

The "scaphium-pocket" and the "pocket-knife" – functional and morphological peculiarities of the uncus of noctuid moths (Insecta: Lepidoptera: Noctuidae)

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Abstract

The uncus is discussed as an additional clasping and pushing hook supposedly having a function in guiding the male genitalia during the copulatory act. A pocket-knife mechanism of the uncus-scaphium complex is described and illustrated. Different "resting positions" of unci are reported from the genera *Phyllodes* BOISDUVAL, 1832, *Eudocima* BILLBERG, 1820, *Hypena* SCHRANK, 1802, *Harita* MOORE, 1882 and *Ricla* WALKER, 1869. The scaphium is discussed as a sheath for terminally sclerotised and fine pointed unci. The scaphium and the scaphial-pockets at the terminal end of the anal cone obviously prevent the anal tube from being damaged by the terminal hook during pre- and postcopulation and in the resting behaviour. Scaphia mainly were found in species with heavily sclerotised terminal hooks of the uncus and are correlated to the length of the uncus as in the genera *Hypena*, *Xoria* NYE, 1975 and *Harita*.

Key words: Hypeninae, Heminiinae, Lepidoptera, male genitalia, morphology, Noctuidae, scaphium, uncus.

Zusammenfassung

Der Uncus wird als zusätzliches Greif- und "Schiebe"-Instrument während der Kopula von Noctuidae beschrieben. Ein "Taschenmesser"-Mechanismus des Uncus-Scaphium-Komplexes wird erstmals beschrieben und abgebildet. Verschiedene Ruhehaltungen der Uncus-Haken werden anhand der Gattungen *Phyllodes* BOISDUVAL, 1832, *Eudocima* BILLBERG, 1820, *Hypena* SCHRANK, 1802, *Harita* MOORE, 1882 und *Ricla* WALKER, 1869 vorgestellt. Das Scaphium wird in seiner Funktion als Schutzschild gegen spitze Uncus-Haken diskutiert. Es wird angenommen, daß das Scaphium und terminal am Analkonus anschließende Scaphialtaschen den eigentlichen Analtrakt vor zufälligen Verletzungen mit spitzhakigen Unci während Prä- und Postkopula und während des Ruheverhaltens schützen. Scaphia finden sich hauptsächlich bei Arten mit spitzhakigen Unci, was an den Gattungen *Hypena*, *Xoria* NYE, 1975 und *Harita* gezeigt werden kann.

Introduction

An internal lock-and-key system with pocket-knife mechanism of the uncus-scaphium complex is described. The function of the uncus during the mating and the function of the scaphium are discussed.

The caudal part of the 10th tergite is called uncus. It is part of the clasping organ or the so called genitalia corpus which – in a general view – consists of a frame (tegumen and vinculum) and a clasping system. The clasping system contains a pair of (normally symmetrical) valves articulating at the sides of the tegumen-vinculum-complex and the uncus which originates at the caudal end of the tegumen.

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According to TUXEN (1956) the term uncus in its recent usage was created by PEYTOUREAU (1895). Formerly GOSSE (1883) used this term for a process of the 8th tergite in Rhopalocera which later was replaced by the term "superuncus".

In primitive Lepidoptera the "uncus" is very difficult to homologize with structures of other Lepidoptera. Normally, in the primitive groups the uncus is not developed as a distinct hook which clearly articulates at the terminal end of the teguminal frame. Large fusions with the tegumen, bifurcations, knob- or lobe-like features of different insertion or shape (e.g. Neopseustidae, DAVIS 1975; Hepialidae, SCHMIDT NIELSEN & ROBINSON 1983) leave the homologization in a smoke-screen. From the point of view of a Noctuidae specialist the primitive forms are not comparable with the typical terminal hook of the clasping apparatus as it is found in Owl moths.

The major part of the 10th tergite forms the uncus, although a part of it is incorporated into the tegumen (SCOBLE 1992).

Around the uncus there occur different accessory or associated structures. These structures are difficult to define and quite different from species to species. The author uses the following definitions of these allied structures:

Socii: A couple of more or less hairy lobes on both sides of the uncus base. The derivation is uncertain (SCOBLE 1992), sometimes they are prominent sometimes they are very small. Generally they are considered to be modifications of the 10th tergite or the inter-segmental membrane of the 9th and 10th abdominal segment, or of the cerci (appendages of the 11th abdominal segment). An impressive example for socii directly deriving from the base of the uncus corpus is *Nolasena ferrifervens* WALKER, [1858] 1857 (LÖDL 1999a).

Gnathos: A pair of sclerites derived from the 10th sternite, closely associated to the uncus. This sclerites may be fused to one single structure or may be reduced or absent. This structure is different from sclerotizations of the anal tube.

Scaphium: Sclerotizations of the dorsal part of the tuba analis.

Subscaphium: Sclerotizations of the ventral part of the tuba analis.

Teguminal processi: These are structures clearly deriving from the tegumen, standing closely to the uncus. A spectacular form of this rare modification was found in *Rhynchina martonhreblyi* LÖDL, 1999c. In this species the uncus is reduced to a weak finger linked to the ventral surface of the tegumen like a hinged arm. The two long teguminal processi are stiff and extend forward. The corresponding features in the female are unclear, the female is not known yet. Clear is that this finger-like uncus cannot have any progressive pushing or clasping function. The directive habit of opening and widening the ostium cave managed by the two teguminal arms is probable.

Material and methods

This study was carried out with conventionally dried specimens from the collections of The Natural History Museum (BMNH) in London, the Naturhistorisches Museum Wien (NHMW) and the Muséum national d'Histoire Naturelle (MNHN) in Paris. Genitalia preparations have been made in the traditional way (mazeration by use of KOH, preparation and isolation of the genitalia tract). The genitalia have been stained with Chlorazol Black.

