Phylogeny of the cactus-feeding phycitines and their relatives (Lepidoptera, Pyralidae) based on adult morphology: Evaluation of adult character-systems in phycitine systematics and evidence for a single origin of Cactaceae-feeding larvae

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The cactus-feeding Phycitinae are a New World group of moth genera that has long been the focus of ecological and biological control related studies, but the group's evolutionary and phylogenetic relationships have remained largely unknown. Here phylogenetic relationships of 15 cactus-associated and 12 allegedly related but non cactus-associated genera of Phycitinae are established based on 64 characters from adult morphology. The resulting phylogeny is the first cladistic higher-level phylogenetic analysis for any group of Phycitinae genera. It is well resolved, albeit weakly supported, and supports the monophyly of a previously suggested group comprised by the true cactus-feeders and the genera *Baphala, Zophodia* and *Rhagea*. A clade comprising all cactus feeders with the non-cactus feeder genus *Rhagea* nested within is retrieved, indicating a single origin of cactus feeding within Phycitinae; however, this clade is poorly supported. Larvae that are predacious on scale insects appear to have evolved at least twice. Evaluations of the different character systems in adult skeletal morphology demonstrate that although some systems contribute little to overall partitioned Bremer support, they might provide critical support at individual nodes. This is supporting earlier workers who suggested that as many characters as possible are needed to establish phylogenetic relationships within Phycitinae. The hitherto scarcely explored region of the pregenitalic abdomen promises to be of considerable importance in phycitine phylogenetics.

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Introduction

Within the Lepidoptera family Pyralidae, the subfamily Phycitinae comprises by far the largest and least known group with more than 4000 described species (Solis & Mitter 1992, Munroe & Solis 1999, Solis 2007). The subfamily was first revised by Ragonot (1885, 1893, 1901), but though the recent decades have seen several higher-level taxonomic works on the subfamily (Roesler 1973, Balinsky 1994, Neunzig 1986, 1990, 1997, 2003, Horak 1997, 2003) and a rise in molecular species-level studies, especially of economically important genera such as *Dioryctria* Zeller (i.e. Du et al. 2005, Roe et al. 2006), higher-level phylogenetic studies on the Phycitinae have proven to be notoriously difficult. As a consequence, since Carl Heinrich's monumental study on New World genera and species (Heinrich 1956), only a few studies have dealt with higher-level evolutionary relationships within the group (i.e. Agenjo 1958, Roesler 1968, 1986, Horak 1997, 2003). One reason for this is the high degree of character homoplasy that apparently exists within the group, especially in classical character systems such as wing venation and male genitalia (Heinrich 1939, 1956, Roesler 1986). Heinrich pointed this out in his publications and in fact noted that the lack of understanding of the higher classification and rela-

tionships within the Phycitinae is "not so much the fault of any entomologist as it is of the phycitids themselves" (Heinrich 1939, p. 332)! Later he stated that attempts to solve the evolutionary relationships of the phycitines "would be a vain and futile performance" (Heinrich 1956). This has influenced students of the group ever since, and the view has generally been that morphology based phylogenetics of the Phycitinae would be very hard to establish. Nonetheless, several workers have made tentative suggestions of close relations between some genera of phycitines (Roesler 1973, Neunzig 1986, 1990, 1997, 2003), and both Roesler (1986) and Horak (1997) suggested that morphological characters can be useful if used carefully and if a study is not relying on one single character system such as genitalic morphology. When engaging in a phylogenetic study, one should of course choose a group that appears to be monophyletic, and select outgroups that do not only allow for character polarization within the ingroup but also are suitable for checking the monophyly of the latter. While the monophyly of the Phycitinae seems well supported by morphological characters (Solis & Mitter 1992) and many genera also appear to be well founded (Heinrich 1956, Roesler 1973, Neunzig 1986, 1990, 1997, 2003, Horak 1997), few genus or tribal level groupings have been suggested and generally not agreed upon (Horak 1997). Agenjo (1958) divided Phycitinae into three tribes, based on the major "wing venation groups" and 14 subtribes based on the "venational divisions" suggested by Heinrich (1956), though these venation based groupings were recognized by Heinrich himself to be artificial (see later). Roesler (1968, 1973) accepted Phycitini as a tribe, and recognized two subtribes, Phycitina and Acrobasiina, within it. But as pointed out by Horak (1997), neither of these groups is supported by good autapomorphies.

One group that appears to be a monophyletic unit is the cactus-feeding phycitines and their closest relatives (Heinrich 1939, 1956, Mann 1969, Neunzig 1997). This group was first recognized by Heinrich in 1939, when he grouped 46 species into 18 genera, including the non-cactus feeding genus *Zophodia* Hübner, and stated that these seem to form a natural unit within the Phycitinae. This view was further elaborated in his revision of all by then known American Phycitinae (Heinrich 1956). That revision was partly built on an overall division based on wing venation, which he acknowledge to be superficial, and a more detailed grouping based on male genitalia. In the latter system he included the genera *Rhagea* Heinrich, *Laetilia* Ragonot and *Baphala* Heinrich as close relatives of the cactus-feeders (including *Zophodia*). He also suggested other groups of genera, such as the *Homoeosoma* Curtis group and the *Mescinia* Ragonot group, as close relatives of the cactus-feeders.

Roesler (1973) synonymized all cactus-feeding genera (but not *Laetilia* and *Baphala*) with the Holarctic genus *Zophodia* and thus tacitly supported the monophyly of the group suggested by Heinrich (1939). He also placed the members of the *Homoeosoma*-group in the same subtribe (Acrobasiina) as *Zophodia* s.l.

Blanchard and Ferguson (1975) erected the genus *Rostrolaetilia* Blanchard and Ferguson for two species previously placed in other genera and seven new species, all from North America. They demonstrated that the genus belongs in the Phycitinae, and based on similarities in male genitalia and lifestyle suggested a close relationship with *Laetilia*, though very little is known about the immature stages of *Rostrolaetilia* (Blanchard & Ferguson 1975, Neunzig 1997).

Neunzig (1997) treated the cactus-feeding genera and allies as defined by Heinrich (1956) in his third fascicle on Phycitinae in the series "The Moths of America North of Mexico", and included the *Homoeosoma*-group (including *Unadilla* Hulst), the *Mescinia*-group (including *Bema* Dyar), and the genera *Barberia* Dyar and *Welderella* Blanchard. He also accepted that *Rostrolaetilia* is closely related to *Laetilia*, and included the genus based on Blanchard & Ferguson (1975). Though Neunzig (1997) thus accepted Heinrich's (1939, 1956) view that the cactus-feeding genera and *Zophodia* are closely related he rejected Roesler's (1973) synomymization. He considered the genera to be too distinct both in terms of morphology and lifestyle to be united in one genus, but he did not reject the idea that they form a monophyletic unit. Neunzig (1997) generally accepted Heinrich's classification, but included the genus *Olycella* Dyar in *Melitara* Walker.

Here, I present a phylogenetic analysis of the cactus-feeding genera and their supposedly closest allies (*Zophodia*, *Rhagea, Baphala, Laetilia* and *Rostrolaetilia*) as defined by Heinrich (1939, 1956), Roesler (1973) and Neunzig (1997). The

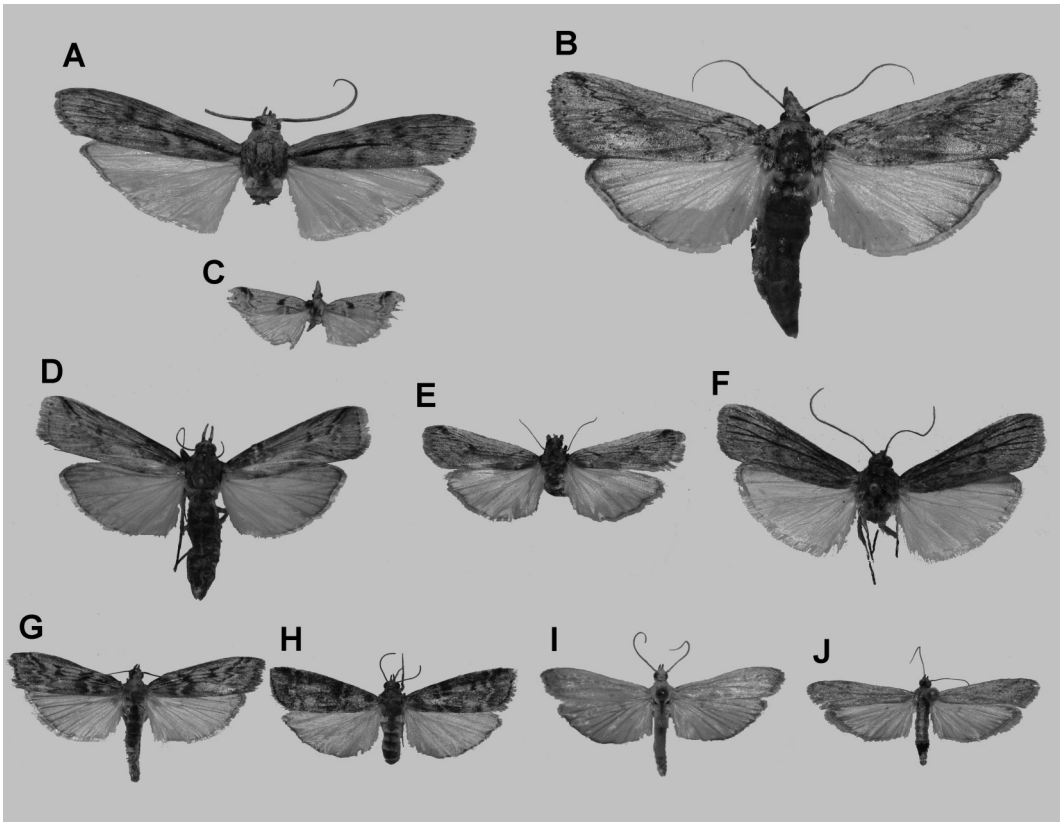

Fig. 1. Representatives of the cactus-feeding Phycitinae and their allies. A *Cactobrosis fernaldialis* B *Melitara dentata* C *Rostrolaetilia placidella* D *Cactoblastis cactorum* E *Yosemitia graciella* F *Eremberga leucopnis* G *Zophodia grosulariella* H *Laetilia zamarcella* I *Homoeosoma electella* J *Patagonia peregrina*.

objectives of the study are: 1) to test the monophyly of the group suggested by Heinrich (and thus determine whether the synomymization suggested by Roesler is systematically justifiable); 2) to test whether enigmatic genera such as *Baphala, Laetilia* and *Rostrolaetilia* are closely related to the cactus-feeders; 3) to identify monophyletic groups within the cactus-feeders and their closest allies; 4) to evaluate the usefulness of various adult morphology character systems in phycitine phylogeny. The original intention was to base this analysis on both adult morphology and molecular characters. However, obtaining suitable material for the molecular part of the study proved to be impossible within the given timeframe for the project. Thus, the present study will probably not be the final word regarding the phylogeny of the cactus-feeding phycitines. On the contrary, I hope that it will inspire other workers to study this fascinating and important group of moths. I also hope that this first higher-level morphology based cladistic analysis of any group of phycitines will demonstrate that adult skeletal morphology can provide useful characters, and thus inspire others to work on other groups of Phycitinae.

