

The larval characterization of the Noctuidae sensu Hampson and of the Nolidae sensu stricto, sensu Hampson and its influence on phylogenetical systematics (Lepidoptera: Noctuidae)

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Abstract

A characterization of the classical Noctuidae sensu Hampson, Boursin, Hartig & Heinicke, Nye and Poole is achieved by considering larval morphology. Larval characters indicate that the Noctuidae sensu Hampson and the Nolidae sensu stricto sensu Hampson are monophyletic. Comparison of the setal maps of the larvae of *Tyria jacobaeae* (Hübner) and *Jocheaera (Apatele auct.) alni* (Linnaeus) with the common chaetogram of the Noctuidae demonstrate this, and suggest, as already supposed from imaginal systematics, that the Arctiidae are the sister-family of the Noctuidae. The choice of unsuitable imaginal character systems plus the failure to include suitable features of the immature stages and especially the wrong interpretation of reversals and the acceptance of using them (as part of a new holomorphy of a quite different taxon) have resulted in the present unsatisfying situation of the higher classification of the Noctuoidea, especially of the Noctuidae.- A larval characterization of the classical Nolidae sensu stricto, sensu Hampson is given. This precludes any combination between these Nolidae and the Noctuidae sensu Hampson. The capacity of phylogenetical systematization is complicated by reversals or limited by them if they will not be used as characters of a completely different and modern taxon (as compared with the "plesiomorphic" more ancient one).

KEY WORDS: Lepidoptera, Noctuidae, phylogenetic systematics, monophyly, larval systematics, imaginal systematics, molecular systematics.

La caracterización larval de los Noctuidae sensu Hampson y de los Nolidae sensu stricto, sensu Hampson y su influencia en la sistemática filogenética (Lepidoptera: Noctuidae)

Resumen

Se consigue una caracterización de los clásicos Noctuidae sensu Hampson, Boursin, Hartig & Heinicke, Nye y Poole considerando la morfología larvaria. Las características larvarias de los Noctuidae sensu Hampson y los Nolidae sensu stricto sensu Hampson indican que son monofiléticos. La comparación de los mapas setales de las larvas de *Tyria jacobaeae* (Hübner) y *Jocheaera (Apatele auct.) alni* (Linnaeus) con el común setograma de los Noctuidae demuestran esto y sugieren, tal y como suponía la sistemática de los imagos, que los Arctiidae son un grupo hermano de los Noctuidae. La elección de caracteres cualitativos inadecuados de los imagos sumando al no haber incluido las características apropiadas de las fases inmaduras y especialmente la interpretación equivocada de los reverses mas la renuncia a usarlos (como parte de un Nuevo holomorfismo de un taxon muy diferente) han desembocado en la actual situación poco satisfactoria de la más alta clasificación de los Noctuoidea, especialmente de los Noctuidae.- Se da una caracterización larval de los clásicos Nolidae sensu stricto, sensu Hampson. Esto impide cualquier combinación entre los Nolidae y los Noctuidae sensu Hampson. La capacidad de la sistemización

filogenética se ve complicada por los reveses o limitada por estos si éstos no son utilizados como caracteres de un taxon completamente diferente y moderno (como comparar con el “plesiomorfo” más antiguo).

PALABRAS CLAVE: Lepidoptera, Noctuidae, sistemática filogenética, monofilia, sistemática larvaria, sistemática de los imagos, sistemática molecular.

Introduction

The stimulation for the present investigation and the results

No one has been more occupied with the systematics and the characterization of the Noctuidae and their subfamilies than KITCHING (1984, 1987), KITCHING & RAWLINS (1998) and YELA & KITCHING (1999).- After the ‘SOS-call’ of YELA & KITCHING (1999: 512) “How, then, can Noctuidae be characterized?” the latest treatment by LAFONTAINE & FIBIGER 2006 (“the lack of any consistent character state to define the Noctuidae sensu lato”) and the convictions of WELLER *et al.*, 1994, KITCHING & RAWLINS, 1998, YELA & KITCHING, 1999 and MITCHELL *et al.*, 2006, the Noctuidae sensu lato, should be most probably polyphyletic.

I myself could not believe this to be the case, especially because I had put so much time into this family and also because in 1999-2000, I had published the summary of more than 40 years experience with the European larvae of the Noctuidae sensu Hampson. After the splitting of the family Noctuidae sensu Hampson by FIBIGER & LAFONTAINE, 2005, I rapidly presented the larval characterization of the Noctuidae sensu Hampson (Beck, lecture at the SEL-congress at Rome 2005) which now is revisited and refined.

In spite of my broad investigations with larvae of the European Noctuidae I was not concerned with this problem before the publication of WELLER *et al.* (1994) of which I was informed by Hasenfuss in 1998. WELLER *et al.* (1994) doubted that the Noctuidae were monophyletic. So shortly before the publication of my books “The larvae of the European Noctuidae, revision of the systematics of the Noctuidae” (BECK, 1999-2000). I was not able to give an original analysis of the matter based on my studies of larval characters, especially because I had not had the opportunity to examine larval material of possible outgroups. I also relied on the results of the investigations of Hasenfuss (pers. comm.), who explained that based on his understanding of larval characters there was no principal distinction between the Arctiidae and Noctuidae. In spite of and stimulated by Kitching and others, I investigated the larval outgroup-material which Hasenfuss kindly lent me and I could find in the unisetose larvae of the genera *Tyria* Hübner and *Utetheisa* Hübner (both Arctiidae) some characters for a monophyletic characterization of the Noctuidae, but on the other hand, an understanding of the presence of so many larval-arctiid traits within the Noctuidae (especially within the Acronictinae) which made it impossible for Kitching (and also for Hasenfuss) to characterize the Noctuidae as monophyletic, based on larval characters.

