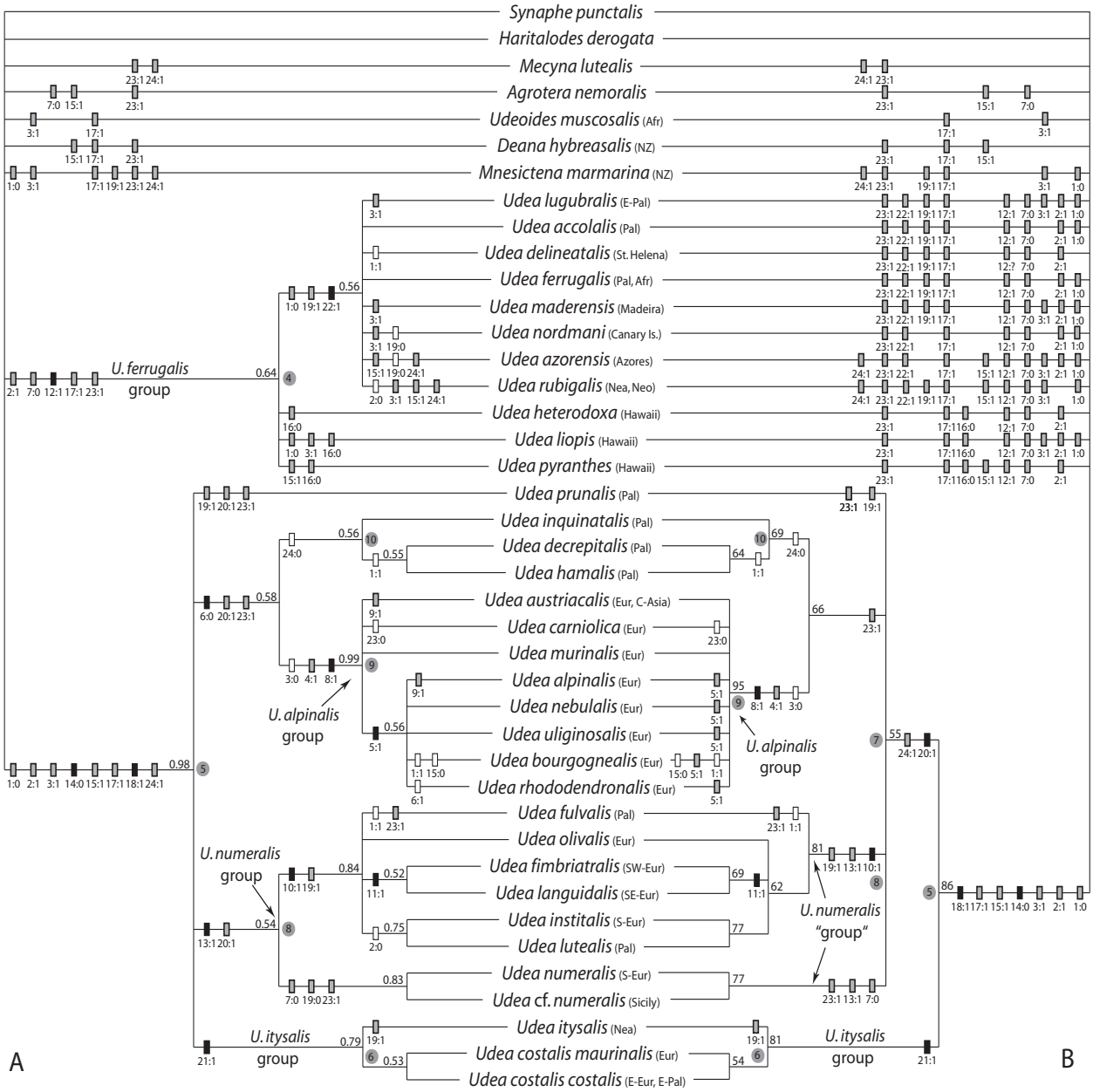

Fig. 5. Phylogenies derived from morphological dataset. **A**: Bayesian inference phylogeny with PP values given above branches; **B**: MP heuristic search phylogeny with JK values given above branches. Boxes upon branches: character transformations (character number : acquired state); black: unique and non-reversal transformations to apomorphic state; grey: homoplastic and non-reversal transformations to apomorphic state; white: reversals to plesiomorphic state (unique or homoplastic); nodes of importance for discussion are numbered 1 – 10 for reference in the text.