In situ preparations of the genitalia tract based on dried specimens have been obtained by using micro tools.

The SEM investigations were carried out by using conventionally prepared specimens (alcohol and as a final stage 99.9 % cooled acetone), coated with gold, on a Jeol 6000/400.

List of species investigated:

Calpinae:

Phyllodes eyndhovii VOLLENHOVEN, 1858

Eudocima salamina (CRAMER, 1777)

Nolasena ferrifervens WALKER, [1858] 1857

Hypeninae:

Hypena proboscidalis (LINNAEUS, 1758)

Hypena varialis WALKER, [1866] 1865

Hiaspis closteroides WALKER, [1866] 1865

Herminiinae:

Bleptinodes perumbrosa (HAMPSON, 1898)

Simplicia rectalis (EVERSMANN, 1842)

Britha bilineata (WILEMAN, 1915)

Britha biguttata WALKER, [1866] 1865

Abbreviations

a	anus	scp	scaphial pocket	tepr	teguminal process
sc	scaphium	soc	socius	u	uncus
sccr	scaphial crown	ta	tuba analis	ub	width of uncus
scl	length of scaphium	te	tegumen	ul	length of uncus

The uncus in the family Noctuidae

The presence of a well developed uncus is an usual trait in the family Noctuidae. The classificatory value of the uncus can be either at tribe or genus level, or at species level.

Reductions of the uncus are found in several genera among many subfamilies. These reductions are strongly believed to be of secondary character, the primary state is a well developed, distinct article inserted in the caudal part of the tegumen.

Within the triline subfamilies several broad and flat forms of unci occur. For example the broad, often rounded unci of the genus complex *Hadula* STAUDINGER, 1889. A similar situation is found with broad, often squarish unci in the genus *Mudaria* MOORE, 1893 (Amphipyridae; HOLLOWAY 1989). The Amphipyridae genus *Athetis* HÜBNER, [1821] exhibits a secondary reduction of the whole uncus. The tegumen in this genus is elongated and expanded into a horseshoe shape (HOLLOWAY 1989). Another example is a genus with uncertain placement among the Hadeninae: *Elusa* WALKER, [1859] 1858 shows reduced or T-shaped unci (HOLLOWAY 1989).

The subfamily Euteliinae exhibits a wide variety of reductions of unci. Sometimes species have unci with bifid apical portions, each part bearing serried ranks of cylindrical setae.

Strange types of unci are also found in the subfamily Stictopterinae, for example in the genus *Diascoides* HOLLOWAY, 1985. This genus exhibits deeply bifid unci with two very slender processes. The unci of the genus *Sigmuncus* HOLLOWAY, 1985 is sinuous or complexly flexed in its vertical plan. The genus *Lophoptera* GUENÉE, 1852 has a variety of different unci forms, some of them are remarkably long and slender.

An enormous enlarging of the unci is found in *Cocytia* BOISDUVAL, 1828 (subfamily Eucocytinae; KITCHING & RAWLINS 1998). The unci is as long as the tuba seminalis, blunt and ventrally broadened with a long thorn at its distal end (SPEIDEL, FÄNGER & NAUMANN 1997).

The Nolidae have been classified recently by HOLLOWAY (1998). Now this family includes the Nolinae and mainly the former noctuid subfamilies Sarrothripinae, Chloephorinae, and Camptolominae. In these groups the unci normally is simple and tiny, often apically hooked. Degenerative forms occur in *Nola* LEACH, [1815] and in the *Iscadia* WALKER, 1857 genus group. A striking modification into a dorsoventral pincer-like structure embracing a cordate pad occurs in *Beana* WALKER, 1862. *Earias* HÜBNER, [1825] exhibits a bifid type of unci.

The obvious diversity of different forms of unci supports the hypothesis of a high potency of analogous developments. Similarities in the unci shape in quite different systematic groups give evidence for the diversity of lineages and the possibility of parallel evolution of features. A good example is a special form of unci in the genus *Sasunaga* MOORE, 1881 (Amphipyridae; HOLLOWAY 1989) and the genus *Acidon* Hampson, 1896 (Hypeninae; LÖDL 1998). Both genera realized a very similar extension of the ventrodorsal part of the unci directly below the terminal hook: a clear analogy.

The mechanical options between the male clasping system unci-scapium and the female papillae anales have been tested by using an "artificially induced precopula" during preparation. The unci and the scapium of *Eudocima salaminia* were found to fit perfectly into the spiny dorsal and ventral furrows situated longitudinally between the papillae. This is described as a secondary lock-and-key in contrast to the primary lock-and-key systems found in the interaction of juxta, aedeagus and vesica on one hand and the sterigma, ductus bursae, caudal part of bursa and cervix bursae on the other hand (MIKKOLA 1992, 1998). The primary lock-and-key clearly works during the copulation and the transfer of the spermatophore. The secondary lock-and-key is supposed to work as a guiding system in the beginning of the copulation. However, MIKKOLA (1998) argues correctly that the lock-and-key systems are not always clear and more or less based on subjective interpretation, which is an evident problem. Lock-and-key systems as holder of a high extent of correlated features on the other hand are very important bearers of evolutive information. So the internal lock-and-keys are of great value for evolutive hypotheses as the pocket-knife situations are, because the bias of analogous coincidences is minimized.