Material

Arctiidae: last-instar larvae of *Tyria jacobaeae* Hübner and of *Utetheisa* Hübner-species (from Central America), preserved in isopropyl-alcohol, both leg. Hasenfuss.

Noctuidae: the setal map (= chaetogram) of *Jocheaera* (*Apatele* auct.) *alni* (Linnaeus) (adapted from AHOLA & SILVONEN, 2005), the common setal map of the ultimate instar larva (BECK, 1999, fig. A21a) which is based on the investigations of the larvae of more than 2000 species of Noctuidae (from: 1- the collection of Beck, 2- the material in the book of CRUMB, 1956, 3- by the experiences with the material of Rawlins, Godfrey and McCabe and, 4- the material of my friend Ahola, 5- additional informations found in the literature on Lepidoptera of Japan, China and India).

Nolidae: newly hatched L1-larvae of *Nola squalida* Staudinger, leg. Rosset, France (IX-2007), L1-larvae of *Meganola togatalis* Hübner, leg. Beck (VI-2008), Spain, Aranjuez.

Methods

Ultimate instar were investigated under the microscope under low magnification (3x5, 3x10), newly hatched L1-larvae of the Nolidae under higher magnification (3x45, 10x45). The important characters were fixed by line-drawings which were then made into the schematic chaetograms or semischematic figs. in this paper.

Abbreviations

A1-A10 = abdominal segments (rings) 1-10. A3-A6/SV-setae: SV-setae on A3 to A6. A9/L-setae: L-setae on A9.

L1-L3, or only L1, L2, L3 = the three lateral setae which surround the spiracles on A1 to A8.

L1-instar = first larval instar.

SV = subventral bristles (= setae) (e. g. 2 SV-setae on T2 and T3 or there only one SV-seta; or 2 SV-setae on A1 or 3 SV-setae on A2).

T1-T3 = thoracic segments (rings) 1-3. T2 / SV-setae, T3 / SV-setae: SV-setae on T2, resp. on T3

St = spiracle (stigma)

The present situation in phylogenetic systematizing of the Noctuidae resp. Noctuoidea by imaginal- and molecular-genetic investigations. Satisfying results of phylogenetic inferences depend on the choice of suitable characters

Because the imagines of the Lepidoptera are notoriously difficult to investigate, the imaginal systematists concentrate on and specialize in one specific organs, e. g. the tympanum, the wing-venation, the genitalia, the antenna, the proboscis, the legs and further characters which are so far unsuitable for phylogenetic conclusions concerning the characterization of the Noctuidae. By doing these selected organ-studies the 'holomorphy' is neglected. For details look at KITCHING (1984, 1987), KITCHING & RAWLINS (1998), YELA & KITCHING (1999), SPEIDEL *et al.* (1996), HOLLOWAY (1998). As examples of the difficulties in these imaginal investigations but also of the choice of some unsuitable larval organs or the restriction to only a special condition of these, with neglect of the whole setal pattern and further traits (e.g. the SV-setae on T2 and T3) we can look at the following sentences taken from YELA & KITCHING (1999): The recently proposed apomorphies (MINET, 1986) which were thought to be good were revealed to be more complex (homoplasious) than previously thought: 1. The small sclerotized band that links the anterolateral elongations of St2 (= sternite of the 2nd abdominal segment) with the corresponding laterotergal sclerite is distinctly widened dorsally. 2. The counter-tympanal cavities are ventrally very close to one another or even broadly contiguous.- However, the former character also occurs in Arctiinae and is not found in many Noctuidae, while the latter feature is present in the majority of Nolidae, Lymantriidae and some Notodontidae, and is not developed in several basal noctuids. "Many larvae of Noctuidae are unique among Noctuoidea in having a cylindrical galeal lobe on the maxillary complex.... However, because some noctuid larvae do not have a cylindrical galeal lobe, the derivation may not be apomorphic for that family.... In addition, noctuid larvae have only a single SV seta on thoracic segments T2 and T3. However the unisetose condition occurs in many notodontids and nolid taxa while a few noctuids have the bisetose condition (see below), probably as a secondary derivation". Additionally YELA & KITCHING (1999) mention a further putative apomorphy for the Noctuidae: the origin of the retractor muscles for the posterior apophyses of the female genitalia (corresponding to the urosomite IX = A9), that anchor in urosomite VII (= A7) rather than in urosomite VIII (= A8) (STEKOLNIKOV, 1967). This is also a condition of no true apomorphy.

In addition to the fact that all these features are not unique for the Noctuidae, the former two imaginal ones and the condition of the galeal lobe of the larvae do not deserve the term "apomorphic".

Apomorphy means an unexchangeable unique (morphological) feature, characteristic only for a certain taxon and not a feature of gradual differences in different taxa.