Materials and methods

Taxon sampling

20 species were included as ingroup taxa in the study, representing 19 of the 22 genera included in the cactus-feeders and their allies by Heinrich (1956) plus *Rostrolaetilia*. Of the three remaining genera, the monotypic *Parolyca* Dyar is known

Table 1. List of genera and species included in the study. For taxa marked with an asterisks (*) only one male and one female were examined. Tot# indicates total number of described species in the genus (ingroup only). CNC Canadian National Collection, CUIC Cornell University Insect Collection, EHSM E. H. Strickland Entomological Museum, GMCSU Gillette Museum Colorado State University, MEM Mississippi Entomological Museum, MSU Montana State University, NMNH National Museum of Natural History, TAMU Texas A & M University.

Species	Tot.#	Larval food source	Collection
Far Outgroups			
Plodia interpunctella, (Hbn.)		Dried vegetable products	EHSM
Pyla aeneoviridella, Rag.		Unknown	EHSM
Dioryctria abietivorella, (Grt.)		Pinaceae	EHSM
Acrobasis tricolorella, Grt.		Rocaceae	EHSM
Near Outgroups			
Mescinia-group.			
*Anderida sonorella**, (Rag.)		Unknown	CNC
Mescinia estrella, B. & McD.		Asteraceae	CNC, CUIC
*Cassiana malacella**, (Dyar)		Unknown	NMNH
*Bema neuricella**, (Zell.)		Fabaceae	NMNH
Homoeosoma-group.			
Homoeosoma electella, (Hulst)		Asteraceae	NMNH, TAMU
Patagonia peregrina, (Heinr.)		Asteraceae	NMNH, EHSM
*Unadilla erronella**, (Zell.)		Asteraceae	NMNH
Phyciodes mucidellus, (Rag.)		Asteraceae	NMNH, MEM, MSU
Ingroups			
Non cactus-feeders			
*Rostrolaetilia ardiferella**, (Hulst)	10	Unknown (presumed predacious)	TAMU, EHSM
Laetilia coccidivora, (Comst.)	12	Predacious (but cactus associated)	TAMU, MEM
*Baphala homoeosomella**, (Zell.)	6	Predacious	NMNH
*Rhagea stigmella**, (Dyar)	2	Crassulaceae	NMNH
Zophodia grosulariella, (Hbn.)	2	Grossulariaceae.	EHSM
True-cactus feeders			
Melitara dentata, (Grt.)	7	*Opuntia* (Cactaceae)	NMNH, CNC, EHSM
*Melitara subumbrella**, (Dyar)	-	*Opuntia* (Cactaceae)	GMCSU
Alberada parabates, (Dyar)	6	*Cylindropuntia* (Cactaceae)	TAMU, CNC, GMCSU
*Nanaia substituta**, (Heinr.)	1	*Cylindropuntia* (Cactaceae)	NMNH
Cactoblastis cactorum, (Berg)	5	*Opuntia* (Cactaceae)	NMNH, MEM
Cahela ponderosella, (B. & McD)	1	*Cylindropuntia* (Cactaceae)	TAMU, CNC
*Rumatha polingella**, (Dyar)	4	*Cylindropuntia* (Cactaceae)	NMNH
	4	*Echinocactus, Echinocereus, Ferocactus, Mammillaria* (Cactaceae)	NMNH, MSU
Yosemitia graciella, (Hulst)			
*Tucumania tapiacola**, Dyar	2	*Opuntia* (Cactaceae)	NMNH
*Eremberga leucorpnis**, (Dyar)	3	*Echinocereus* (Cactaceae)	NMNH
*Salambona analamprella**, (Dyar)	1	*Opuntia* (Cactaceae)	NMNH
*Sigelgaita chilensis**, (Heinr.)	3	*Eulychnia, Trichorereus* (Cactaceae)	NMNH
Ozamia clarefacta, Dyar	6	*Opuntia* (Cactaceae)	NMNH, TAMU
Cactobrosis fernaldialis, (Hulst)	4	*Ferocactus* (Cactaceae)	MSU, CNC
*Echinocereta strigalis**, (B. & McD.)	1	*Echinocereus* (Cactaceae)	NMNH
Taxa discussed but not formally included in the analysis			
*Welderella parvella**, (Dyar)		Unknown	NMNH
*Barberia affinitella**, Dyar		Unknown	NMNH
*Olyca phryganoides**, Walker		*Opuntia* (Cactaceae)	NMNH
*Amalafrida leithella**, (Dyar)		*Opuntia* (Cactaceae)	NMNH

from very few specimens and had to be excluded as material was not available. Material of the two genera *Olyca* Walker and *Amalafrida* Heinrich were available, but not all characters could be scored. Hence, these two genera were not included in the cladistic analyses, but the specimens were examined and a tentative assessment of their phylogenetic relationships is made. Since so little is known about the phylogenetic relationships of the Phycitinae, identifying good outgroups posed a problem. Therefore a double outgroup approach was chosen. Eight of the 10 additional genera included by Neunzig (1997) were chosen as "near" outgroup since these generally have been considered to be close to the taxa included here in the ingroup (Heinrich 1956, Roesler 1973, Neunzig 1997). As was the case with *Olyca* and *Amalafrida*, two of the genera, *Barberia* and *Welderella* were available, but not all characters could be scored. The two genera were therefore not included in the cladistic analyses. They were examined and will be included in the discussion. Four phycitine genera that have never been suggested to be close to the ingroup were chosen as "far" outgroups: *Acrobasis* Zeller*, Dioryctria, Pyla* Grote and *Plodia* Guénée. Heinrich (1956) placed *Plodia* in the same major group as the ingroup and near outgroup taxa based on wing venation, but placed all four 'far' outgroup genera far from these based on male genitalia. Roesler (1973) placed *Acrobasis* and *Dioryctria* in the same subtribe, Acrobasiina, as *Zophodia, Laetilia, Homoeosoma* and *Phycitodes*. In most cases one species from each genus (generally the type species) was examined. But for *Melitara* two species, *M. dentata* and *M. subumbrella*, were included. These represent the two old genera *Melitara* and *Olycella* united by Neunzig (1997) in one genus. Including representatives of both old genera allows testing of this hypothesis. A subset of the cactus-feeders and some close relatives are shown in Fig. 1. A full list of taxa included in the study with total number of species in each of the ingroup genera and larval food sources listed (after Heinrich 1956, Mann 1969, Neunzig 1997, 2003) is given in Table 1.

Character scoring

Both males and females were examined for potential characters. Pinned specimens were examined using a Leitz Wetzlar Stereomicroscope (max 100x magnification). Head characters were generally scored directly this way, but the heads of some specimens were examined in a JEOL JSM-6301FXV scanning electron microscope (SEM) to allow better comparison and illustration of the characters. Wing venation was examined by placing the spread specimen upside down under a stereo microscope and placing a droplet of xylene on the wing. Characters from pregenitalic abdomen and genitalia of both sexes were scored using a stereomicroscope after the abdomina had been macerated in 10% KOH and stained in Chlorazol Black in a 70% ethanol solution. Generally, only one male and one female from each species (the species marked with an asterisk* in Table 1) could be examined as these species are rare in collections. To avoid miss-scorings caused by a single aberrant specimen, the character scorings (especially wing venation) were checked against the literature (Heinrich 1956 and Neunzig 1997). For the two genera *Nanaia* and *Mescinia* only male specimens were available. But the text and excellent figures in Heinrich (1956) allowed me to confidently score characters relevant to females.

The nomenclature follows Wootton (1979) and Kristensen (2003) with minor modifications for Pyralidae following Neunzig (1997).

Phylogenetic analyses

Phylogenetic analyses were carried out in PAUP* 4.10b (Swofford 2002) and TNT 1.0 (Goloboff *et al*. 2003) using maximum parsimony and a heuristic search algorithm with TBR branch swapping and 1000 random replications.100 trees pr. step were saved in TNT, whereas the default 10 trees pr. step were saved in PAUP*. Character transformations were analyzed in MacClade 4.0 (Maddison and Maddison 2000). Clade robustness in the final cladogram was evaluated using Bremer support (BS) (Bremer 1988, 1994). Bremer support values were calculated in TreeRot 2.0 (Sorensen 1999) in conjunction with PAUP*. To examine the contribution of the different character systems, and hence evaluate their importance in this study and give an estimate of their usefulness in phycitine phylogenetics, the dataset was divided into five overall partitions based on the overall character systems: Head, wings, pregenitalic abdomen (including male A8), female genitalia and male genitalia. Partition Bremer support (PBS) (Baker and DeSalle 1997, Baker *et al.* 1998, Gatesy *et al.* 1999) for each partition was calculated in TreeRot