Palaearctic *U. costalis* (Eversmann, 1852) and *U. maurinalis* (Curtis, 1934). Our results support that the latter two taxa are closely related to *U. itysalis* and therefore belong to the *itysalis* group. For the North American *U. itysalis*, Munroe (1966) distinguishes 10 subspecies. The European *U. maurinalis* is regarded as endemic to the French Alpes Maritimes and had been originally described as a subspecies of *itysalis*. Leraut (2008) treats *maurinalis* as a subspecies of *U. costalis*, but does not provide evidence for this taxonomic change. In contrast to the restricted distribution of *maurinalis*, *costalis* occurs from Eastern Europe to the East Palaearctic (Speidel 1996; Sinev 2008). Our finding of a closer relationship of *maurinalis* to *costalis* than to *itysalis* supports Leraut's (2008) hypothesis. However, the confusing taxonomic situation in the *U. itysalis* group deserves further study.

According to our own investigation of type material, character state 21 : 1 (ductus bursae with projection at anterior end), an autapomorphy of the *U. itysalis* group, is also present in the North African *U. tachdirtalis* (Zerny, 1935). Additionally, the apomorphy is present in the Nearctic *U. beringialis* Munroe, 1966,

which was not explicitly included in the *U. itysalis* group by MUNROE (1966).

5.5. *Udea alpinalis* group + (*Udea numeralis* group + species around *Udea decrepitalis*)

(node 7 in Figs. 4–6)

Sister to the *U. itysalis* group is a monophylum that shows weak to solid statistical support (55% JK in MP phylogeny of morphological dataset; 1.00 PP, 99% JK in molecular and 1.00 PP in combined phylogeny). It can be recognised by one unique apomorphic character state, the presence of an accessory signum anterior of ductus bursae (20 : 1).

5.6. *Udea numeralis* group

(node 8 in Figs. 4–6)

The *U. numeralis* group is well supported in the Bayesian phylogenies of the molecular and the combined datasets, but the molecular data alone do not support the inclusion of *U. lutealis* and *U. olivalis*. In the combined analysis, the species group includes the latter two species and can be recognised by two apomorphic character states: 10 : 1 (praephallus with sclerotised, granulated area) and 13 : 1 (praephallus ventrally with longitudinal, twined split). In this scenario, a reversal (10 : 0) is observed for the *U. numeralis* + *U.* cf. *numeralis* subclade. In contrast, the Bayesian inference of the morphological data results in 13 : 1 being the only apomorphic character state for the *U. numeralis* group, whereas character state 10 : 1 is apomorphic for the sister group of the *U. numeralis* + *U.* cf. *numeralis* subclade. The question whether *U. lutealis* + *U. olivalis* (in Fig. 6) or *U. numeralis* + *U.* cf. *numeralis* (in the Bayesian phylogeny of Fig. 5) is sister to the remaining species of the *U. numeralis* group cannot be answered here and should be addressed in future studies of this large species group.

Character state 11 : 1 (praephallus with sclerotised, granulated area present distad from posterior end) is recognised as an autapomorphy for the clade *U. fimbriatralis* + *U. languidalis*. *Udea* cf. *numeralis*, originating from Sicily, shows features of genital morphology different from *U. numeralis* (Hübner, 1796) and is therefore kept separate from it. Our morphological investigations indicate that the Mediterranean and Near East taxa *U. catilualis* (Hampson, 1900) and *U. praepetalis* (Lederer, 1869) are closely related to *U. numeralis* due to the presence of a single cornutus (7 : 1) and probably form a species complex which is in need of taxonomic revision.