The above cited feature, "bisetose" condition (of the SV-group on T2 and T3) in some Noctuidae: "probably as a secondary derivation", is now clarified. This bisetose condition in the Noctuidae is to be found at very different positions in the system (often very closely in related genera and subgenera, present in one and missing in the other, see below). It is to be understood as a reversal (in the molecular-genetical sense of returning the temporary suppression of the operator-genes, BECK, 1992: 10; POOLE, 1995) and not as a secondary derivation. On the contrary, the unisetose conditions in Notodontidae and "Nolidae" and in the Noctuidae sensu Hampson are convergent. In the Nolidae sensu stricto *Nola squalida* Staudinger has in the L1-instar on T2, T3 each one SV-seta, fig. 11.

The reasons the imaginal systematists as yet cannot find "exclusive" autapomorphies within the family for characterizing this are: 1. the choice of unsuitable (equivocal) characters. 2. Possibly the imaginal morphology as a whole does not provide such characters at the family level of the Noctuidae.- For comparison, curiously, at superfamily level there are good autapomorphies, larvally as well as imaginally: the two MD-setae on the metathorax of the larvae of the Noctuoidea (exception Oenosandriidae) and the position of the tympanum on the metathorax.- These are also signs to look for suitable characters as autapomorphies: a clearly different and simple construction and/or a specific position of certain characters are more suitable than the differentiation of very complex characters, e. g. of the tympanum which itself is exposed to a heavy pressure of selection and adaptation. Instead, the "simple" characters of a chaetogram (which are stabilised through a long period of evolution) are easily to be examined and so very suitable to control a large sample.

But in nearly all characters there lurk homoplasies, either as convergences or as reversals. The many exceptions from "good" apomorphies are often due to reversals of plesiomorphic conditions, which, within the family, can occur anywhere and with very different frequency, independently of the degree of evolution. Therefore a characterization of higher taxa is often achieved only by a combination of several autapomorphic characters.

The present attempt by LAFONTAINE & FIBIGER, 2006 (based on MITCHELL *et al.* [2005] 2006), to integrate the otherwise well characterised families Arctiidae, Nolidae, Lymantriidae as subfamilies within a much larger family of Noctuidae, has to be rejected. The LAQ (= Lymantriidae, Arctiidae, Quadrifine Noctuidae) - clade of molecular systematical investigations (MITCHELL *et al.*, 2006) can just as well be interpreted as a sister-relationship at least of the Arctiidae to the Noctuidae sensu Hampson.

The consequences for the new systems, for the Noctuidae, resp. Noctuoidea (FIBIGER & LAFONTAINE, 2005; LAFONTAINE & FIBIGER, 2006) but also for the present systematic conclusions by molecular-genetical investigations are evident. The latter with its quantitative methods is not compatible with systematics which are based on some qualitative and essentially morphological characters. Just as for molecular-genetical investigations genes responsible for morphogenesis are not taken into consideration, present results are unreliable and very contradictory - sometimes in congruence with systematics according to (undoubted) morphological characters and sometimes not.

Value of reversals for elucidating descendance. Restrictions for applying the rules for phylogenetic systematizing or enlargement of the rules?

The phenomenon of reversals in its modern, molecular-genetically founded sense was unknown to HENNIG (1950).- Although Hennig postulated that plesiomorphic characters are not allowed for phylogenetic decisions, these (in the sense of reversals) are of high value in understanding the evolutionary history of a taxon, similar to the biogenetic rule of Haeckel. But, while the latter is an obligatory phenomenon for all taxa in the embryonic development of the respective higher taxon, e. g. a class or phylum, the reversals can appear at each level of evolution and with different frequency and unpredictable occurrence. E. g. within the Noctuidae in the genus *Autographa* Hübner, out of nine species investigated, the larvae of five species have three SV-setae on A1 (the condition of the

quadrifine series of subfamilies of the Noctuidae) and in the other species there are only two SV-setae (the condition of the trifine series of subfamilies of the Noctuidae). Within the Glottulini one genus, *Brithys* Hübner, shows on T2 and T3 two SV-setae each (a character of the Arctiidae), and the genus *Polytela* Guenée one SV-setae each (a character of the Noctuidae). In *Syngrapha* Hübner sensu auctorum, some species have two SV-setae, and others only one seta on T2 and T3.

Hitherto the reversals make it impossible for phylogenetic systematics to apply their theoretical tools everywhere (see the problems with the phylogenetical characterization of the Noctuidae). While phylogenetic systematics appears convincing in theory, in practice its successful application is restricted to suitable taxa (especially with a low number of species) or, exceptionally, when there are exact positions of certain characters (see above Noctuoidea) especially if there are undoubted apomorphic characters to higher (and speciose) taxa also.

But instead of ignoring the reversals (the present praxis) there is the possibility of using them as characters in a new context (holomorphis) of a completely different and more modern taxon (as compared to the ancient taxon where the “reversal-character” in question appeared for the first time and as a common part of its holomorphis).

Larval investigations and results, choice of suitable characters

After larval investigations on a very broad sampling of taxa (more than 2000 species) one finds (nearly) no autapomorphy without exception. The reason is the phenomenon of reversals and parallelisms.