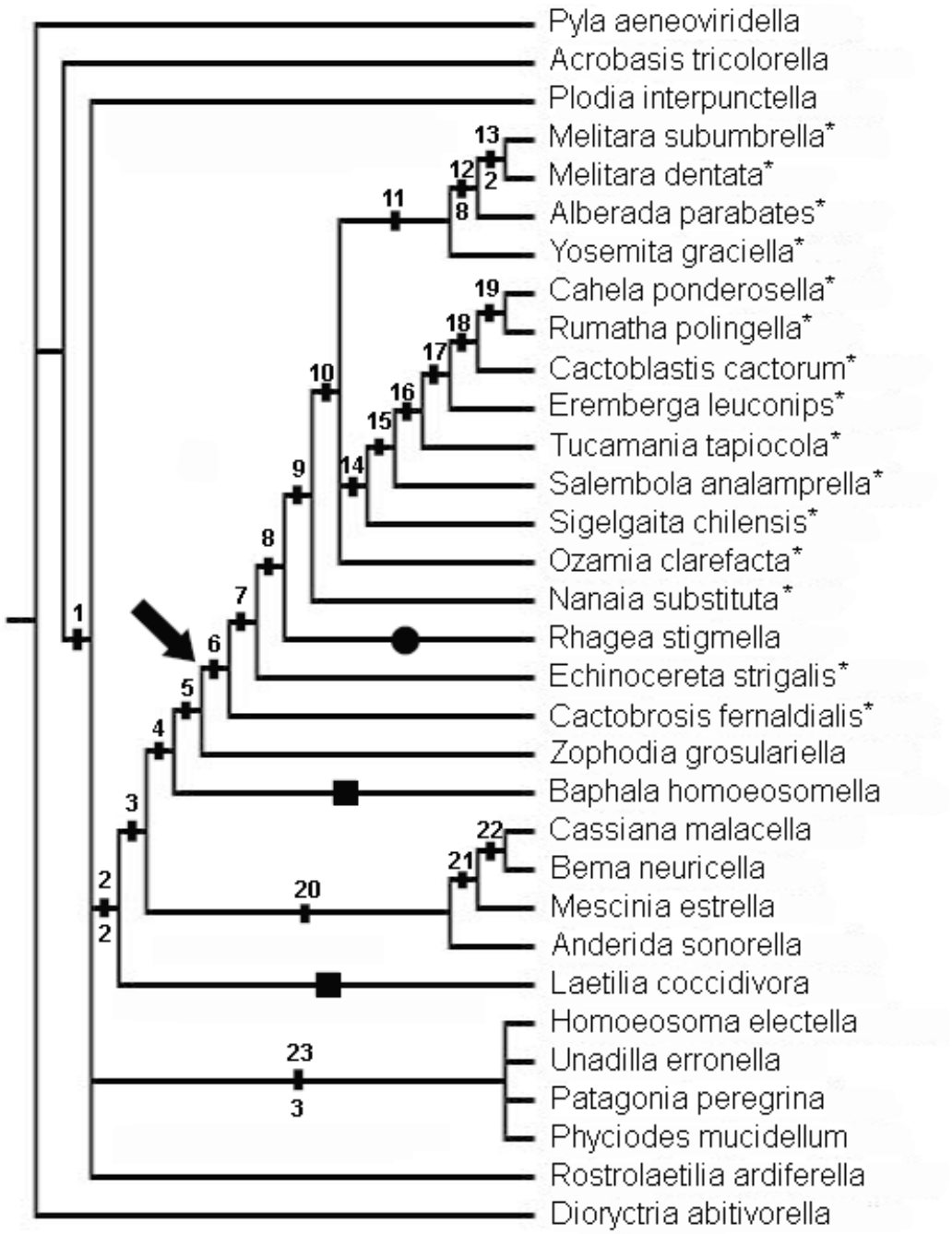

Fig. 2. Strict consensus tree of the 12 most parsimonious trees, 252 steps long. CI = 0.2835, RI = 0.5935. Numbers above the nodes are clade numbers as used in the text, numbers below the nodes are Bremer Support values above 1. The arrow indicates the evolution of Cactaceae-feeding, the closed circle indicates a shift from Cactaceae-feeding to Crassulaceae-feeding. A filled square indicates predacious larvae. Species with Cactaceae-feeding larvae are marked with an asterisk (*).

2.0. Additionally, the dataset was reanalyzed multiple times excluding one or more data partitions.

Results

64 characters were scored: 15 were from the head region, 12 from the wings, 15 from the pregenitalic abdomen, 8 from female genitalia, and 14 from male genitalia. 56 characters were binary and 10 were multistate. Of the 10 multistate characters, 7 were treated as unordered, and three (characters 15, 22 and 63) were treated as ordered. All characters had equal weight. The full list of characters is given in Appendix 1, and the character matrix is given in Appendix 2.

The phylogenetic analysis of all characters resulted in 12 equally parsimonious trees, 252 steps long. The strict consensus of these trees is shown in Fig. 2. The BS and PBS values for each clade and the list of apomorphies are given in Table 2. An overview of the number of clades supported or contradicted by each data partition, and each partition's contribution to the overall support can be found in Table 3. Cladograms from reanalyses of the dataset with different partitions excluded are shown in Figs 3 and 4.

Discussion

Overall phylogenetic patterns

The strict consensus tree in Fig. 2 is generally well resolved, but few clades are well supported (Table 2). As a consequence only these well supported clades and a few others are discussed here.

Clade 1 as defined here comprises the ingroup taxa, the near outgroup taxa and the far outgroup taxon *Plodia interpunctella*. The group is held together by several homoplastic characters and one unique apomorphy: 24:0, hind wing veins M_{2+3} fused for their entire length. This is basically the character used by Heinrich (1956) to define his "Venation Group 2", a group comprising many

Table 2. Bremer support, partitioned Bremer support and apomorphy list for the clades in the cladogram in Fig. 2. Characters in bold are unique apomorphies, characters in italics have a CI value of at least 0.5. F female genitalia character, H head characters, M male genitalia characters, P pregenitalic abdomen characters, T thoracic (wing) characters.

Clade	Bremer Support	Partitioned Bremer Support	List of apomorphies Character	CI	Change
1	1	H: -0.238095	12	0.200	0 -> 1
		T: 2.321429	*15*	*0.500*	*0 -> 1*
		P: 0.988095	17	0.333	0 -> 2
		F: -0.940476	**24**	**1.000**	**1 -> 0**
		M: -1.130952	31	0.333	1 -> 0
			37	0.250	0 -> 1
			40	*0.500*	*0 -> 1*
			48	0.111	0 -> 1
			59	0.143	0 -> 1
2	2	H: -0.089744	17	0.333	2 -> 1
		T: 1.807692	23	0.167	0 -> 1
		P: -0.217949	25	0.200	0 -> 1
		F: 0.551282	50	0.333	0 -> 1
		M: -0.051282	55	0.333	0 -> 1
			61	0.333	0 -> 1
			62	0.286	2 -> 1
3	1	H: -0.176768	9	0.222	2 -> 0
		T: 0.439394	35	0.250	0 -> 1
		P: 1.479798	41	0.250	0 -> 1
		F: -0.196970	42	0.250	0 -> 1
		M: -0.545455			
4	1	H: 0.030055	5	0.333	0 -> 1
		T: 0.319672	*15*	*0.500*	*1 -> 2*
		P: 1.396175	28	0.333	1 -> 0
		F: -0.071038	38	0.200	0 -> 1
		M: -0.674863	44	0.333	0 -> 1

Clade	Bremer Support	Partitioned Bremer Support	List of apomorphies Character	CI	Change
5	1	H: -0.135739	23	0.167	1 -> 0
		T: 0.561856	45	0.167	0 -> 1
		P: 1.424399	47	0.286	0 -> 1
		F: -0.214777	58	0.200	0 -> 1
		M: -0.635739	62	0.286	1 -> 0
6	1	H: -0.001718	20	0.200	0 -> 1
		T: 0.448454	32	0.167	1 -> 0
		P: 1.475945	33	0.200	1 -> 0
		F: -0.194158	34	0.167	1 -> 0
		M: -0.728522	57	0.250	0 -> 1
7	1	H: -0.154244	5	0.333	1 -> 0
		T: 0.773292	42	0.250	1 -> 0
		P: 1.402692	45	0.167	1 -> 0
		F: -0.333333			
		M: -0.688406			
8	1	H: -0.271930	36	0.200	1 -> 0
		T: 0.615789	46	0.286	0 -> 2
		P: 1.250877	60	0.250	0 -> 1
		F: -0.128070			
		M: -0.466667			
9	1	H: -0.015152	**13**	**1.000**	**0 -> 1**
		T: 0.479798	17	0.333	1 -> 0
		P: 1.459596	47	0.286	1 -> 2
		F: -0.227273	57	0.250	1 -> 0
		M: -0.696970	63	0.200	0 -> 1
			64	0.200	0 -> 1
10	1	H: -0.263833	8	0.333	1 -> 0
		T: 0.783401	33	0.200	0 -> 1
		P: 1.417679	48	0.111	1 -> 0
		F: -0.294872	49	0.143	1 -> 0
		M: -0.642375	50	0.333	1 -> 0
11	1	H: 1.227273	9	0.222	0 -> 1
		T: -0.166667	14	0.333	0 -> 1
		P: -1.469697	46	0.286	2 -> 1
		F: 0.863636	47	0.286	2 -> 1
		M: 0.545455	60	0.250	1 -> 0
12	8	H: 2.599688	2	0.250	0 -> 1
		T: 1.556075	*15*	*0.500*	*2 -> 3*
		P: 1.054517	20	0.200	1 -> 0
		F: 0.344237	26	0.167	0 -> 1
		M: 2.445483	33	0.200	1 -> 0
			39	**1.000**	**0 -> 1**
			41	0.250	1 -> 0
			43	*0.500*	*0 -> 1*
			51	0.333	0 -> 1
			52	0.222	1 -> 0
			58	0.200	1 -> 0
			64	0.200	1 -> 0
13	2	H: 1.300000	**3**	**1.000**	**0 -> 1**
		T: 2.400000	19	0.333	0 -> 1
		P: -0.300000	25	0.200	1 -> 0
		F: -0.400000			
		M: -1.000000			
14	1	H: 0.164269	8	0.333	0 -> 1
		T: 0.377698	11	0.250	0 -> 1
		P: 0.799760	23	0.167	0 -> 1