A further argument refers to the different extent of lock-and-key mechanisms. As in the field of mechanics the definition of "lock" includes a wide range of differently delicate systems. There are locks which can be opened by a simple metal tool and there are locks which are in need of complexly built keys with dozens of details fitting exactly in the

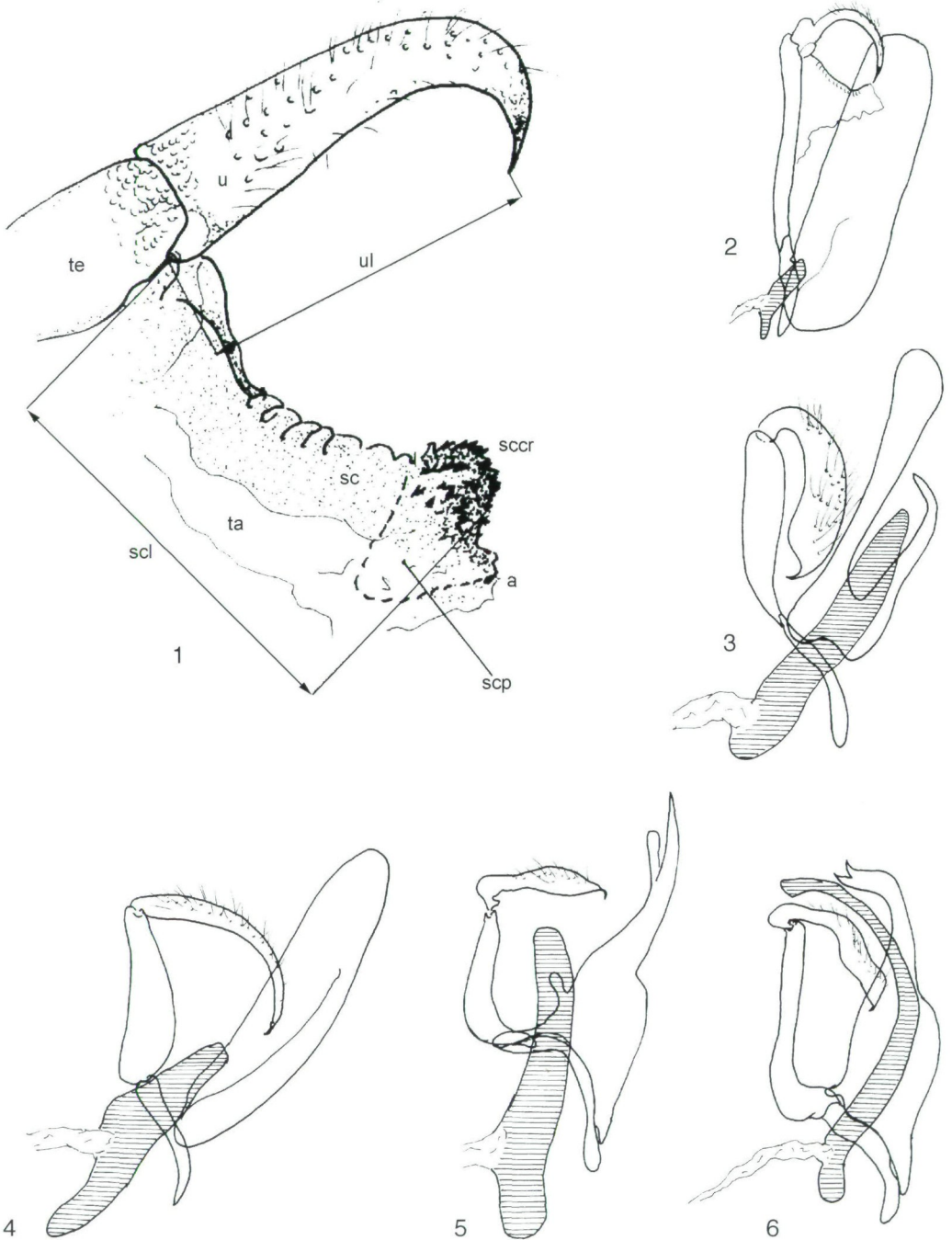
corresponding locking device. Male and female genitalia operate the same wide ranges of various systems which differentiate clearly in their delicateness and perfection. However, the simple as well as the complex systems can be called "lock-and-key" systems so far we find evidence of clearly corresponding features. Just the extent of accordance is varying. Additionally it is possible that the clasping function of the uncus is suppressed or replaced in some species by a pushing function similar to those found in other Lepidopteran families, like the Zygaenidae (NAUMANN 1987). Especially species with pirate-hooked unci or species with helmet structures on the dorsal surface of their unci could use this tool for pushing upwards the papillae anales complex of the female. This behaviour would help to open the ostium area. It is most likely that further studies will bring to light several well differentiated systems of behaviours of the early stage copula.