A very suitable and easily controlled character system is the chaetogram of primary-setosed larvae (resp. in secondary-setosed larvae that of the primary-setosed L1-instar of these). The hypothesis put forth here is that there existed during the evolution within the Lepidoptera a common and regular setal map (chaetogram) of the primary setae (which already had been developed in the ancestors) in which the positions of the bristles are very consistent (HASENFUSS, 1963); this concerns the setae on the whole integument of the body (including the head) and represents, together with the shape of the larva, the mouthparts and a few additional characters, the external “holomorphis”. KITCHING & RAWLINS (1998: 365) write of the importance of the study of the larvae in order to construct a more stable system: “One of the most intractable problem in Lepidoptera classification has been the phylogeny of the quadrifid lineages of Noctuoidea. This is due to great homogeneity in adult morphology and widespread homoplasy in virtually every character system. Features of the immatures have been much more informative, but resolution of phylogenetical problems has been hindered by the absence of vouchered immatures for the vast majority of world genera. Understanding of relationships between and among the major subgroups awaits further research.”

But as demonstrated below: It is not necessary to have the larvae of all described species of the Noctuidae (resp. Noctuoidea) to make important conclusions about the phylogeny and higher classification of noctuid families and superfamilies; for many taxa some representative species (esp. the larvae of type species) are sufficient.

In spite of the critics of HEINICKE (1962) the beginning of the substitution of the Hampsonian system of the Noctuidae by a more natural system (BECK, 1960), was made possible by the investigation of less than 1 % of the then known 25000 species of the world Noctuidae.

In very speciose taxa (e. g. in the family Noctuidae, today with more than 35000 described species, KITCHING & RAWLINS, 1998) it can be nearly impossible to find unique synapomorphies common to all included taxa.

Comparison of the setal map of primary - setosed larvae of Arctiidae with those of Noctuidae

The following comparison of the setal maps of the Arctiidae (*Tyria jacobaeae*) with that of the Noctuidae *Jocheaera* (*Apatele* auct.) *alni* and with the common setal map of the Noctuidae - larvae shows the congruences and differences between both families.

	Arctiidae	Noctuidae	exceptions (= reversals) within the Noctuidae
number of T2,T3/SV-setae	2	1	Some
number of L3-setae on A1-A6 or only on A3-A6	2	1	Some
number of A9/L-setae	2	1	three (<i>J. alni</i> , <i>Ufeus</i> Grote, Agaristinae: <i>Sarbanissa transiens</i> Walker)
number of A7-A9/SV-setae or only A7/SV-setae	2	1	Some
number of A3-A6/SV-setae (on the outside of the prolegs)	4	3	Some
number of L-setae on the anal-prolegs	4	3	None
heteroid order of crochets	often	very rare	2 records (also in some Euteliinae, pers. comm. D. Wagner)
homoid order of crochets	rare	common	
Secondary setation	very often	rare	in Acronictinae with Pantheini, and in Dilobinae, Raphiinae, and in <i>Conistra</i> (<i>Dasyampa</i>) 'Hadeninae'
Primary setation	?rare	common	see the exceptions above

Table 1.– Comparison of the setal maps of the larvae of primary - setosed Arctiidae and Noctuidae

Characterization of the larvae of the Noctuidae sensu Hampson

1. The primary-setosed larvae of the Noctuidae are to be understood as the continuation (trend) of the respective development within the Arctiidae. Therefore the numerical setal pattern (the relations of distances between setae here are not taken into consideration, e. g. the close condition of D1 and D2 on T2 and T3) of the primary setosed larvae of the Noctuidae is on the whole very close to that of the respective Arctiidae. The main differences for the Noctuidae (distinguishing them from the Arctiidae) are: one SV-seta each on T2 and T3, one L3-seta each on A1 to A6, one L-seta on A9, one SV-seta on A7 (to A9), 3 SV-seta on the outside of the prolegs on A3-A6 and only three L-setae on the outside of the anal-proleg.
2. The disturbing and scattered occasional presence of arctiid characters within the Noctuidae has to be marked as reversals of the plesiomorphic arctiid-condition and has either to be neglected (the praxis hitherto) or used as part of a new holomorphis (that of the Noctuidae) for characterization of the Noctuidae.
3. These arctiid-characters are the occasional presence of two SV-setae each on T2, T3; of two L3-setae each on A3-A6 or on A1-A6; two L-setae on A9 [hitherto at the Noctuidae only at *Jocheaera alni*, at *Ufeus* spp. and at *Sarbanissa transiens*, an Agaristinae (which has 3 L-setae on A9!)]. Further arctiid features are four SV-setae on the abdominal - prolegs and two SV-setae on A7 (to ?A9).
4. At present we have only one character which is unique and thus autapomorphic for the Noctuidae-larvae as compared with the Arctiidae - the absence of an additional seta (the seta Lx of the Arctiidae in the figs. 4 and 5) on the outside of the anal - proleg, basally of the L-setae-group, figs. 4-6. This character has also to be controlled for consistency in further material of primary setosed larvae of the Arctiidae.
5. The homoid character of the crochets of the prolegs of the Noctuidae (fig. 6) is shared also with some Arctiidae (Syntomidae); most Arctiidae are characterized by heteroid crochets (figs. 4 and 5). This arctiid character has been found within the Noctuidae only three times, with *Scoliopteryx libatrix* Linnaeus, with *Gyrtothripa*, a Sarrothripinae, and some Euteliinae (pers. comm. D. Wagner). This character within the Noctuidae has also to be ignored as reversal of a plesiomorphic condition.
6. The secondary setation of the Arctiidae - larvae is also found within the Acronictinae (including the

Pantheini), with the Raphiinae, with the Dilobinae and within the “Xyleninae / Hadeninae” in *Conistra (Dasycampa)* Hübner.