Clade	Bremer Support	Partitioned Bremer Support	List of apomorphies Character	CI	Change
		F: -0.077938	26	0.167	0 -> 1
		M: -0.263789	32	0.167	0 -> 1
15	1	H: -0.208160	1	0.333	0 -> 1
		T: 0.524896	*15*	*0.500*	*2 -> 3*
		P: 1.477870	34	0.167	0 -> 1
		F: -0.144537	46	0.286	2 -> 1
		M: -0.650069	47	0.286	2 -> 0
			63	0.200	1 -> 0
16	1	H: -0.069697	7	0.333	0 -> 1
		T: 0.469697	41	0.250	1 -> 0
		P: 0.948485	52	0.222	1 -> 0
		F: -0.124242			
		M: -0.224242			
17	1	H: -0.115504	*15*	*0.500*	*3 -> 2*
		T: 0.509302	48	0.111	0 -> 1
		P: 0.934109	49	0.143	0 -> 1
		F: -0.103101	60	0.250	1 -> 0
		M: -0.224806			
18	1	H: -0.105797	23	0.167	1 -> 0
		T: 0.517391	62	0.286	0 -> 1
		P: 1.088406	64	0.200	1 -> 0
		F: -0.215942			
		M: -0.284058			
19	1	H: -0.077957	11	0.250	1 -> 0
		T: -0.048387	47	0.286	0 -> 2
		P: 0.940860	58	0.200	1 -> 0
		F: 0.283602			
		M: -0.098118			
20	1	H: 0.108333	**56**	**1.000**	**0 -> 1**
		T: -0.191667			
		P: -0.233333			
		F: 0.183333			
		M: 1.133333			
21	1	H: 0.476190	*4*	*0.500*	*0 -> 1*
		T: -0.428571	25	0.200	1 -> 0
		P: -0.333333	27	0.167	1 -> 0
		F: 0.238095	55	0.333	1 -> 0
		M: 1.047619	62	0.286	1 -> 0
			64	0.200	0 -> 1
22	1	H: -0.291667	*10*	*0.500*	*1 -> 0*
		T: 0.875000	19	0.333	0 -> 1
		P: 0.041667	21	0.333	0 -> 1
		F: 0.041667	53	0.250	0 -> 1
		M: 0.333333			
23	3	H: -0.445736	**6**	**1.000**	**0 -> 1**
		T: 5.569767	*16*	*0.500*	*0 -> 1*
		P: -0.042636	18	0.400	1 -> 0
		F: -1.833333	27	0.167	1 -> 0
		M: -0.248062	36	0.200	1 -> 0
			45	0.167	0 -> 1
			48	0.111	1 -> 0
			49	0.143	1 -> 0
			52	0.222	1 -> 2
			54	0.333	0 -> 1
			59	0.200	0 -> 1
			61	0.333	0 -> 1

genera not included here. The results of the current analysis is thus in accordance with Heinrich. However, much more data are needed to corroborate this. A possible character defining this group excluding *Rostrolaetilia* could be 40:1, male sternite 8 reduced to a short, anterior structure (possibly representing only the sternal antecosta). This character state is absent in *Acrobasis, Pyla, Dioryctria* and *Rostrolaetilia*, but present in all other included taxa. However, Heinrich (1956) does illustrate numerous modifications of the male sternum 8, some of which may bear similarities to what is observed here. Despite the number of characters supporting this clade, it receives low Bremer support.

Clade 2 is one of the few clades in the cladogram that receives a Bremer support of more than 1. The clade comprises the *Mescinia*-group and all the genera included by Heinrich (1956) in the cactus-feeders group in broad sense together with *Laetilia* as the sister group of the other taxa. Characterwise the clade is only weakly supported by several homoplastic characters.

Clade 4 comprises *Baphala, Zophodia* and the true cactus-feeders (including the non cactus-feeder *Rhagea*). This clade is only supported by a few homoplastic characters. But interesting support come from characters 5:1, flagellum of male antenna basally with patch of scale-like sensilla, and 15:2, mandibles reasonably well developed as a pointed rod. Character 5 has been suggested by Heinrich (1939, 1956) and Neunzig (1997) as possible indication of relationship between *Baphala, Zophodia, Cactobrosis* Dyar and *Ozamia* Ragonot. But the present results indicate that the presence of this character may be plesiomorphic in the three former and a parallel development in the latter. Character 15 suggests that fairly well-developed mandibles are unique to this clade, though further developments of these structures have happened within the clade. It should also be noted that well-developed mandibles (though different from what has been observed in the Phycitinae) within Pyraloidea have been described from a member of Crambidae (Rouchy 1964). The Bremer support of 1 is, however, very low.

Clade 5, though only supported by highly homoplasious characters, should be mentioned as it is almost synonymous with *Zophodia* as defined by Roesler (1973). Thus the current results support Roesler's synomymization from a purely systematically point of view. The clade is, however, poorly supported and may well be challenged in the future. Furthermore, the genera in this clade show considerable morphological and biological diversity. It therefore seems most reasonable to retain the genera for the moment.

Clade 6 is also poorly supported, but deserves to be discussed as it comprises all the cactus-feeding genera and the Crassulaceae-feeding genus *Rhagea*. It therefore appears that the habit of feeding on Cactaceae is due to one evolutionary event, with a later host shift to Crassulaceae.

Clade 12 appears as the best supported clade in the cladogram. The monophyly of *Melitara* and *Alberada* Heinrich is supported by several more or less homoplastic characters including: 15:3, the presence of large, hook-shaped mandibles and: 43:1, female dorsum 8 short and in lateral view triangular (paralleled only in *Cactoblastis cactorum*), and one unique apomorphy: 38:1, antecosta of male tergum 8 with latero-posterior "shoulders". The Bremer support of 8 is the highest in the analysis, and the clade is the only one that receives positive support from all five data partitions. Both Heinrich (1939, 1956) and Neunzig (1997) proposed that *Melitara* and *Alberada* are closely related. The current results strongly support that suggestion.

Clade 13 comprises the representatives of the two genera united by Neunzig (1997) in *Melitara*. Though supported only by two homoplastic char-

Table 3. Parameters for the individual data partitions.

Character system	Clades with positive support	Clades with negative support	Overall contribution to total PBS
Head	7	16	3.244
Wings	19	4	20.515
Pregen. ab.	17	6	16.984
Female gen.	7	16	-2.866
Male gen.	5	18	-3.689

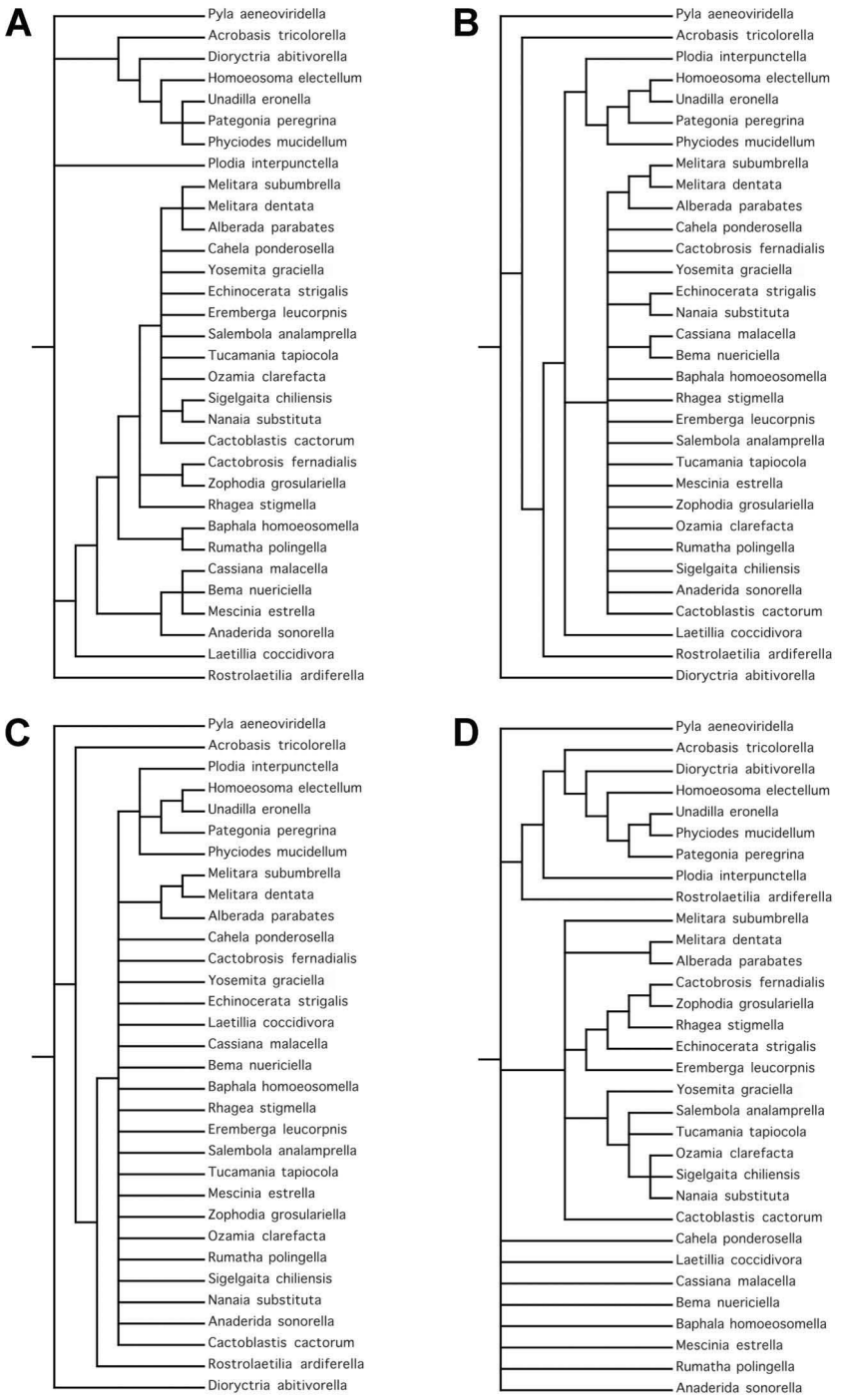

Fig. 3. Strict consensus trees of four analyses of partial datasets. A Excluding wing and pregenitalic characters (232 trees, 138 steps). B Excluding genitalic characters (301 trees, 138 steps). C wing and pregenitalic characters only (3791 trees, 84 steps). D Genitalic characters only (404 trees, 86 steps).

acters and one unique apomorphy: 3:1, female antenna bipectinate, the current results support that decision.

Clade 20 comprises the members of the *Mescinia*-group, a group of genera thought to be closely related (together with the Central American genus *Apatunga* Heinrich) by Heinrich (1956) and Neunzig (1997). Though Heinrich did not formally include *Bema* in this group he noted that its male genitalia are of the '*Mescinia* type'. The clade is supported by one unique apomorphy: 56:1, uncus in dorsal view narrow and pointed. The Bremer support is only 1. The internal phylogeny of the *Mescinia*-group is uncertain, especially because neither *Apatunga* nor *Barberia* were included in the present cladistic analysis.