We found the longitudinal split in the praephallus, an autapomorphy for the *U. numeralis* group, to be also present in the afore mentioned *U. catilualis* (W-Pal) and *U. praepetalis* (W-Pal) as well as in *U. ardekanalis* Amsel, 1961 (W-Pal), *U. bipunctalis* (Duponchel, 1832) (W-Pal), *U. confinalis* (Lederer, 1858) (W-Pal), *U. cyanalis* (La Harpe, 1855) (Pal), *U. tritalis* (Christoph, 1881) (E-Pal), *U. sviridovi* Bolshakov, 2002 (W-Pal) and *U. zernyi* (Klima in Zerny, 1940) (W-Pal).

5.7. *Udea alpinalis* group

(node 9 in Figs. 4–6)

Apart from the apomorphic character state of sexual dimorphism in form of darker hind wings of females (5 : 1) in species of the *U. alpinalis* group, wing pattern elements are largely reduced or with little contrast. A second apomorphy, the presence of a sclerotised ridge on the praephallus (8 : 1), was also found for this species group. In the Bayesian analysis of the morphological data, character state 8 : 1 is an apomorphy for the group as a whole, whereas 5 : 1 is apomorphic for a weakly supported subgroup (0.56 PP) comprising *U. alpinalis*, *U. nebulalis*, *U. uliginosalis*, *U. bourgognealis* and *U. rhododendronalis*.

Phylogenetic relationships of *U. rhododendronalis* are unstable among the different analyses: It is weakly supported to be the sister group (0.54 PP, 53% JK) of the species around *U. decrepitalis* in the analyses of the molecular dataset, whereas in the Bayesian phylogeny of the morphological dataset the species is part of the subgroup within the *U. alpinalis* group. In the combined analysis, *U. rhododendronalis* is the well supported sister (0.99 PP) to the remaining species of the *U. alpinalis* group. *U. rhododendronalis* differs from the other *U. alpinalis* group species in the presence of a strongly sclerotised ductus bursae in the female genitalia and of several long, well-developed, needle-shaped cornuti in the male phallus. We suppose that no close relative of this species is included in our taxon sample, which would at least be partly responsible for the differing relationships found among our phylogenetic analyses. *Udea rhododendronalis* is probably a close relative of the North American *U. vacunalis* (Grote, 1881), a species with similar genital morphology and the typical plain-coloured, almost immaculate wings (see MUNROE 1966).

Another species belonging to this species group is the Caucasian *Udea cretacea* (Filipjev, 1925). FILIPJEV (1925) clearly stated that the females of *U. cretacea* are much smaller and their wings have a more