Just as the enigmatic occurrence of so many secondary - setosed larvae within the Acronictinae and also with *Dasycampa* Guenée (*Conistra* Hübner auctorum) is now better understood, so too is recognition that the primary setosed larva of *Jocheaera alni* has also many characters of the primary setosed Arctiidae-larvae - as reversals.

The Nolidae - Noctuidae - relations

It is curious that the conclusions to the different combinations between the Nolidae sensu stricto, sensu Hampson and Noctuidae sensu Hampson have been based on very dubious, putative and unsuitable characters (for the desired taxonomic level): first and foremost on the boat-shaped cocoon and its two-walled construction (see also BECK, 1999), then on the “bar”- shaped retinaculum (KITCHING & RAWLINS, 1998), on the direction of the branches of the split muscle 4 in the valva and the presence of an adenosma (which often is missing!), the ventral prothoracic gland of the larva (SPEIDEL *et al.*, 1996).

The broad investigation of HOLLOWAY (1998), aiming to prove the monophyly of the Nolidae (with the subfamilies Sarrothripinae, Chloephorinae, Camptolominae and Nolinae), failed.

Larval characters of the Nolidae sensu Hampson

In KITCHING & RAWLINS, 1998 (here fig. 7) *Meganola minuscula* shows a large setosed wart behind the spiracle (= St), combination of the setae L1 and L2 (because L2, usually below the spiraculum, is missing). In STEHR, 1987, *Nola sorghiella* Riley (fig. 8) shows the two characters of the mature larvae of the Nolidae: the complete absence of the A3-prolegs and the secondary setation on verrucae of which the verruca behind the spiraculum represents the fused (primary) setae L1 and L2 (the verruca below the spiracle is situated in the L3-position and thus refers to seta L3); this same constellation of features is distinct in the schematic setal maps of Ahola, fig. 9 and Hasenfuss, fig. 10 (in BECK, 1999). But all these figures which are very close also to setal patterns of some Arctiidae (KITCHING & RAWLINS, 1998, fig. 19. 14 F, G: *Virbia rosenbergi* and *Nyctemera apicalis*) give no clear answer about the monophyly of the Nolidae sensu Hampson.

The L1 - larvae of the Nolidae have never been investigated. The L1 - larva of *Nola squalida* (Staudinger, 1870), fig. 11, shows the combination of the seta L1 (usually behind the spiracle) with L2 (usually ventral of the spiracle) to a joint wart ventrocaudal to the spiracle, further one SV-setae each above the thoracic legs on T2 and T3, and possibly an autapomorphic position of the SD1-bristle dorsocaudal of SD2 on T1, also visible in the mature larva of *Meganola albula* (Denis & Schiffermüller), fig. 12; the prolegs on A3 are missing from the first instar; the other prolegs on A4 to A6 are completely developed (of the same size) from the L1 - instar.

The chaetotaxy of the second to last instar of *Nola cuculatella* (Linnaeus), fig. 10, with one setal wart below the spiracle (and the absence of a wart or pinaculum behind the spiracle in the normal position of the L1 setae) shows variability. Both possibilities, that of *Meganola minuscula* as well as that of *Nola cuculatella* are fundamentally different from the chaetotaxy of the Noctuidae sensu Hampson, in which the positions of the three setae (SD1, L1, L2) around the spiracles on A1 to A8 are clearly separated in all instars (fig. 3); that holds true even for larvae of the Acronictinae (including the Pantheinae auctorum). The missing prolegs on A3 (from the L1 - to the last instar) is an additional reliable autapomorphy for the Nolidae sensu stricto and forbids a combination with the cited subfamilies of the Noctuidae (above) and also with the Arctiidae. These characters argue strongly against the definitions of the Nolinae / Nolidae of many authors (e. g. KITCHING & RAWLINS, 1998) based on the characters mentioned above.

From these results it is at once clear that the Nolidae sensu stricto, sensu Hampson should never have been combined with the Noctuidae (KITCHING, 1984, SPEIDEL *et al.*, 1996) and, for the same

reasons, there should never have been combinations of some subfamilies of the Noctuidae (Chloephorinae, Sarrothripinae, Eariadinae) with the Nolidae (KITCHING & RAWLINS, 1998). If we had taken into consideration the two convincing and absolute larval autapomorphies we never would have the present confusion in the systematics of the Noctuidae as well as in the Noctuoidea.

How to unmask reversals

To make use of reversals for the phylogenetical systematics it is necessary to recognize them. In the chapter above "Value of reversals for elucidating the descendance - ..." some easy examples for recognizing reversals are listed. In all cases the unusual occurrence of the "plesiomorphic" condition beside the progressive apomorphic one in closely related taxa is the first hint for a reversal.

A more complex and at first glance not recognizable reversal which is of enormous importance to the present phylogenetical reasoning within the Plusiinae is the occurrence of the complete series of prolegs from A3 to A6 in the larvae of the Abrostolini, contrary to all the other Plusiinae in which the larvae only have prolegs on A5 and A6. This larval! character stimulated all the imaginal systematists (see KITCHING, 1987) to give the Abrostolini a basic and ancestral position within the tribes of the Plusiinae contrary to the opinion of BECK, 1999, who gives evidence for the Abrostolini as a very derived perhaps the most derived position within the Plusiinae: The larvae of the Abrostolini share all the other characters of the Plusiinae, especially those which have been developed depending on the possession of only two pairs of prolegs on A5 and A6, e. g. the tapered body cephalad of A5 towards the head, the dorsad arched body cephalad of A5 and, most conspicuous, the elliptic head in lateral view, a very specialised and derived pattern of the larvae and, last but not least, imaginally a very derived valva as compared with the rectangular valva of European Plusiinae. The only conclusion therefore is that the occurrence of four pairs of prolegs from A3 to A6 - in presence of all the other derived characters of the Plusiinae at the Abrostolini - is a reversal.