The subfamily Hypeninae

The revision of the genus *Hypena* SCHRANK, 1802 of the Ethiopian Region and Madagascar (LÖDL 1994a, 1995) was the first step to a definition of the monophyly of the Hypeninae s.str. The different morphological lines within the type genus of the Hypeninae could be recognized and the author was able to define a sister group (*Dichromia* GUENÉE, 1854) as a distinct genus (LÖDL 1994b). Closely related genera like *Harita* MOORE, 1882 (LÖDL [1997] 1996), *Ricla* WALKER, 1869 (LÖDL 1997b) and *Xoria* NYE, 1975 (LÖDL 1997a) could be added to this monophyletic complex of genera. *Ricla* was found to be the African "part" of the genus *Harita*. The genus *Acidon* HAMPSON, 1896 was then discovered as the far end of the "typical *Hypenas*" (LÖDL 1998). To this genus complex the genus *Hiaspis* WALKER, [1866] 1865 (formerly placed in the Calpinae) was added (LÖDL 1998) (Fig. 4). One of the synapomorphic features of the *Hypena*-group is a firm and coarse corium on the dorsal surface of the tuba analis (Figs. 1, 7-11). This scaphium may consist of two symmetrical, sclerotised strips at the base or may be a ribbed corium. The distal end of the scaphium is quite often formed like a knob, covered with spines and sclerotised teeth. Sometimes it extends to a scaphial pocket which trims the sclerotised and fine pointed terminal hook of the uncus in a harmless resting position. Obviously this morphological cooperation of blunt scaphial crown (Fig. 10) and scaphial pocket with the terminal hook of the uncus prevents the anal tube from being pierced. The length of the uncus (measured from the uncus base to the tip of the terminal hook) is highly correlated to the length of the scaphial rib with the crown. The more sclerotised the uncus, the more structured and strictly formed is the scaphium and its crown on the dorsodistal end of the anal tube. A typical pocket-knife situation is found in the genus *Xoria*. A long and slender uncus fits perfectly into a bent, coarsely skinned scaphium and a scaphial pocket for the bill-like terminal hook (Figs. 7-8).

A glimpse at the subfamily Herminiinae

The Herminiinae are in a similar "poor" condition in regard to monophyletic fixations as the Hypeninae have been. An interesting approach to the systematics of this group of noctuids, characterized by a prespiracular hood of the tympanum has been made by OWADA (1987). In this review the characters – mainly of the Japanese species – are listed and described.



Figs. 1 - 6: (1) Uncus-scapium-device in *Hypena* sp. – *a* anus; *sc* scaphium; *sccr* scaphial crown; *scl* length of scaphium; *scp* scaphial pocket; *ta* tuba analis; *te* tegumen; *u* uncus; *ul* length of uncus. (2 - 6) Lateral view of in situ positions of male genitalia (aedeagi marked), (2) *Harita* sp., (3) *Bleptinodes perumbrosa*, (4) *Hiaspis closteroides*, (5) *Britha biguttata*, (6) *Britha bilineata*.

Normally the uncus within the subfamily Herminiinae is very well developed. While characterized as "hook-shaped" in the Hypeninae the uncus of the Herminiinae is mostly "club-shaped" with a knee at its basal part and is normally densely covered with long and thick setae on the dorsal surface (Fig. 3). The big and club-shaped uncus characterizes in particular a truly monophyletic group within the Herminiinae: the genus group *Idia* HÜBNER, [1813]. Some of the typical *Herminia* LATREILLE, 1802 wear a "casuar helmet", the genus *Hipoepa* WALKER, [1859] 1858 wears a halberd-shaped process on the dorsal surface of the uncus. A clearly analogous feature is found in the Hadeninae *Dictyestra dissectus* WALKER, 1865 (HOLLOWAY 1989: fig. 78).

In *Simplicia rectalis* (EVERSMANN, 1842) a club-shaped uncus is found which is flattened dorsoventrally and fits into a longitudinal groove of the corium of the anal tube.

"Resting positions" of the uncus

Different taxa exhibit different artificial "resting positions" of the uncus. This are – presumably – secondary in situ positions of the uncus in relation to the remaining copulatory system and to the abdominal lumen. Although there is no evidence that these positions are strictly identical to the "natural" resting positions apart from the mating habit, it is clear that some of the findings are due to "biological mechanisms". Especially the "secondary lock-and-key systems" of uncus and scaphium have a high reliability. The same is true for the scaphial pockets of the *Hypena*-group which show a clear correlation to the length of the uncus and its terminal "arming". This correlation and the frequency of lock-and-key evidences between uncus and accessory systems make a coincidence based on analogy most unlikely.

Unci with a fine pointed and sclerotised terminal hook normally require a corresponding "system of assistance" in the anal cone. This frequently is a scaphial shield and other trimming systems for hiding the fragile and skinny anal tube. Moreover the scaphium itself can obviously become part of a clasping system (*Eudocima salaminia*) which supports the clasping procedure in the initial state of the copulation.

The scaphial rib trims the sclerotised uncus in a harmless resting position. Several types of uncus-scaphium relations have been observed:

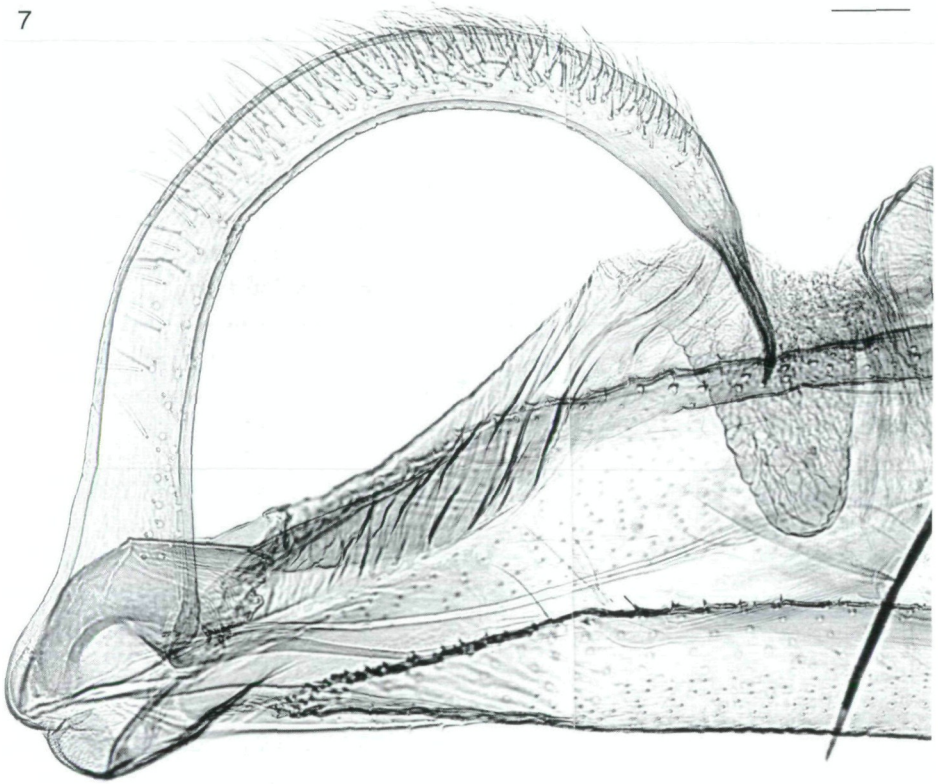
Corium type with a scaphial crown and a scaphial pocket for the terminal hook of the uncus (*Hypena*-type) (Figs. 1, 7-11).