Clade 23 comprises the representatives of the *Homoeosoma*-group. The group appears well supported by several more or less homoplastic characters and one unique apomorphy: 6:1, male antennae with a basal notch (see Neunzig 1997, plate D2). The close relationship based on this character was suggested by both Heinrich (1956) and Neunzig (1997). But since Roesler (1973) seems to illustrate this character state in several Palaearctic genera (*Ectohohoesoma, Patagoniodes, Rotrudosoma* and *Pararotruda*) the notched male antenna is probably an apomorphy for a larger group including these genera.

The positions of Olyca, Amalafrida, Barberia and Welderella.

Olyca, Amalafrida and *Barberia* all have a large, hook-shaped gnathal head (character 61:1). The nature of *Welderella's* gnathos could not be determined with satisfaction in the preparations available for this study. This indicates that the three former genera all belong in the group defined by clade 2 in Fig. 2. Furthermore, *Amalafrida* and *Olyca* both show strong affinities with clade 4 and the true cactus-feeders. In both taxa the mandibles are present as pointed rods (character 15:2), the maxillary palpus show affinities with other cactus-feeders (characters 13:1, 14:1), the male of *Olyca* has a slightly serrate antenna (character 1:1), the male of *Amalafrida* has bipectinate antenna (character 2:1), the female dorsum 8 has an anterior incision (character 44:1), both posterior and anterior apophyses show similarities with other cactus-feeders (characters 46:2, 47:2), the male tegumen has paired sclerotized lobes (character 55:1) and the gnathos head is split (character 62:0). In combination these characters all clearly demonstrate that the two genera belong in the cactus-feeders.

Barberia has the same narrow, triangular uncus found in the *Mescinia* group (character 56:1), indicating a close relationship with this clade. This relationship has previously been suggested by Shaffer (1968) and Neunzig (1997).

The phylogenetic position of *Welderella* remains problematic. Neunzig (1997) suggested that the genus might be close to *Laetilia* and *Rostrolaetilia* based on male genitalia. But I have not found any characters linking any of the three genera. The reduction of the male S8 does link *Welderalla* to clade 1 excluding *Rostrolaetilia*. Two other characters related to female genitalia (characters 47:2, 50:1) do indicate a closer relationship with the lower part of clade 5. However, the small mandibles (character 15:1) do not support a close relationship with the cactus-feeders. For the time being, the position of this genus remains a mystery.

Evolution of specialized larval feeding habits

As mentioned above, the results support a single origin of cactus-feeding larvae within the phycitines as the most parsimonious distribution of this feeding habit would be that it evolved at the base of clade 6 and is reversed in *Rhagea* (Fig. 2). The poor support of the groups within clade 6 in general does not allow a confident assessment of the evolution of host-plant associations within the cactus-feeding phycitines. Whereas a host plant shift from Cactaceae to Crassulaceae appears fairly simple as both plant families often occur in the same kind of habitats (e.g. Raven *et al.* 1999), the possible shift from Grossulariaceae (the food plants of *Zophodia*, the putative sister-group of clade 6 (Fig. 6)) to Cactaceae is harder to explain. This indicates that Grossulariaceae-feeding larvae could be a specialization of *Zophodia*.

The genera *Laetilia* and *Baphala* both have larvae that are predacious on scale insects (Heinrich 1956, Neunzig 1997). Though similar and highly specialized in lifestyle, the predacious larvae in these two genera appear to have evolved independently.

Data partitions and evaluation of different character systems

Several authors have pointed out that phycitines display a very high degree of homoplasy in their

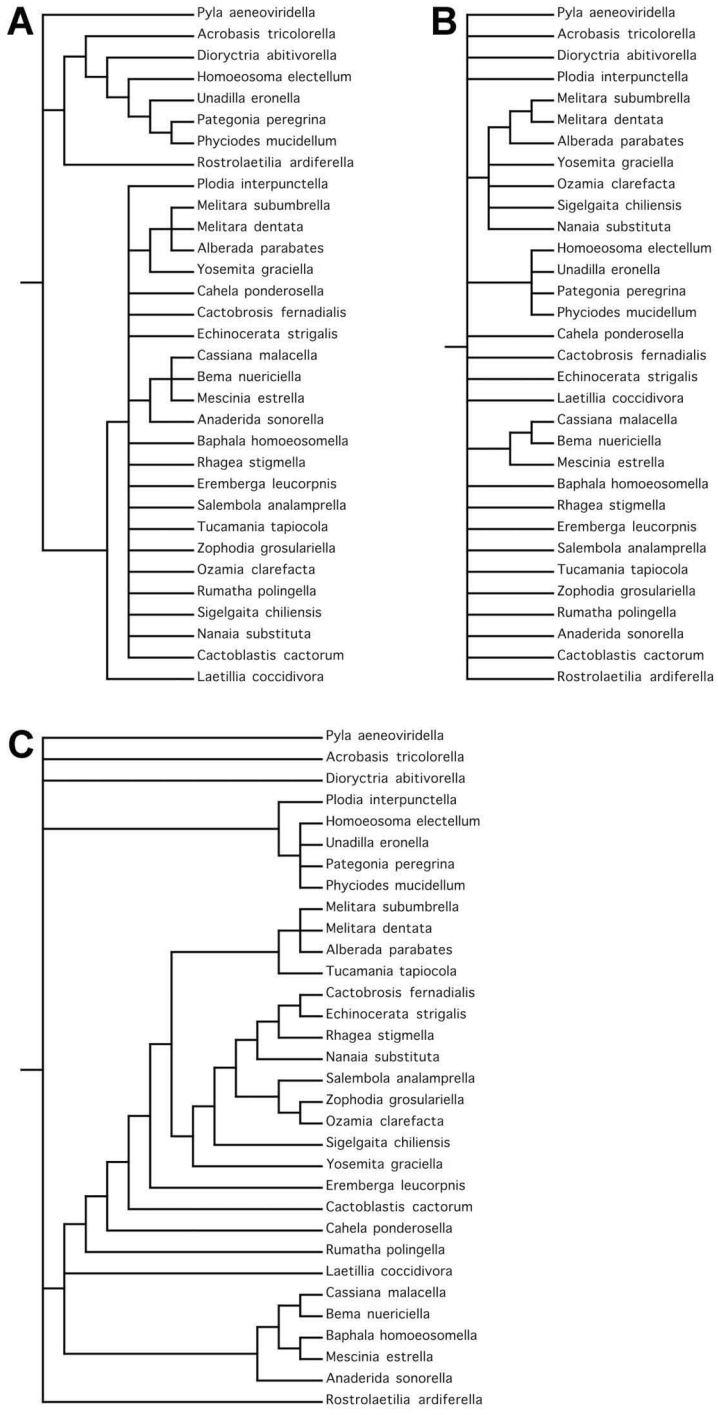

Fig. 4. Strict consensus trees of three analyses of partial datasets. A Excluding wing characters (36 trees, 197 steps). B Excluding pregenitalic characters (1912 trees, 195 steps). C Excluding head characters (20 trees, 199 steps).

adult morphology, and as a consequence relying on a single or few adult character systems such as wing venation or male genitalia would most likely result in a misleading phylogeny and thereby an unnatural classification (Heinrich 1956, Roesler 1986, Horak 1997, 2003). The present results strongly support these assumptions. Dividing the dataset into five partitions and examining their contribution to the overall support of the results through partitioned Bremer support (Table 3) reveals that characters related to the head are fairly ambiguous, yielding an overall contribution to PBS of 3.2, but supporting only 7 clades and disagreeing in 16. The characters related to wings and pregenitalic abdomen are contributing the majority of the support, the former supports 19 clades and disagrees in 4, the latter supports 17 clades and disagrees in 6. These character systems yield an overall contribution to PBS of 20.5 and 17 respectively. On the other hand, the female and male genitalic characters are strongly contradicting the overall result, the former supporting 7 clades and contradicting 16, the latter supporting 5 and contradicting 18, with an overall contribution to PBS of -2.9 and – 3.7 respectively.

This demonstrates that there is a high degree of homoplasy in the dataset, and could furthermore lead to the conclusion that genitalic characters are of lesser importance in reconstructing phycitine phylogeny, a view also put forward by Roesler (1986). However, reanalyzing the phylogeny with one or more datasets excluded show that this is not the case. When characters from the wings and pregenitalic abdomen are excluded from the dataset (Fig. 3A), the analysis still recovers clade 4 (Fig. 2) as a monophyletic unit. The *Mescinia*-group is also recovered as a monophyletic sister group of the clade 4, and *Laetilia* is the sister of clade 4 + *Mescinia* gr. Furthermore, the *Homoeosoma*-group is recovered as monophyletic. When genitalic characters are excluded from the analysis the result is far less resolved (Fig. 3B), but the overall pattern still reflect the combined results fairly well. Of the major clades, only the *Homoeosoma*-group, the *Melitara – Alberada* clade, clade 1 and clade 2 are recovered, and clade 2 shows almost no internal resolution. When wings and pregenitalic abdomen are analyzed alone the result is even less resolved (Fig. 3C), only clade 1, the *Melitara – Alberada* clade and part of the *Homoeosoma*-group are recovered, and most taxa within clade 1 are placed in a large polytomy. When genitalia characters are analyzed alone (Fig. 3D), the result appears more resolved than that of wings and pregenitalic abdomen. However, a closer examination reveals that compared to the full dataset analysis, only the *Homoeosoma*-group is recovered. The rest of the "genitalia only" tree bears little similarity to the tree in Fig. 2.