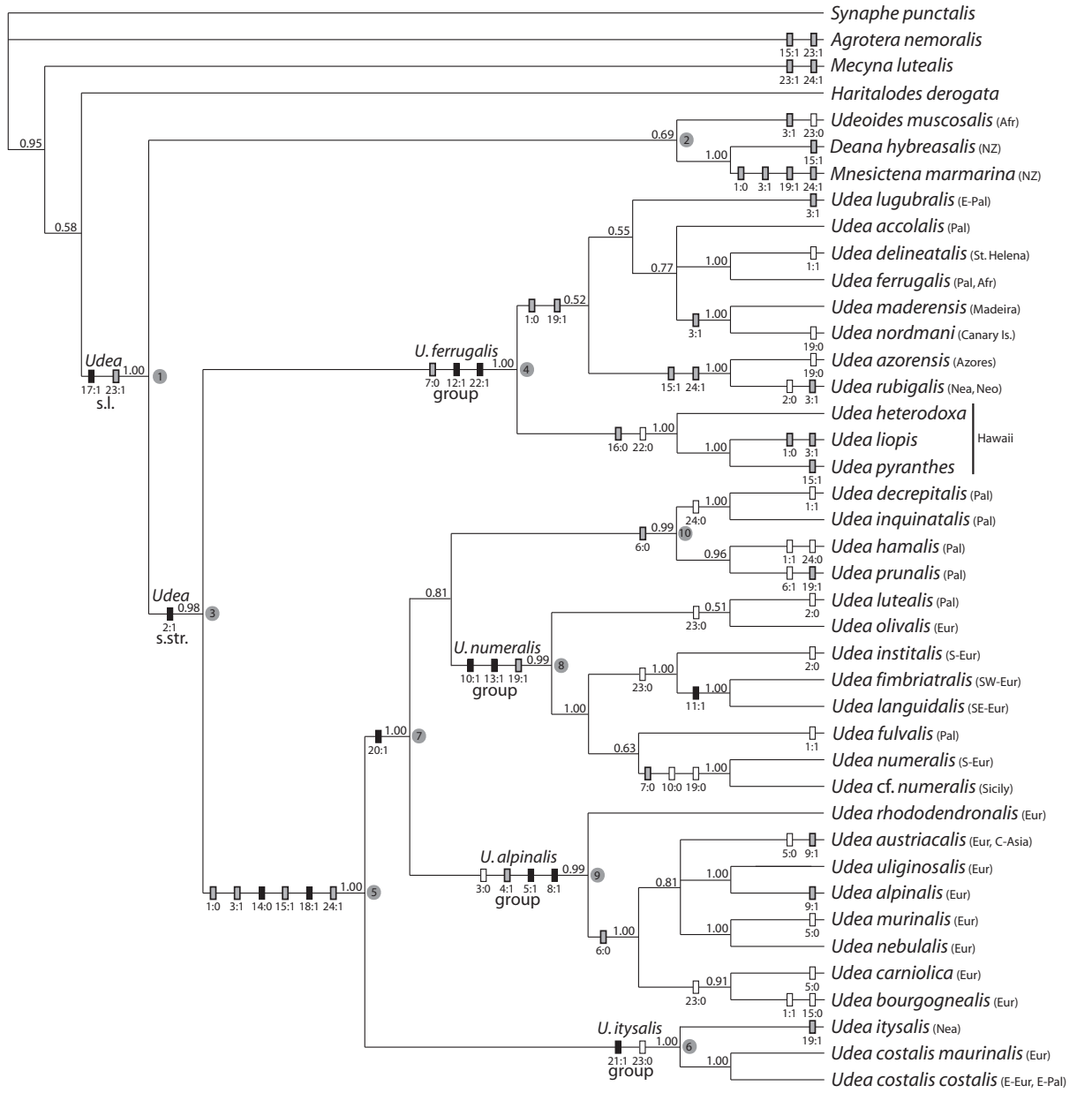

Fig. 6. Bayesian inference phylogeny of combined dataset. PP values given above branches. Boxes upon branches: character transformations (character number : acquired state); black: unique and non-reversal transformations to apomorphic state; grey: homoplastic and non-reversal transformations to apomorphic state; white: reversals to plesiomorphic state (unique or homoplastic); nodes of importance for discussion are numbered 1 – 10 for reference in the text.

pointed apex, which agrees with the sexual dimorphism found in the *U. alpinalis* group.

Wing reduction in the *alpinalis* group is paralleled in *U. hageni* Viette, 1952, endemic to Tristan da Cunha. In contrast to the *alpinalis* group, male *U. hageni* have reduced wings, while females are still unknown. We already provided arguments that *U. hageni* belongs to the *U. ferrugalis* group (see 5.2.). Thus, wing reduction in *U. hageni* is considered as having evolved independently.

All species of the *U. alpinalis* group are continental in distribution. The European species are restricted to or at least associated with mountain regions. *U. carniolica*, *U. murinalis* and *U. bourgognealis* are endemic to the European Alps.

5.8. Species around *Udea decrepitalis*

(node 10 in Figs. 4 – 6)

Apart from the taxa that we consider "species groups" herein, we found a moderately to well supported clade in the analyses of the molecular and combined datasets (0.84 PP, 61% JK; 0.99 PP) that includes 4 of the sampled species: *U. decrepitalis*, *U. hamalis*, *U. in-*

quinatalis and *U. prunalis*. This clade is perhaps sister to the *U. numeralis* species group, as indicated in Fig. 6, and supported by 0.81 PP. In the Bayesian phylogeny of the morphological dataset (Fig. 5), this clade (without *U. prunalis*) forms a monophylum together with the *U. alpinalis* group, supported by the unique apomorphy 6:0 (absence of cornuti in phallus). *Udea prunalis* differs in genital anatomy from the other three members of this clade in possessing cornuti and in the ductus bursae being partly sclerotised.