Scaphium with two symmetric shields or ribs (e.g. *Phyllodes* or part of the *Hypena*) (Figs. 12-14).

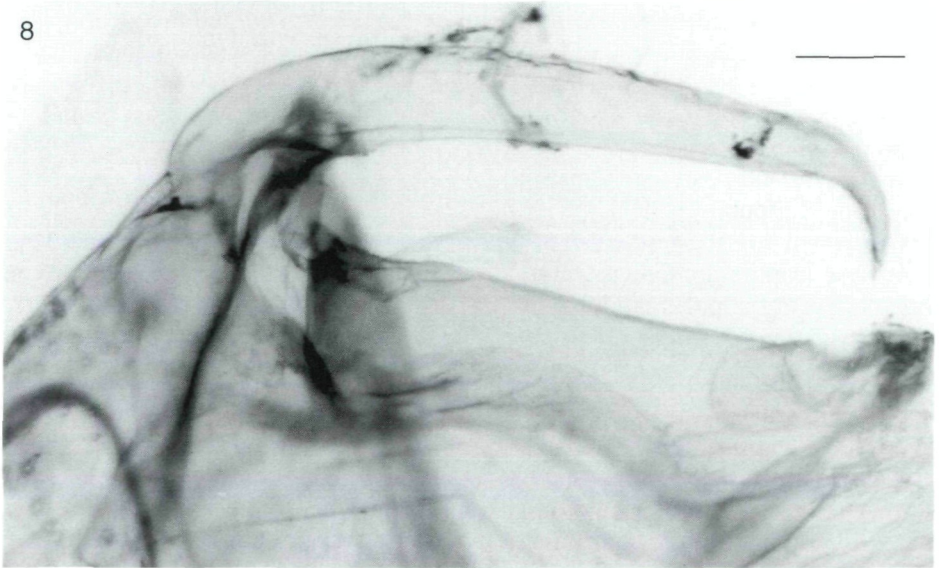
Stringent lock-and-key situation between uncus and scaphium, pocket-knife insertion of the uncus in the scaphial shield (*Eudocima*) (Fig. 15).

Beside this, species with less curved unci and unci which do not wear harmful terminal hooks frequently lack a scaphium. In these cases the anal tube is skinny and flabby. Big and club shaped unci often have a rounded ventral surface and their terminal tip – although fine pointed – is not long enough to have a damaging influence on the anal tubes (Figs. 3, 16). The "*Idia*"-type of unci, also found in the herminiine genus *Simplicia* GUENÉE, 1854 has been discussed several times by LÖDL (1996a, b, c, 1997d, 1999d). In

7



8



Figs. 7, 8: (7) *Harita* sp., Noctuidae Brit. Mus. slide No. 8853, uncus resting scaphial pocket. Scaphium recognizable as a ribbed trim. (8) *Hypena* (*Pseudodichromia*) *laetalimaior* LÖDL, 1995, gen.praep. M.Lödl 187, uncus and scaphial shield with scaphial pocket.

these groups no scaphial shield is found, no scaphial pocket mechanism for the terminal part of the uncus could be recognized at the present.

Pocket-knife positions are also found. A special pocket-knife situation could be observed in *Britha bilineata* (WILEMAN, 1915) (Fig. 6): The uncus is situated with its rounded dorsal margin within the upcurved dorsal margin of the aedeagus. It could be possible that the rounded, indented dorsal surface of the uncus plays an additional role in protruding the aedeagus during the copulation.

Within the subfamily Calpinae the species *Eudocima salaminia* exhibits a classic form of pocket-knife situation in combination with a scaphial sclerotization. A perfect lock-and-key mechanism between the uncus and the form of the scaphium was observed, and it is most likely that this is a "normal" resting position due to the high coincidence of the lock-and-key mechanism (Fig. 15).

A curious resting position of an uncus was observed in the genus *Phyllodes* BOISDUVAL, 1832. The terminal hook of the uncus was inserted in the distal opening of the aedeagus and deeply stuck in the protruding vesica (Fig. 13).