Of the three data partitions that yield a positive contribution to the total partitioned Bremer support, characters from the pregenitalic abdomen seem to be of greatest importance. When wing characters are excluded (Fig. 4A), the *Homoeosoma*-group is recovered, and *Plodia* is included in clade 2 and clade 3 which are otherwise recovered. The *Melitara – Alberada – Yosemitia* clade, and the *Mescinia* group are likewise recovered, but placed in a large polytomy in clade 3. When pregenitalic abdomen characters are excluded (Fig. 4B), only the *Melitara – Alberada* group, the *Homoeosoma*-group and part of the *Mescinia*-group are recovered, and most taxa are placed on a large, basal polytomy. When head characters are excluded (Fig. 4C) the result is still well resolved and bears overall similarity to the total analysis. Principal differences are: Clade 1 is not recovered, *Plodia* is the sister group of the *Homoeosoma*-group, *Baphala* is removed from the cactus-feeders s.l. and placed within the *Mescinia*-group, the *Mescinia*-group is not necessarily the sister group of the remaining cactus-feeders s.l., and the internal phylogeny of the cactus-feeders s.l. differs somewhat from that of the total analysis.

The apparent importance of the pregenitalic abdomen for reconstructing phycitine phylogenies is not entirely surprising, since a wide variety of sexual secondary characters are found in males of many groups (i. e. Dickens 1936, Heinrich 1956, Horak 1997, T. J. Simonsen & A. D. Roe unpublished). Horak (1997) pointed out that though these characters have been assumed to display a high degree of homoplasy, their structure (if they are present) is often constant within genera, but varies at higher level and might as such be of phylogenetic importance.

The results presented here demonstrate that even within a small group of Phycitinae, such as the cactus-feeders and their closest relatives, there is a high degree of character homoplasy. The results underline the importance of employing as many character systems as possible when studying phycitine phylogeny and evolution. In this study, only pinned museum specimens were readily

available, hence only classical characters from skeletal adult morphology could be included. Therefore, molecular characters from both mitochondrial and nuclear genes should be combined with the present adult morphology in a future revision. Given the low support most clades received, and the sensitivity to character sampling demonstrated above, there is little doubt that inclusion of molecular data will change some of the results. Ideally, characters from larvae and pupae should be included in a future study as well, but as the immature stages of many taxa are very poorly known (if at all), this does not seem possible at the moment.

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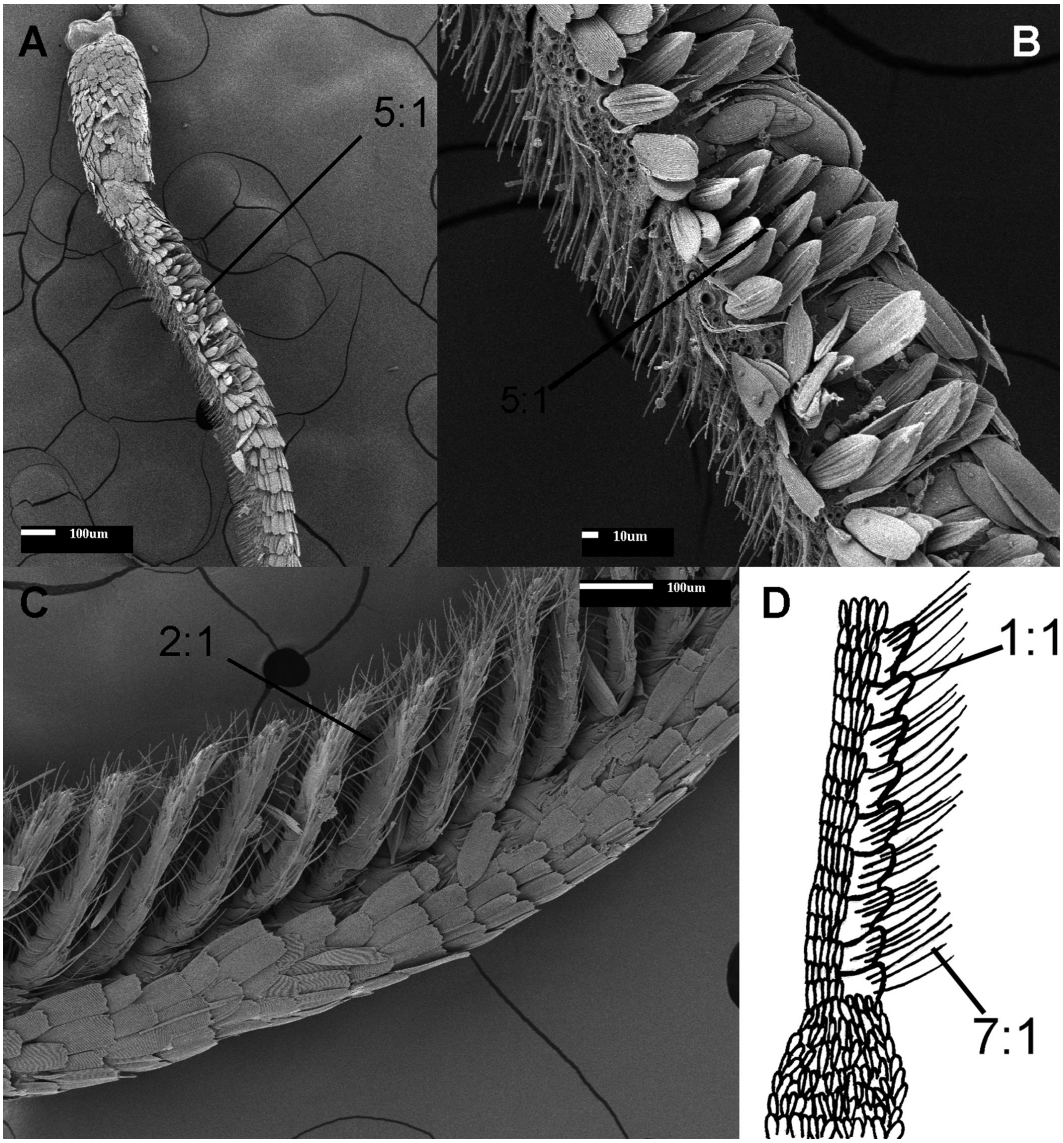

Fig. 5. Antenna characters. A Base of antenna of male *Zophodia grosulariella*. B Detail of A. C Antenna flagellum of male *Alberada parabates*. D Base of antenna of *Echinocereta strigalis* (redrawn after Neunzig 1997).

Appendix 1. List of Characters

Head:

1: Male antenna serrate: 0 = absent, 1 = present (Fig. 5D).
2: Male antenna bipectinate: 0 = absent, 1 = present (Fig. 5C).
3: Female antenna bipectinate: 0 = absent, 1 = present.
4: Male antenna with dorsal spine-like sensilla: 0 = absent, 1 = present (Neunzig 1997, fig. 20c).
5: Flagellum of male antenna basally with patch of scale-like sensilla: 0 = absent, 1 = present (Fig. 5A, B).

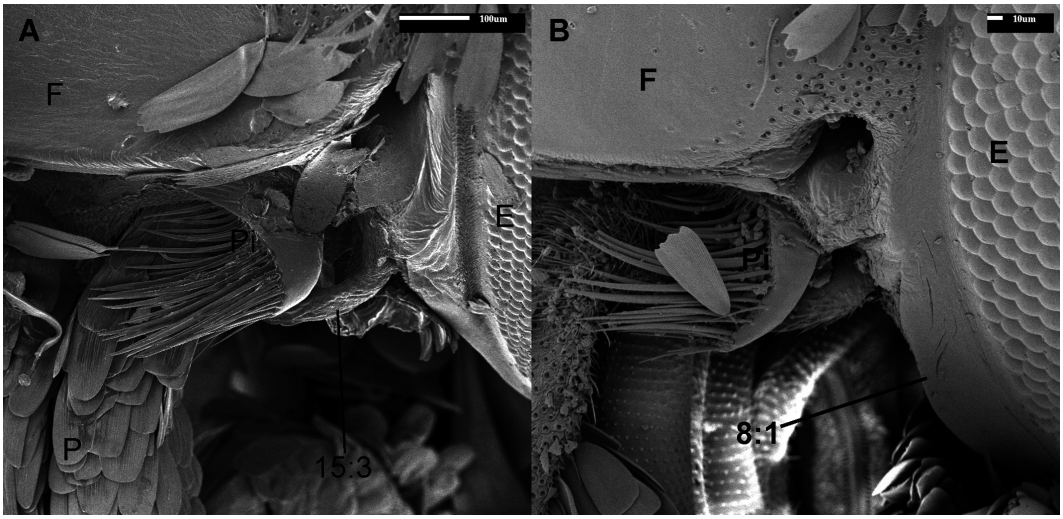

Fig. 6. Mandible and eye-ridge. A *Alberada parabates*. B *Zophodia grosulariella*. Abbreviations: E Eye. F Frons. P Proboscis. Pi Pilfers.

6: Male antenna with a basal notch: 0 = absent, 1 = present (Neunzig 1997, plate D2).
7: Hair-like sensilla on antenna almost as long as segments are wide: 0 = absent, 1 = present (Fig. 5D).
8: Sharp ridge between eye and labial palpus: 0 = absent, 1 = present (Fig. 6B).
9: Position of chaetosomata with respect to eye: 0 = anterior to dorso-basal corner of eye, 1 = over corner, 2 = posterior to corner.
10: Ocellus present: 0 = absent, 1 = present.
11: Ocellus placed in an anterior incision of chaetosomata: 0 = absent, 1 = present (Fig. 7).
12: Basal segment of labial palpus with a conspicuous ventral fan of scales: 0 = absent, 1 = present.
13: Terminal segment of maxillary palpus with a fan-shaped tuft of scales: 0 = absent, 1 = present.
14: Terminal segment of maxillary palpus pointed outwards: 0 = absent, 1 = present.
15: Size and shape of mandibles: 0 = almost absent, 1 = small triangular lobe, 2 = pointed rod, 3 = long, curved rod (ordered) (Fig. 6A).

Wings:

16: FW: Small ventral fold basally on costa in both sexes: 0 = absent, 1 = present.
17: FW: Rs_{2+3} and Rs_4: 0 = diverge before the end of Rs_1, 1 = diverge well after the end of Rs_1, 2 = Rs_{2+3} and Rs_4 fused for their entire length (Fig. 8).
18: FW: M_{2+3}: 0 = fused for their entire length, 1 = diverge before the wing margin, 2 = entirely separate (Fig. 8).
19: FW: M_{2+3} if not fully fused: 0 = diverged for more than half their length, 1 = diverged for less than half their length (Fig. 8).