At present, it is unclear whether this clade is more closely related to the *U. numeralis* species group or to the *U. alpinalis* species group, or to neither of them. Furthermore, no apomorphic character states that would allow recognition of its members could be found for this clade. Therefore, we avoid the term "species group" for this putative monophylum and we suggest further research including additional, potentially closely related taxa and an extended set of data.

All four species are mainly found in temperate and boreal climates, but *U. prunalis* also occurs in Southern Europe. *U. inquinatalis* is holarctic in distribution (MUNROE 1960; SPEIDEL 1996; SINEV 2008).

6. Conclusions

The results of this study show that the European *Udea* species do not form a monophyletic group in itself. Instead, four species groups are observed (the *ferrugalis*, *itysalis*, *numeralis* and *alpinalis* group), each containing *Udea* species occurring in Europe as well as in other parts of the Holarctic region. We find at least one morphological apomorphy for each of these four species groups, allowing placement of further species not studied herein. The *U. ferrugalis* group comprises all herein investigated island species, suggesting considerable long-distance dispersal abilities of members of this species group. Island colonisation by the ancestor species seems to have taken place via ocean currents, as in the cases of *U. azorensis* (Azores), sister taxon to the New World *U. rubigalis*, and of *U. delineatalis* (St. Helena), sister of the Old World *U. ferrugalis*. The *U. alpinalis* group is characterised by sexual dimorphism, with females being smaller than males, and consists of species distributed in mountainous regions and including all species endemic to the European Alps. The species around *U. decrepitalis* were discovered to form one additional clade with high molecular support, but without morphological apomorphies. We are able to place two of the three previously known *Udea* species groups – the *U. itysalis* group (MUNROE 1966) and the *U. lugubralis* group (YAMANAKA 1988) – in our phylogenetic results, but the relationships of the *U. orbicentralis* group (INOUE et al. 2008) remain unknown. Altogether, we are able to place 54 of the 213 described *Udea* species into species groups.

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8. References

CALENDINI F., MARTIN J.-F. 2005. PaupUP v1.0.3.1 A free graphical frontend for Paup* Dos software.

CLAVIJO A.J.A. 1990. Systematics of black and white species of the genus *Diaphania* Hübner, 1818 (Lepidoptera: Pyralidae: Pyraustinae). – Ph.D. thesis, Department of Entomology, McGill University, Montreal. Pp. i–xi & 1–215, figs. 1–159.

DUGDALE J.S. 1988. Lepidoptera – annotated catalogue, and keys to family-group taxa. – Fauna of New Zealand, Wellington **14**: 1–262.

FILIPJEV N. 1925. Lepidopterologische Notizen. – Russkoe Entomologceskoe Obozrenie, St. Petersburg **19**(1): 47–52.

HANNEMANN H.-J. 1964. Kleinschmetterlinge oder Microlepidoptera II. Die Wickler (s.l.) (Cochylidae und Carposinidae). Die Zünslerartigen (Pyraloidea). Pp. i–viii & 1–401, pls. 1–22 in: DAHL F., Die Tierwelt Deutschlands, 50. Teil. – Gustav Fischer, Jena.

HASENFUSS I. 1960. Die Larvalsystematik der Zünsler (Pyralidae). – Abhandlungen zur Larvalsystematik der Insekten, Berlin **5**: 1–263.

HAYDEN J.E. 2009. A new genus of Caribbean Odontiinae with Palaeotropical affinities (Lepidoptera: Crambidae). – Journal of the Lepidopterists' Society **63**(4): 185–208.

HUELSENBECK J.P., RONQUIST F. 2001. MrBayes: Bayesian inference of phylogenetic trees. – Bioinformatics **17**(8): 754–755.