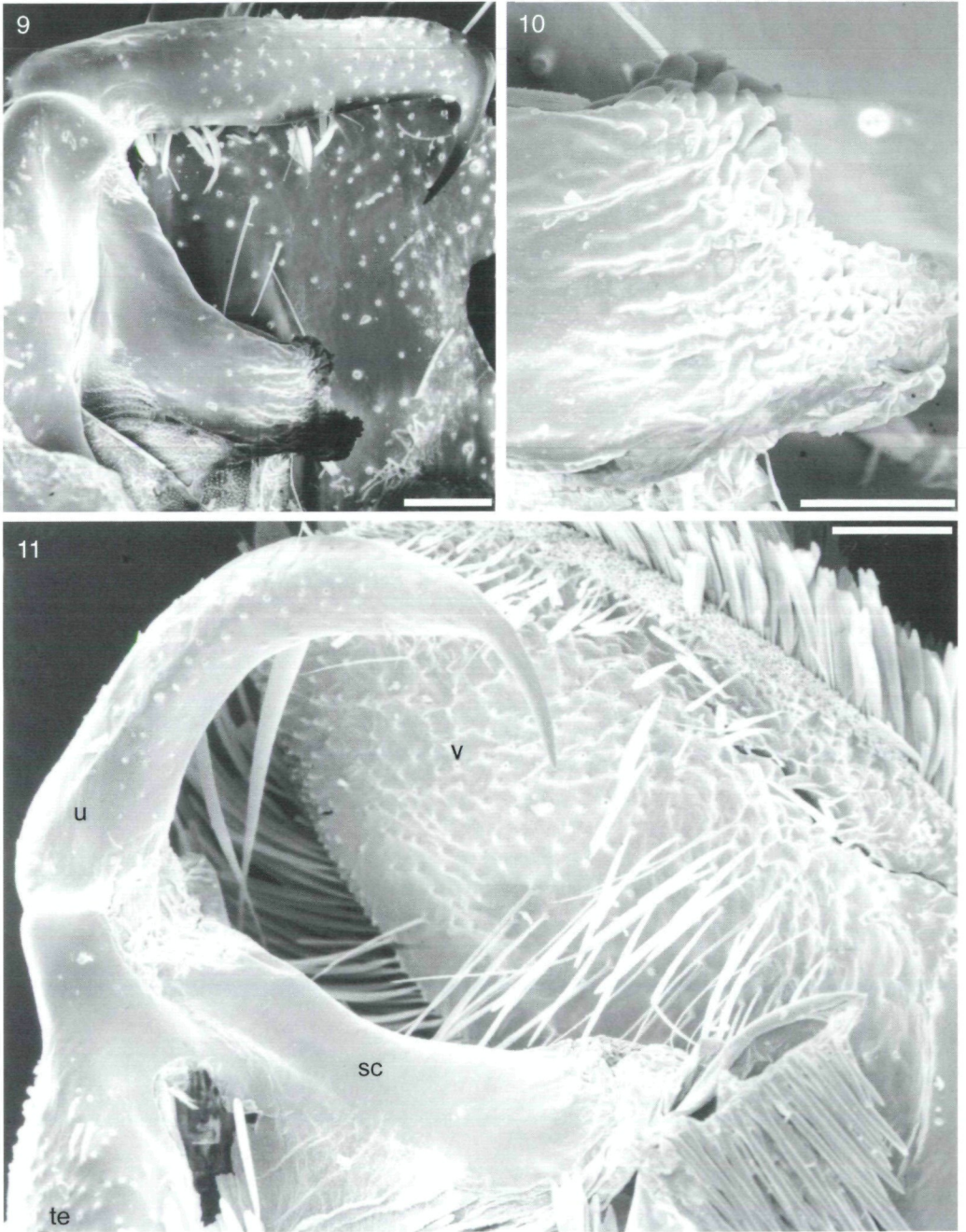
Discussion

The uncus is an additional clasping hook supposedly having a function in guiding the male genitalia during the copulatory act.

The pocket-knife mechanism of the uncus-scaphium complex is described and illustrated above. Different "resting positions" of unci are reported from the genera *Phyllodes*, *Eudocima* BILLBERG, 1820, *Hypena* SCHRANK, 1802, *Harita* MOORE, 1882, *Xoria* NYE, 1975, *Acidon* HAMPSON, 1896, *Britha* WALKER, [1866] 1865. In one specimen of the genus *Phyllodes* the terminal hook of the uncus was inserted in the distal opening of the aedeagus and deeply stuck in the protruding vesica.

The scaphium is discussed as a sheath for terminally sclerotised and fine pointed unci. The scaphium obviously prevents the anal tube from being damaged by the terminal hook in pre- and postcopulation and probably during the resting behaviour. Scaphia were mainly found in species with heavily sclerotised terminal hooks of the uncus and correlated to the length of the uncus as in the genera *Hypena*, *Xoria*. Additionally the scaphia are discussed as a possible part of a clasping system which cooperates with the uncus in grasping for the papillae anales of the female.

The mechanical options between the male clasping system uncus-scaphium and the female papillae anales were tested by using an "artificially induced early stage copula" during preparation. The uncus and the scaphium of *Eudocima salaminia* were found to fit into the spiny dorsal and ventral furrows situated longitudinally between the papillae perfectly. This is described as a secondary lock-and-key in contrast to the primary lock-and-key systems found in the interaction of juxta, aedeagus and vesica on one hand and the sterigma, ductus bursae, caudal part of bursa and cervix bursae on the other hand. The primary lock-and-key clearly works during the copulation and the transfer of the spermatophore. The secondary lock-and-key is supposed to work as a guiding system in the beginning of the copulation. Lock-and-key options should be generally accepted as a possible evolutive strategy. It may take place, but