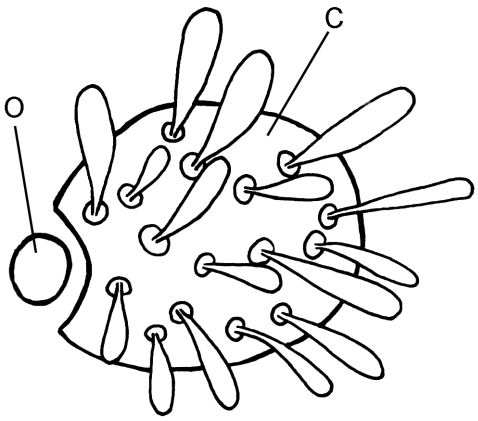

Fig. 7. Character 11:1. Ocellus (O) placed in an anterior incision of chaetosomata (C).

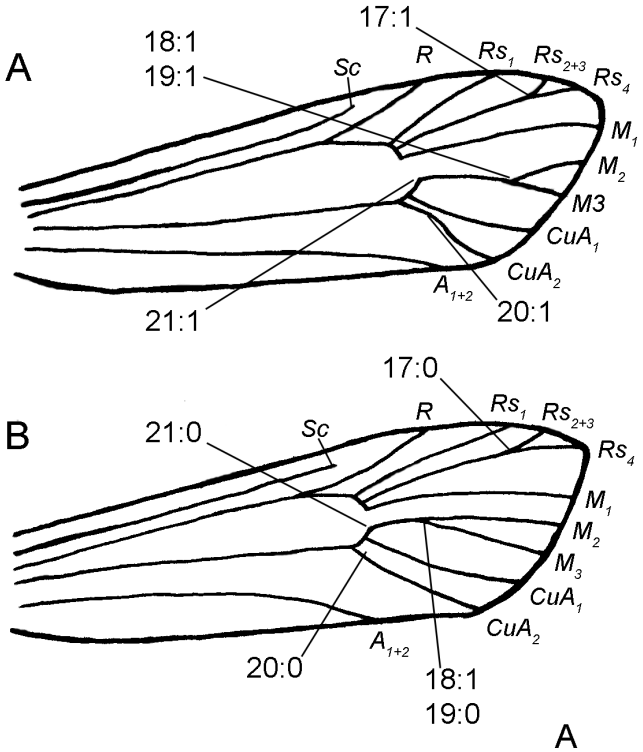

Fig. 8. Forewing venation characters exemplified by A *Cassiana malacella* and B *Zophodia grosulariella*. Overall wing shape stylized.

20: FW: CuA_1 and CuA_2 close together at base, CuA_2 then sigmoidly swung away from CuA_1: 0 = absent, 1 = present (Fig. 8).
21: FW: Cell projected further posteriorly than anteriorly: 0 = absent, 1 = present (Fig. 8).
22: HW: Sc+R and Rs: 0 = fully separeted, 1 = Sc+R and Rs fused basally but diverge before wing margin, 2 = fused for their entire length (ordered) (Fig. 9).
23: HW: M_1: 0 = basally free from stem of Sc+R+Rs, 1 = M_1 connected to stem by a small cross vein (Fig. 9).
24: HW: M_{2+3}: 0 = fused for their entire length, 1 = diverge before the wing margin (Fig. 9).
25: HW: CuA_1 and M_{2+3} fused basally: 0 = absent, 1 = present (Fig. 9).
26: HW: Cell distally with vestigial anterior cross vein: 0 = absent, 1 = present (Fig. 9).

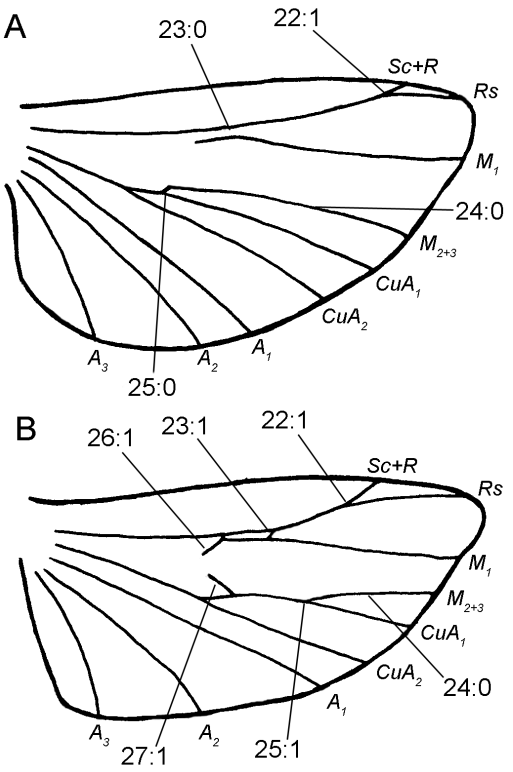

Fig. 9. Hind wing venation characters exemplified with by A *Homoeosoma electella* and B *Rhagea stigmella*. Overall wing shape stylized.

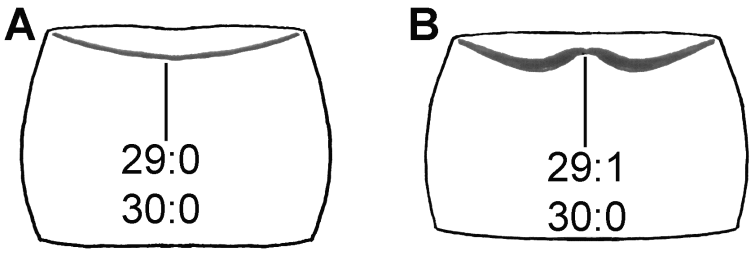

Fig. 10. Antecosta (Ac) of Tergum 3 (T3).

27: HW: Cell distally with vestigial posterior cross vein: 0 = absent, 1 = present (Fig. 9).

Pre-genitalic abdomen

28: T3 antecosta: 0 = ring shaped, 1 = M-shaped (Fig. 10).
29: T3 antecosta: 0 = entire, 1 = split centrally
30: S3 antecosta: 0 = membranous, 1 = sclerotized
31: S3 antecosta: 0 = entire, 1 = split centrally
32: T4 antecosta: 0 = entire, 1 = split centrally
33: T5 antecosta: 0 = entire, 1 = split centrally
34: T6 antecosta: 0 = entire, 1 = split centrally
35: Male T8 with a well defined bridge between antecosta and tergal plate: 0 = absent, 1 = present (Fig. 11).
36: Bridge of male T8: 0 = short and wide, 1 = more than twice as long as wide (Fig. 11).
37: Antecosta of male T8 sclerotized, wide and

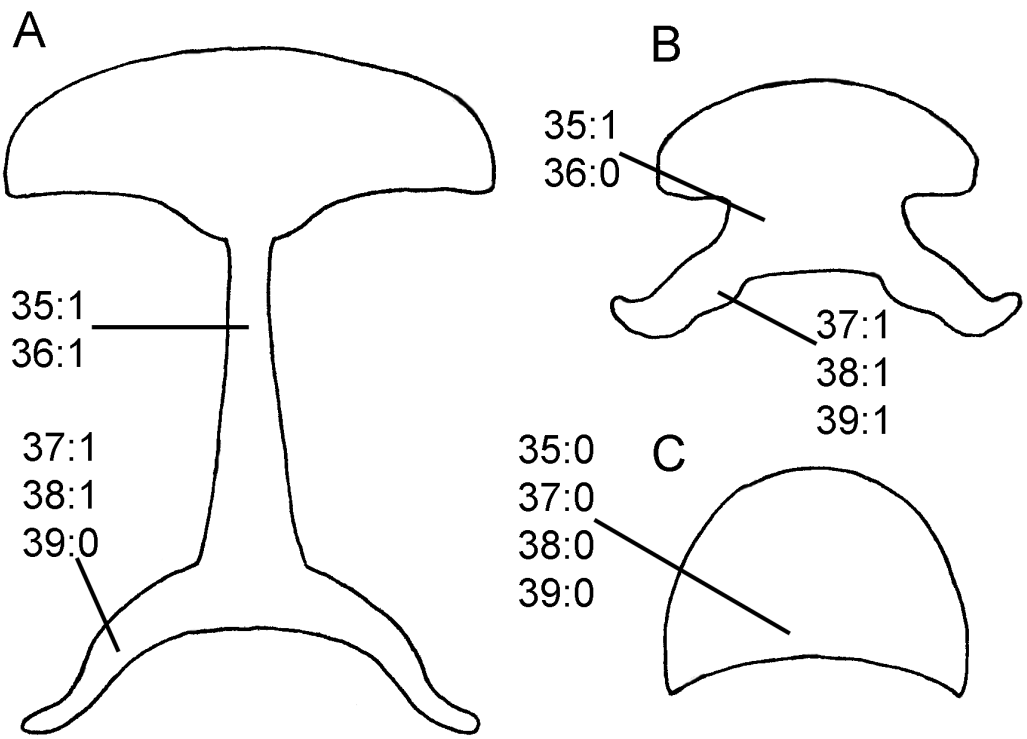

Fig. 11. Tergum 8 (dorsal view). Male characters exemplified by A *Ozamia clarefacta*, B *Melitara subumbrella* and C *Unadilla erronella*.

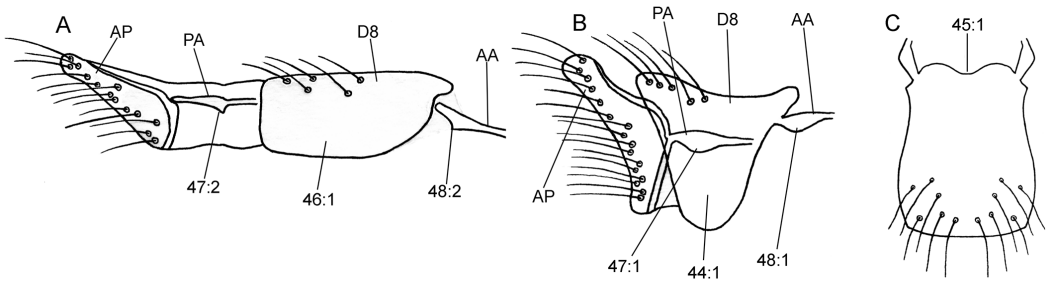

Fig. 12. Female genitalia characters exemplified by A *Sigelgaita chilensis* (lateral view), B *Melitara dentata* (lateral view) and C *Echinocereta strigalis* (dorsum 8 dorsal view). Abbreviations: AA Anterior apophysis. AP Anal papilla. D8 Dorsum 8. PA Posterior apophysis.

free from plate laterally: 0 = absent, 1 = present (Fig. 11).

