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Artificially induced wing folding in trifine and quadrifine noctuids with special reference to the function of the posterior notal wing process (Lepidoptera: Noctuidae)

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Abstract

Aim of this comparative morphological study in the family Noctuidae is the investigation of the function of the wing base structures during wing folding. The forewings and hindwings of representatives of the Noctuidae subfamilies Calpinae, Catocalinae and Noctuinae were artificially moved into their natural resting positions. The changes in position of the various wing base structures are described and figured with detail using light optic methods. Particular attention was paid to the "posterior notal wing process" which is an important taxonomic feature on specific as well as on higher taxonomic level. Because of strucural pecularities we assumed that this notal wing process had a key function in forewing folding. This theory cannot be proved by the existing studies, for detailed investigations show that the posterior notal wing process does not participate in wing folding. For the first time the process of hindwing folding is desribed and illustrated in detail.

Zusammenfassung

Die vorliegende vergleichend-morphologische Studie innerhalb der Familie Noctuidae verfolgt das Ziel, die Funktion der einzelnen Flügelbasisstrukturen während der Faltung der Vorder- als auch der Hinterflügel zu untersuchen. Die Vorder- und Hinterflügel von Vertretern der Unterfamilien Calpinae, Catocalinae und Noctuinae werden künstlich in ihre Ruheposition bewegt. Die Positionsveränderungen der Flügelbasistrukturen werden detailliert beschrieben und photographisch dokumentiert. Besondere Aufmerksamkeit wird dem posterior notal wing process gewidmet, der sowohl auf Art- als auch auf höherem Niveau von taxonomischer Relevanz ist. Aufgrund struktureller Besonderheiten liegt die Annahme nahe, daß dieser notal wing process eine Schlüsselfunktion in der Vorderflügelfaltung übernimmt. Diese Hypothese kann durch die vorliegenden Studien nicht bestätigt werden, weil detaillierte Untersuchungen zeigen, daß der posterior notal wing process an der Flügelfaltung überhaupt nicht beteiligt ist. Zum ersten Mal gelingt es, die Faltung der Hinterflügel zu analysieren und zu dokumentieren.

Key words: forewing, hindwing, Lepidoptera, morphology, Noctuidae, posterior notal wing process, wing base, wing base structure, wing folding.

1. Introduction

Wing folding is achieved by a complex arrangement of sclerites, membranes and bending cuticles. A basic work dealing with the morphology of the wing base structures in fore- and hindwings was first published by SHARPLIN (1963b, c). It contributed to the standardization of the terminology of the wing base sclerites. LÖDL (2000) gave a first survey on the sclerite arrangement of the forewing in the family Noctuidae whereas PAUMKIRCHNER & LÖDL (2002a, 2002c) present a detailed study of the wing sclerites and of participating elements in fore- and hindwing bases in the family Noctuidae. A general summary of the morphology of the wing base is found in MATSUDA (1970) and SCOBLE (1992).

This paper was the result of a consequent investigation of the process of forewing and hindwing folding. A first attempt to the understanding of wing folding was presented by SHARPLIN (1964a).

Published by MC. FARLAND (1979) three main types of resting positions are observed within the order Lepidoptera:

- 1. The tectiform type: the forewings are held over the body like a roof. Most primitive Lepidoptera, but also many members of higher nocturnal groups like Noctuidae and Arctiidae show this type.
- 2. The planiform type: this type is characterized by holding the wings plane on the substrate. The hindwings are visible. This resting posture is typical for several Geometrids.
- 3. The typical resting posture of butterflies is the veliform one. The wings are vertically held over the body. As a result the dorsal surfaces touch and the ventral surfaces of the hindwings are visible.

In between different intermediate stages are possible GRAHAM (1950).

The genus *Catocala* SCHRANK, 1802 and *Noctua* LINNAEUS, 1758 are both characterized by the planiform type of resting posture. The genus *Phyllodes* BOISDUVAL, 1832 represents the tectiform type of resting positions.

Aim of this paper is to demonstrate the participation of the various wing base structures during wing folding and to clarify if there are differences in the main resting positions. Special attention is paid to the **posterior notal wing process** which is of high taxonomic value on special as well as on high taxonomic level. Due to its complex construction consisting of branches, membranes and **bending cuticles**, this notal wing process seemed to be predistinated for playing a central role in wing folding. Especially the large areas of **bending cuticle** in the **posterior notal wing process** permitting an extraordinary flexibility (SHARPLIN, 1963a) support this theory. The process of hindwing folding is investigated for the first time.

This paper is a valueable contribution to the understanding of wing folding, to the demonstration of the responsible sclerites and to the clarifying of misunderstandings caused by the wrong description of vein bases by SHARPLIN (1964).