Knölke S., Erlacher S., Hausmann A., Miller M.A., Segerer A.H. 2005. A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. – Insect Systematics & Evolution **35**: 401 – 409.

Inoue H. 1982. Pyralidae. Pp. 307 – 404 (vol. 1) & 223 – 254 (vol. 2), pls. 36 – 48, 228, 296 – 314 in: Inoue H., Sugi S., Kuroko H., Moriuti S., Kawabe A. (eds.), Moths of Japan vols. 1 & 2. – Kodansha, Tokyo.

Inoue H., Yamanaka H., Sasaki A. 2008. Revision of *Udea orbicentralis*-complex from Japan, with descriptions of four new species (Pyralidae, Pyraustinae). – Tinea, Tokyo **20**(2): 85 – 94.

Kristensen N.P. 2003. Skeleton and muscles: adults. Pp. 39 – 131 in: Kristensen N.P. (ed.), Lepidoptera, Moths and Butterflies. Vol. 2: Morphology, physiology, and development. In: M. Fischer (series ed.), Handbook of Zoology. Volume IV Arthropoda: Insecta, Part 36. – Walter de Gruyter, Berlin & New York.

Landry B. 1995. A phylogenetic analysis of the major lineages of the Crambinae and of the genera of Crambini of North America (Lepidoptera: Pyralidae). – Memoirs on Entomology International, Gainesville **1**: 1 – 242.

Leraut P.J.A. 2008. Ébauche d'une liste des pyrales de France [Lepidoptera, Pyraloidea]. – Revue Française d'Entomologie (N.S.) **29**[2007](4): 149 – 166.

Maes K.V.N. 2006. *Udeoides* gen.n., a new genus of Spilomelinae from Africa (Lepidoptera: Pyraloidea, Crambidae). – Belgian Journal of Entomology, Bruxelles **8**(2): 127 – 137.

Mally R., Nuss M. 2010. Phylogeny and nomenclature of the box tree moth, *Cydalima perspectalis* (Walker, 1859) comb. n., which was recently introduced into Europe (Lepidoptera: Pyraloidea: Crambidae: Spilomelinae). – European Journal of Entomology **107**(3): 393 – 400.

Minet J. 1982. Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). – Bulletin de la Société Entomologique de France **86**[1981]: 262 – 280.

Müller K., Müller J., Neinhuis C., Quandt D. 2008. PhyDE – Phylogenetic data editor, Version 0995. – URL: http://www.phyde.de/.

Munroe E.G. 1950. The generic positions of some North American Lepidoptera commonly referred to *Pyrausta* Schrank. – The Canadian Entomologist **82**: 217 – 231.

Munroe E.G. 1966. Revision of the North American species of *Udea* Guenée (Lepidoptera: Pyralidae). – Memoirs of the Entomological Society of Canada **49**: 1 – 57.

Munroe E.G. 1983. Pyralidae (except Crambinae). Pp. 67 – 76 & 78 – 85 in: Hodges R.W., Dominick T., Davis D.R., Ferguson D.C., Franclemont J.G., Munroe E.G., Powell J.A. (eds.), Check List of the Lepidoptera of America North of Mexico Including Greenland. – E.W. Classey Ltd. and the Wedge Entomological Research Foundation, London.

Munroe E.G. 1989. Changes in classification and names of Hawaiian Pyraloidea since the publication of Insects of Hawaii, Volume 8, by E.C. Zimmerman (1958) (Lepidoptera). – Bishop Museum Occasional Papers, Honolulu **29**: 199 – 212.

Munroe E.G. 1995. Pyraustinae. Pp. 34 – 79 in: Heppner J.B. (ed.), Atlas of Neotropical Lepidoptera. Checklist: Part 2. Hyblaeoidea - Pyraloidea - Tortricoidea 3. – Association for Tropical Lepidoptera & Scientific Publishers, Gainesville.