General rule: there is cause for suspicion of a reversal when besides the sum of derived characters there is one (or some) of very ancestral "plesiomorphic" character.

Discussion and conclusions

We now have characterizations of the Noctuidae sensu Hampson and of the Nolidae sensu stricto, sensu Hampson as monophyletic families based on larval morphology.

Conclusions for the phylogenetic systematics, e. g. of the Noctuoidea

1. Within a family very rich in species it is nearly impossible to find an apomorphy as synapomorphy, obligatory for all taxa (I am holding my breath and crossing my fingers that a Noctuidae larva having the arctiid additional basal seta on the anal-proleg will be found).
2. Therefore we have to work with the combination of several apomorphic characters and especially to have in mind the common trend of evolution within the family or within the subfamily and the respective holomorphs, see the example of the Plusiinae.
3. The mentioned reversals, in the modern sense unknown to Hennig, have not to be ignored for phylogenetical reasoning (as plesiomorphic conditions) if the new context of these reversals with an otherwise advanced holomorph is pointed out. On the other hand these reversals give some evidence for the phylogenetic history of the group.
4. Phylogenetic systematics are based on consistent apomorphic characters. This is a contradiction to the principle and the basis of evolution, the inconsistency of species. Analogous to this inconsistency we have a collective inconsistency in higher taxa with some or many species: As the example of the Noctuidae demonstrates, there is nearly no character of common consistency. This experience with imaginal characters led to the present problems in the systematics of the Noctuoidea and to the crisis in the systematics (of the Lepidoptera) over all: it is impossible by means of phylogenetic

systematics to construct a complete phylogenetical system (of the Lepidoptera) if there is no positive use of the reversals for phylogenetical systematizing. Otherwise the phylogenetical systematics as a whole would be primarily of theoretical importance.

After the present larval investigations we now have in the Noctuoidea three monophyletic families Noctuidae, Nolidae and Arctiidae of which the latter larvally is postulated as the sister-family of the Noctuidae [the suggested imaginal-systematical conclusions for this are to be found in: Hampson (in KITCHING, 1984: 182, fig. 2), KITCHING (1984: 224, fig. 4), SPEIDEL, FÄNGER & NAUMANN, 1996, fig. 1]. The other families of the Noctuoidea here are not under consideration.