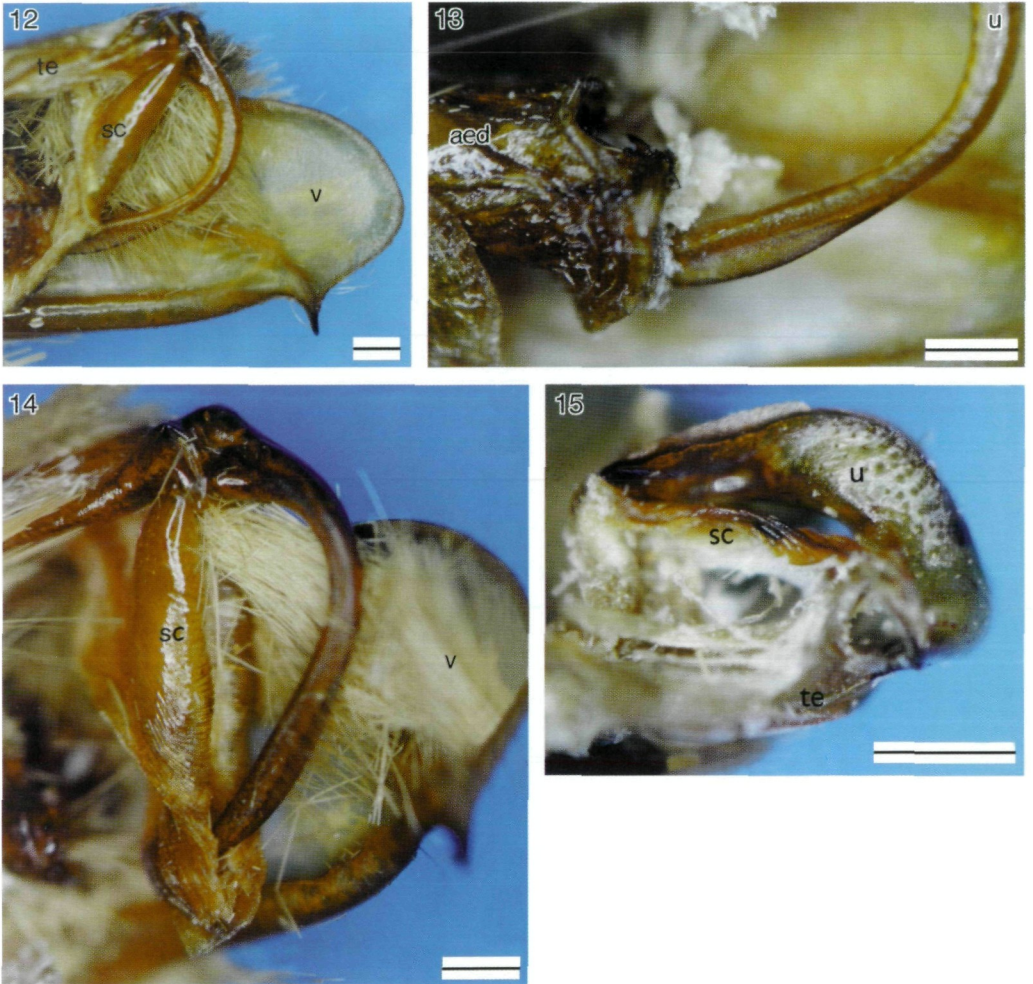


Figs. 9 - 11: Scanning microscope studies of the uncus of *Hypena* sp., (9) *Hypena viridifascia* FLETCHER, 1963, uncus and scaphium. Scale = 0.1 mm, (10) *dto.*, detail of distal end of scaphium: "scaphial crown". Scaphial pocket hidden in the grooved area. Scale = 0.05 mm, (11) *Hypena proboscidalis* LINNAEUS, 1758, uncus and scaphium. Scaphium well recognizable as a sclerotised shield. Scale = 0.1 mm. Abbreviations: *sc* scaphium; *te* tegumen; *u* uncus; *v* valve.

not necessarily. The author is convinced that several of the evolutionary hypotheses are true for a selection of cases (MIKKOLA 1992):

Sexual selection by female choice, genitalic recognition and stimulation effects, pleiotropic mechanisms (primary and secondary ones), as well as sperm competition within the male sex are the main effects on the compatibility of genitalia. MIKKOLA (1992) proposes correctly that sexual selection by the females and genitalic stimulation are primarily effective in the early stage of the copula. The physiological and genetic compatibility factors are exclusively working within or after the copulation, the external genitalia or the emancipated behaviour of the sexes (primarily the females) just can effect precopulative situations. Lock-and-keys as coadaptative situations become a feature by themselves. The tendency of coevolution and forming more or less detailed lock-and-keys is quite different even within related groups of moths. An example: The *Harita*-type of male genitalia with extraordinary long valves with parallel margins, pirate-hook-shaped, long and fine pointed unci and very small aedeagi is found in both, the genus *Harita* and the genus *Ricla* WALKER, 1869 (Figs. 2, 7). These are allopatric sister groups, *Harita* is found in Asia, *Ricla* is found in the Ethiopian Region. This type of male genitalia (LÖDL [1997] 1996: figs. 12-18; LÖDL 1997b: fig. 14; LÖDL 1997c: fig. 6) obviously matches the simple female genitalia with weak and skinny and flabby bursae as well as the complex systems of variously shaped and structured female genitalia in *Ricla* (LÖDL 1997b: fig. 15; LÖDL 1997c: fig. 4-5). So this is a convincing proof for the existence of quite different evolutive strategies of two obvious compatible genitalic systems. One key fits two completely different lock systems! The small and tiny aedeagi could bear the solution for this problem. This generalized feature enables the female genitalia to walk on different evolutive strategies without necessarily induced coadaptation. The tiny vesicas simply can transfer the spermatophore in both types of females, isolation mechanisms are supposed to be evolved on different fields but definitely not in a lock-and-key between male and female. The big cornuti which are mainly found in the genus *Ricla* seem to fit better in the huge bursae of their females than into the skinny and flabby bursae of the genus *Harita*.