Munroe E.G, Solis M.A. 1998. The Pyraloidea. Pp. 233 – 256 in: Kristensen N.P. (ed.), Lepidoptera, Moths and Butterflies. Volume 1: Evolution, systematics, and biogeography. In: Fischer M. (series ed.), Handbook of Zoology. Volume IV Arthropoda: Insecta, Part 35. – Walter de Gruyter, Berlin & New York.

Mutanen M., Wahlberg N., Kaila L 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. – Proceedings of the Royal Society B: Biological Sciences, London **277**: 2839 – 2848.

Nuss M. 1999. Revision der Gattungen der Scopariinae (Lepidoptera: Pyraloidea, Crambidae). – Nova Supplementa Entomologica, Berlin **13**: 3 – 151.

Nuss M., Karsholt O., Meyer M. 1998. A taxonomic revision of the Scopariinae from the Macaronesian Region (Lepidoptera: Pyraloidea: Crambidae). – Entomologica Scandinavica **28**[1997](4): 509 – 551.

Nuss M., Landry B., Vegliante F., Tränkner A., Mally R., Hayden J., Segerer A., Li H., Schouten R., Solis M.A., Trofimova T., de Prins J., Speidel W. 2011. Global Information System on Pyraloidea. – URL: http://www.pyraloidea.org.

Regier J.C., Zwick A., Cummings M.P., Kawahara A.Y., Cho S., Weller S., Roe A., Baixeras J., Brown J.W., Parr C., Davis D.R., Epstein M., Hallwachs W., Hausmann A., Janzen D.H., Kitching I.J., Solis M.A., Yen S.-H., Bazinet A.L., Mitter C. 2009. Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. – BMC Evolutionary Biology **9**: 280.

Robinson G.S. 1976. The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. – Entomologist's Gazette, London **27**: 127 – 132.

Sinev S.Ju. 2008. Catalogue of the Lepidoptera of Russia [in Russian]. – KMK Scientific Press, St. Petersburg and Moscow. 424 pp.

Solis M.A., Mitter C. 1992. Review and preliminary phylogenetic analysis of the subfamilies of the Pyralidae (sensu stricto) (Lepidoptera: Pyraloidea). – Systematic Entomology **17**: 79 – 90.

Solis M.A., Maes K.V.N. 2003. Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea Lepidoptera). – Belgian Journal of Entomology **4**[2002]: 53 – 95.

Speidel W. 1996. Pyraloidea [part]. Pp. 166 – 183, 187 – 196 & 319 – 327 in: Karsholt O., Razowski J. (eds.), The Lepidoptera of Europe. A distributional checklist. – Apollo Books, Stenstrup.

Sutrisno H. 2002a A preliminary study on relationships among selected Australian members of the tribe Spilomelini (Lepidoptera: Crambidae: Spilomelini). – Zoological Science, Tokyo **19**(8): 915 – 929.

Sutrisno H. 2002b. Cladistic analysis of the Australian *Glyphodes* Guenée and allied genera (Lepidoptera: Crambidae; Spilomelinae). – Entomological Science, Tokyo **5**(4): 457 – 467.

Swofford D.L. 2000. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates.

Viette P. 1952. Lepidoptera. – Results of the Norwegian scientific expedition to Tristan da Cunha 1937 – 38, Oslo **23**: 1 – 19, pls. 1 – 3, map.

Wahlberg N., Wheat C.W. 2008. Genomic outposts serve the phylogenomic pioneers: Designing novel nuclear markers for genomic DNA extractions of Lepidoptera. – Systematic Biology **57**(2): 231 – 242.

Wolff N.L. 1971. Lepidoptera. – Zoology of Iceland **3**(45): 1 – 193, pls. 1 – 15. Copenhagen & Reykjavik.

Yamanaka H. 1988. Revision of the *Udea lugubralis*-complex (Lepidoptera: Pyralidae) from Japan, with description of a new species. – Tinea, Tokyo **12**(12): 105 – 112.

Zimmerman E.C. 1958. Lepidoptera: Pyraloidea. – Insects of Hawaii **8**: i – xii & 1 – 456. Honolulu.