38: Antecosta of male T8 laterally lyre shaped: 0 = absent, 1 = present (Fig. 11).

39: Antecosta of male T8 with latero-posterior "shoulders": 0 = absent, 1 = present (Fig. 11).

40: Male sternite 8 reduced to a small, anterior structure (antecosta): 0 = absent, 1 = present.

41: The reduced male sternite 8 shaped as a triangular three dimensional structure: 0 = absent, 1 = present.

42: A pair of large, lateral scale tufts present anteriorly on male A8 (between antecosta of T8 and S8: 0 = absent, 1 = present.

Female genitalia

43: Sclerotization of dorsum 8 in lateral view: 0 = cylindrical or flattened, 1 = high and clearly triangular (Fig. 12B).

44: Sclerotization of dorsum 8 in dorsal view with a centro-anterior incision: 0 = absent, 1 = present (Fig. 12C).

45: Sclerotization of dorsum 8: 0 = cylindrical, 1 = flattened and clearly longer than high (Fig. 12A).

46: Base of posterior apophysis: 0 = narrow, 1 = clearly diamond shaped thickened, 2 = thickened with a ventral point (Fig. 12).

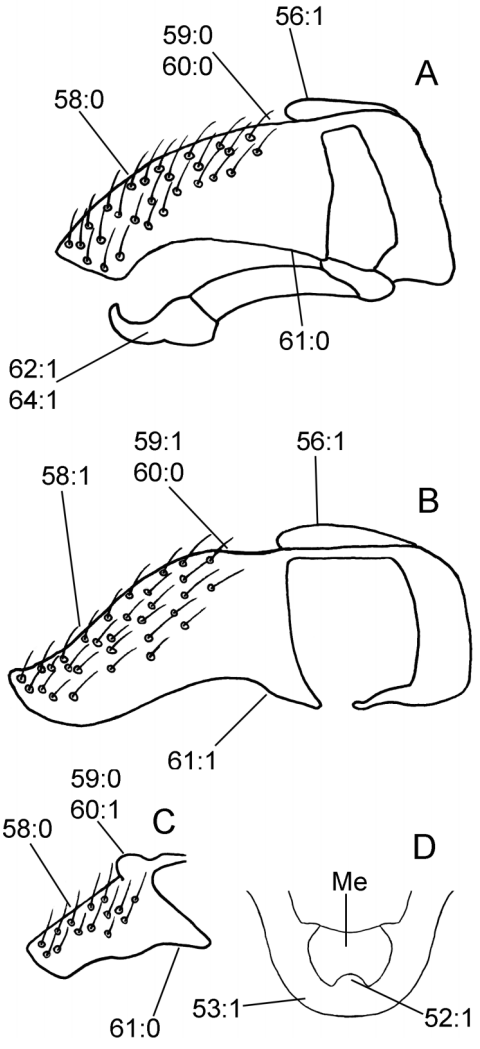

Fig. 13. Tegumen, uncus, gnathos and saccus. Male genitalic characters exemplified by A *Melitara dentata* (tegumen, uncus and gnathos, lateral view), B *Rhagea stigmella* (tegumen and uncus, lateral view, gnathos removed), C *Rumatha polingella* (uncus, lateral view, tegumen and gnathos removed) and D *Melitara dentata* (saccus, dorsal view). Me membranous central area of saccus.

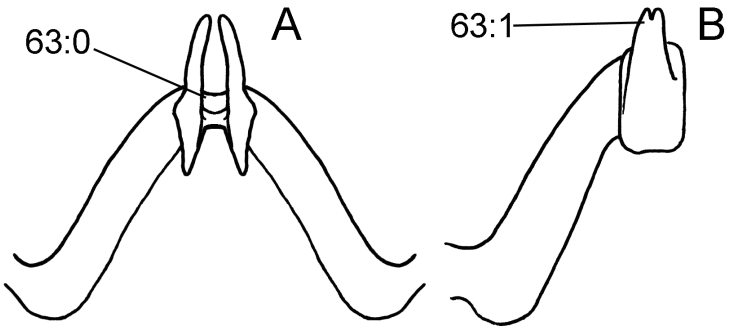

Fig. 14. Gnathos. Male genitalic characters exemplified by A *Melitara dentata* (gnathos, ventral view) and B *Cahela ponderosella* (gnathos, ventral view, left gnathal arm removed).

47: Base of anterior apophysis: 0 = narrow, 1 = clearly diamond shaped thickened, 2 = thickened with a ventral point (Fig. 12)
48: Bursa ostium sclerotized ventrally: 0 = absent, 1 = present.
49: Bursa ostium sclerotized dorsally: 0 = absent, 1 = present.
50: Ductus seminalis originates anteriorly on corpus bursae: 0 = absent, 1 = present.

Male genitalia

51: Saccus with a ventro-central hump proceeding into central membranous area: 0 = absent, 1 = present (Fig. 13D).
52: Saccus in dorsal view: 0 = rounded, horseshoe shape, 1 = longer and more rectangular, 2 = more triangular pointed (Fig. 13D)
53: Saccus in lateral view dorso-ventrally very narrow: 0 = absent, 1 = present.
54: Saccus in lateral view curved upwards: 0 = absent, 1 = present.
55: Tegumen dorsally with paired sclerotized lobes: 0 = absent, 1 = present (Fig. 13).
56: Uncus in dorsal view: 0 = broad and rounded triangular, 1 = more narrow and pointed.
57: Uncus in lateral view recurved, "duck-bill" like: 0 = absent, 1 = present (Fig. 13B).
58: Dorsal base of uncus in lateral view with a flat "dent": 0 = absent, 1 = present (Fig. 13B).
59: Dorsal base of uncus in lateral view with a pair of rounded "bumps": 0 = absent, 1 = present (Fig. 13C).
60: Ventral margin of ventro-basal corner of uncus with a basal "hump": 0 = absent, 1 = present (Fig. 13B).
61: Gnathos with a large, hook-shaped head: 0 = absent, 1 = present (Fig. 13A).
62: Gnathal head: 0 = split except dorsally, 1 = more fused but always with split tip, 2 = fully fused (ordered) (Fig. 14).
63: Gnathos: 0 = curved downward distally, 1 = very straight, head pointed posteriorly (Fig. 13A).
64: Dorsal valve margin: 0 = straight or slightly curved, costa continuing to the tip of valva, 1 = convexly curved, costa terminating abruptly before valve tip (Fig. 15).

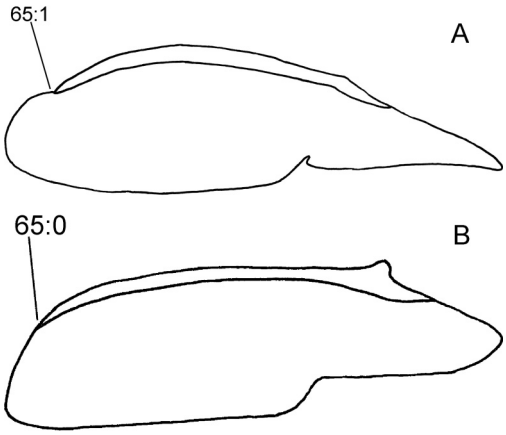

Figure 15. Valve. Male genitalic characters exemplified by A *Cassiana malacella* (outside view) and B *Cahela ponderosella* (outside view).

Appendix 2. Character Matrix

Pyla_aeneoviridella	0000000121000000002-0000101101111110-0—0--0000001100000000001200
Acrobasis_tricolorella	0000000101000000010001010011011111 0-0—0--0010000000100000000--0
Dioryctria_abitivorella	0000000111000010 02-0000100111111110-1000-0001100000110000010 0--0
Plodia_interpunctella	00000001-101001020-00200000000-111110--1000000011001000000000--0
Melitara_subumbrella	0110000011011130011001000110010000101111001101100010001001001000
Melitara_dentata	0110000011011130011001000110010000101111001101100010001000001010
Homoeosoma_electellum	0000010121000011 20-0110000010101110-1001000010000001 0000-0101200
Alberada_parabates	0100000011011130010001001110010000101111001101100010001000001010
Cahela_ponderosella	1000001110-1102001010100111001001110110100010120100000010000011100
Cactobrosis_fernadialis	0100100101010020110111001110010000111101110110011101001011001000
Yeosemita_graciella	0000000011011120010101001010010110101101100101100001001001001001
Echinocerata_strigalis	1000001111110020110101001000010000111101100100111100001011001000
Laetillia_coccidivora	0000000121010010110001101011010111 0-1001000000011100001000001100
Cassiana_malacella	0001000100-1001011111110100101011111110011100010111011001000010 01
Bema_nuericiella	0000000100-1001010-0111000010101111 1---11?0010000101100100001101
Baphala_homoeosomella	0000100111010020111001 10{01}0000101111111011101010111010000001 01100
Unadilla_eronella	0000010121000011 20-1010000010101110-0001000010010002110000101100
Rhagea_stigmella	0000000101010020110001101110010000101101000102111101001011011000
Eremberga_leucorpnis	1000001121111020010101101110010111101101000101111010001011001001
Pategonia_peregrina	0000010121010011 20-0010000010101111010010000100000000100001012 00
Phyciodes_mucidellum	0000010121010010210002000001010111010010000100000021100001012 00
Salembola_analamprella	1000000101101130010101101110010111111101110101000101001001011001
Tucamania_tapiocola	1000001001111030010101101110001000101101000101000000001001011001
Mescinia_estrella	0001000101010010110-0110000101111111111011100000111010001001010 01
Zophodia_grosulariella	0000100101010020010001001010010111111001110110101101001001001000
Ozamia_clarefacta	0000100001011020010101001010010011111101110002200001001001011010
Rumatha_polingella	0000000101011020010101101010010110101001000100211000001000101200
Sigelgaita_chiliensis	0100000111111020010101101110010110101101100112200011001011011011
Nanaia_substituta	01?0000101111020010101001000010000111001100102211101001001011011
Anaderida_sonorella	0000000101010010010001101011010000111001110000011101001101001100
Cactoblastis_cactorum	1000001101111120010101001110010111101101001101010000001001001110
Rostrolaetilia_ardiferella	0000000121000010010010010110?? ---0-1000-0000001100001000000--0