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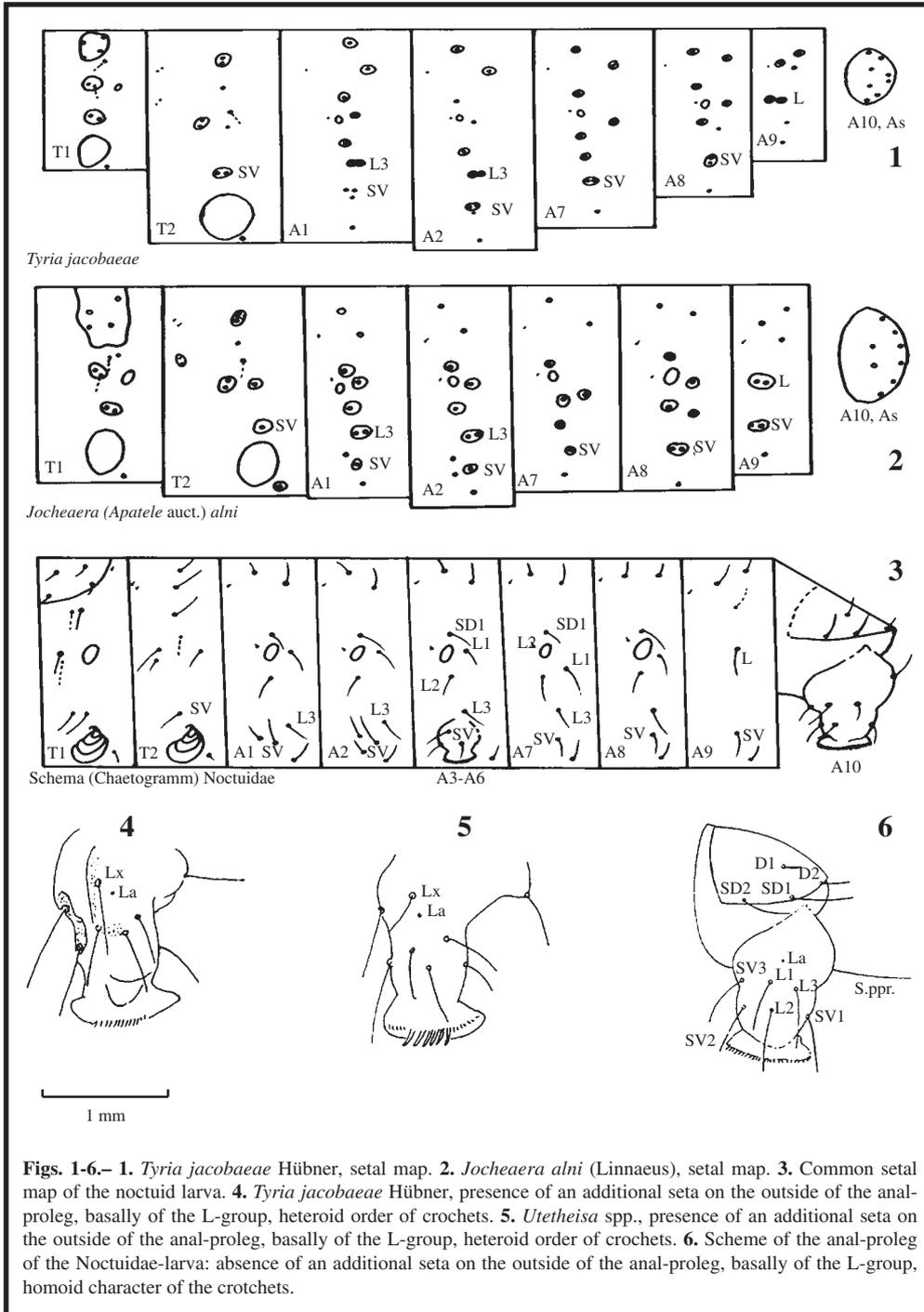
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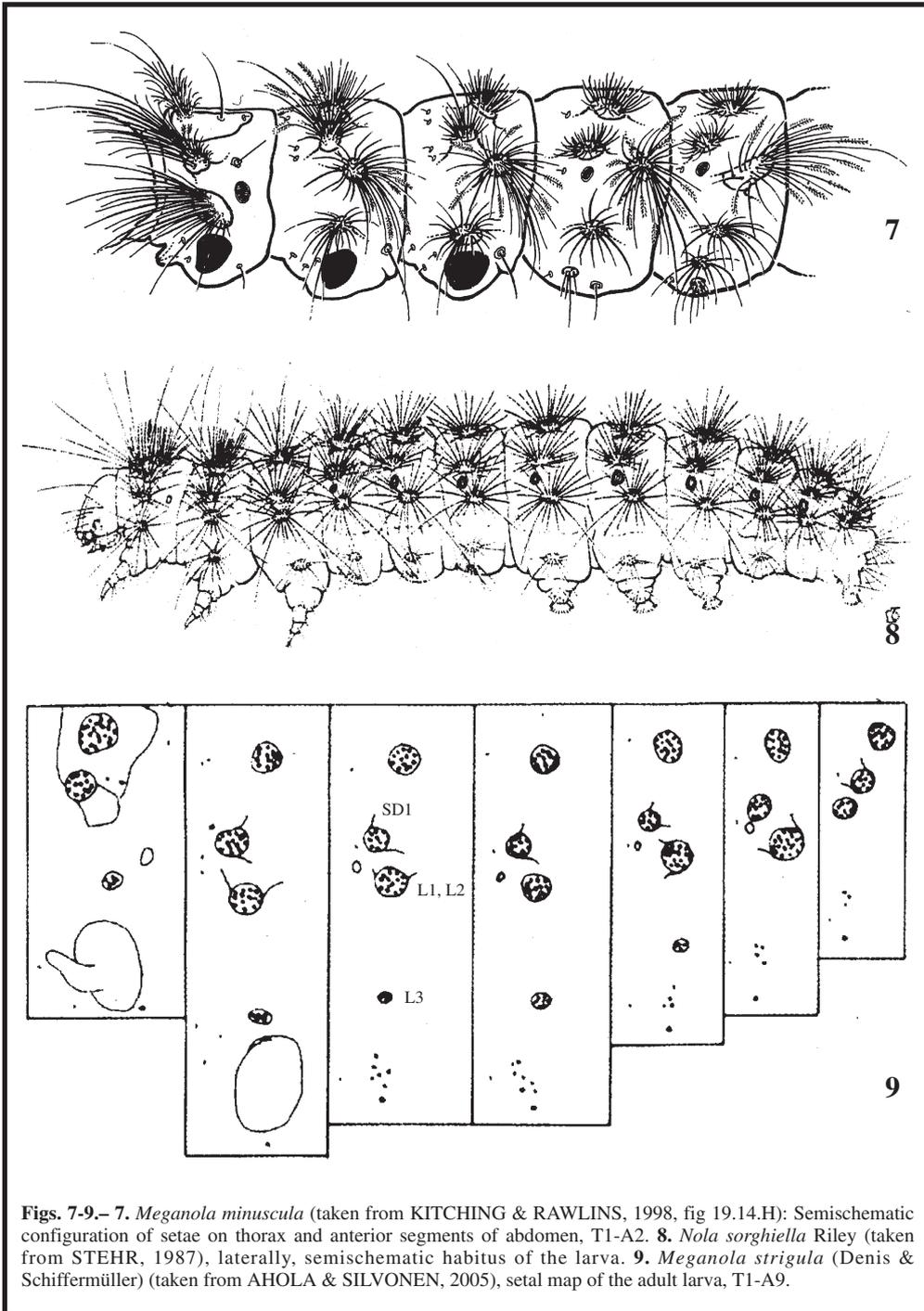
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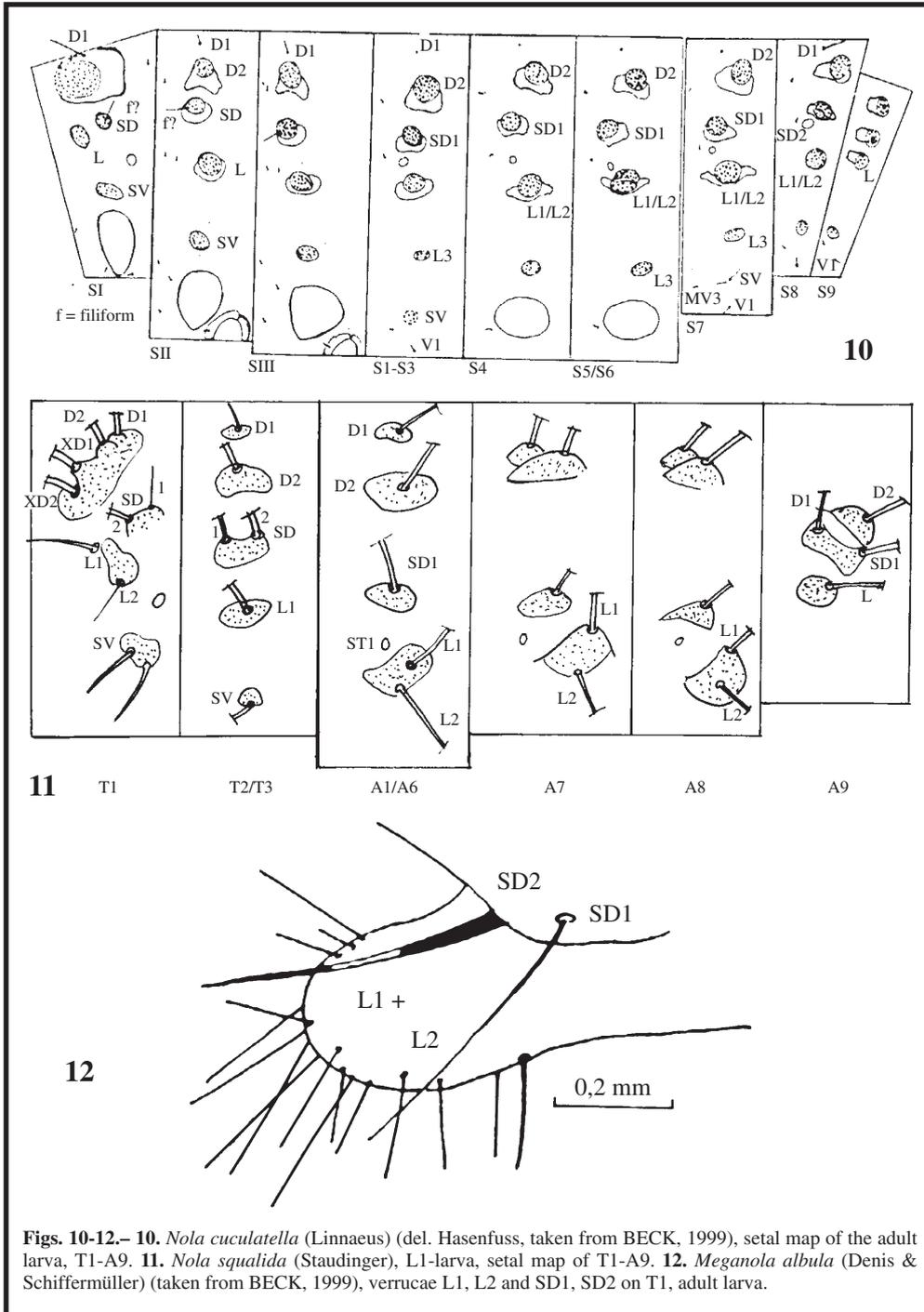
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Figs. 1-6.— 1. *Tyria jacobaeae* Hübner, setal map. 2. *Jocheaera alni* (Linnaeus), setal map. 3. Common setal map of the noctuid larva. 4. *Tyria jacobaeae* Hübner, presence of an additional seta on the outside of the anal-proleg, basally of the L-group, heteroid order of crochets. 5. *Utetheisa* spp., presence of an additional seta on the outside of the anal-proleg, basally of the L-group, heteroid order of crochets. 6. Scheme of the anal-proleg of the Noctuidae-larva: absence of an additional seta on the outside of the anal-proleg, basally of the L-group, homoid character of the crochets.



Figs. 7-9.— 7. *Meganola minuscula* (taken from KITCHING & RAWLINS, 1998, fig 19.14.H): Semischematic configuration of setae on thorax and anterior segments of abdomen, T1-A2. 8. *Nola sorghiella* Riley (taken from STEHR, 1987), laterally, semischematic habitus of the larva. 9. *Meganola strigula* (Denis & Schiffermüller) (taken from AHOLA & SILVONEN, 2005), setal map of the adult larva, T1-A9.



Figs. 10-12.— **10.** *Nola cuculatella* (Linnaeus) (del. Hasenfuss, taken from BECK, 1999), setal map of the adult larva, T1-A9. **11.** *Nola squalida* (Staudinger), L1-larva, setal map of T1-A9. **12.** *Meganola albula* (Denis & Schiffermüller) (taken from BECK, 1999), verrucae L1, L2 and SD1, SD2 on T1, adult larva.