As a result of the presented observations the male uncus can be accepted as a multi-functional organ. It is presumed that the uncus is an active clasping and guiding tool during the mating act. The different forms and sizes of the organ in relation to the remaining genitalia corpus lead to the option that the usage of this tool is also quite different. Beside the clasping function (outside on the female abdomen in precopulative action or on the dorsal surface of the rim between the protruding papillae in the early stages of copula) a mechanoreceptive sensitivity is likely. Furthermore a "pushing function" of the uncus is possible, in pushing upwards the papillae anales complex of the female to open the sterigma cave and the ostium. The widening of the sterigma cave and the ostium area is done by different tools then, e.g. by the lamina dorsalis and lamina ventralis in the Zygaenidae (NAUMANN 1987) or by juxta and transtilla in the Noctuidae, if they are complexly developed. A function in retaining, extracting or rearranging the vesica or even the aedeagus itself is also possible. The illustrations on the genus *Phyllodes* make obvious that at least from a mechanical standpoint the uncus can be left in such a position by the moth making an arrangement or a self-manipulation of the aedeagus with its vesica possible. Unfortunately we have no further knowledge about the artificial character of



Figs. 12 - 15: In situ positions of uncus and allied components of male genitalia. Scale = 0.5 mm, (12) *Phyllodes eyndhovii*, lateral view of uncus and sclerotised scaphium, (13) *Phyllodes eyndhovii*, detail of uncus stuck in the distal portion of the scaphial tube, inserted in the distal opening of the aedeagus, (14) *Phyllodes eyndhovii*, different specimen, lateral view of uncus with distal end inserted in skinny sac at the end of the scaphial shield, (15) *Eudocima salaminia*, lateral view of uncus inserted in corresponding sclerotisations of the scaphial shield. Scaphial tube and tegumen opened, white traces of muscles are visible. Abbreviations: *aed* aedeagus, *sc* scaphium; *te* tegumen; *u* uncus; *v* valve.

this position. Furthermore we do not know how the anaesthetica influence an unnatural, artificial holding of the different parts of the copulatory system. In addition to the well known primary lock-and-key systems in male and female genitalia lock-and-key mechanisms have been observed for the clasping process in the beginning of the copula and lock-and-key between structures of the male genitalia (uncus-scapium complex).

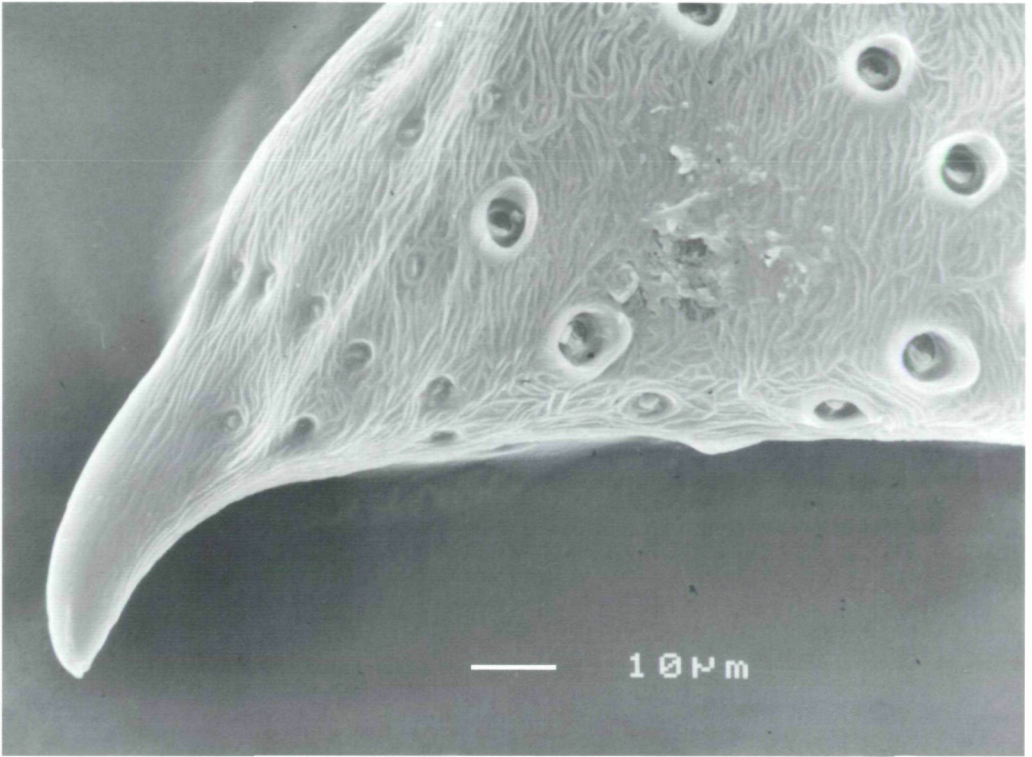


Fig. 16: Scanning microscope studies of the terminal end of the uncus of *Simplicia rectalis*.

Acknowledgements

I am very much indebted to the colleagues of the BMNH who generously helped as ever. In particular I thank David Carter, Dr Jeremy Holloway, Martin Honey, Dr. Malcolm Scoble. Thanks are also due to Dr. Joel Minet (MNHN) for loan of material. I am also very much indebted to Dr. Sabine Gaal-Haszler (NHMW) and Dr. Kristensen (ZMUC) for reading the manuscript.

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Zeitschrift/Journal: [Annalen des Naturhistorischen Museums in Wien](#)

Jahr/Year: 2000

Band/Volume: [102B](#)

Autor(en)/Author(s): Lödl Martin

Artikel/Article: [The "scaphium-pocket" and the "pocket-knife" - functional and morphological peculiarities of the uncus of noctuid moths \(Insecta: Lepidoptera: Noctuidae\). 7-21](#)