2. Material and method

The results of this paper have been obtained by light optic methods. First, dried specimens have been cleaned step by step with small brushes. Cleaning is necessary along the whole dorsal and ventral surfaces and along the sides of the thorax. For the investigation of the function of the different wing base structures during wing folding, the wings were prepared with 70% alcohol. By using a hypodermic needle allowing an exact dosage little drops of alcohol were put on the ventral and dorsal wing surfaces. Then the wings were moved step by step into the natural resting position. The photographic documentation of the different steps of movement were done with an Olympus stereomicroscope SZX 12. Special care has to be paid to the avoidance of reflection caused by alcohol.

List of species investigated:

Material of the Natural History Museum in Vienna was used.

Material for the investigation of the process of forewing folding:

Calpinae:

The genus *Phyllodes* BOISDUVAL, 1832 *Phyllodes imperialis* DRUCE, 1888 *Phyllodes verhuellii* VOLLENHOVEN, 1858

Catocalinae:

The genus *Catocala* SCHRANK, 1802 *Catocala elocata* (ESPER, 1787 (1788) *Catocala puerpera* (GIORNA, 1791). *Catocala sponsa* (LINNAEUS, 1767)

Noctuinae:

The genus Noctua LINNAEUS, 1758 Noctua fimbriata (SCHREBER, 1759) Noctua pronuba (LINNAEUS, 1758)

Material for the investigation of the process of hindwing folding:

Catocalinae

The genus *Catocala* SCHRANK, 1802 *Catocala puerpera* (GIORNA, 1791) *Catocala sponsa* (LINNAEUS, 1767)

Noctuinae The genus Noctua LINNAEUS, 1758 Noctua pronuba (LINNAEUS, 1758)

3. Results

The chapter presenting the results of this study is splitted into four parts. The first part deals with the process of forewing folding containing on the one hand a general survey of wing movement and on the other hand the pecularities within the investigated genera. In the second part the process of hindwing folding is demonstrated in a detailed way for the first time. The third part contains a tabule comparing the differences of forewing folding within the investigated genera. The fourth part of this chapter is the photographic part giving evidence to the presented results.

3.1. The process of forewing folding

General survey of forewing folding (Fig. 1-3)

All investigated species are characterized by the same general course of forewing folding. Pecularities and deviations are mentioned later in this paper. Although the prepared species of the genus *Catocala* SCHRANK, 1802, *Noctua* LINNAEUS, 1758 and *Phyllodes* BOISDUVAL, 1832 have different resting positions, there are no obvious differences in wing folding.

The genus *Catocala* is a representative of the planiform resting position. The wings are horizontally held over the body. The forewings are moved backward as far as the outer margins of fore- and hindwings form a straight line. Thorax and hindwings are partly visible. The genus *Noctua* also belongs to the planiform resting position type, but in comparison to the genus *Catocala* the hindwings are completely covered by the forewings. A representative of the tectiform type is the genus *Phyllodes*. The wings are held over the body like a roof.

First, a general survey of forewing folding:

The tergopleuralmuscle called PDC abc after EATON (1988), t-p 13 and 14 after MATSUDA (1970) and M 85 after SNODGRASS (1933) inserting on the **third axillary sclerite** contracts. This muscle is well developed and is covered by the membrane of the **third axillary sclerite**. It consists of three parts: the upper bundle which originates on the episternum, and the middle and the lower bundle which both insert on the epimeron after RHEUBEN & KAMMER (1987). EATON (1988) also mentions three fasciculi, but two originate on the episternum whereas only one has its origin on the epimeron. Due to the contractive force of the tergopleuralmuscle the proximal part of the **third axillary sclerite** is pulled forward. The anterior part of the sclerite is now the most distal, the posterior part the most proximal one. As a result the proximal edge of the sclerite either lies along the processus of the **first and second axillary sclerites** or covers the tips of those both processus. Additionally, the **third axillary sclerite** is arched upwards.

The movement of the **third axillary sclerite** is transmitted to the majority of the wing base and the vein bases so that the whole forewing is moved backward. The part of the wing consisting of the anal, the median and the cubital veins also follows the movement of the sclerite, is arched upwards and covers - according to the resting position - either partly or completely the posterior notal wing process.

The first median plate is partly covered by the radial plate and the median and cubital vein bases.

The anterior part of the wing - the **humeral plate** and the costal and the subcostal veins - tips forward. The **humeral plate** - not mentioned by SHARPLIN (1964) in the context with wing folding - turned out to be a central element in this process. During wing folding a gap arises between the **humeral plate** and the costal vein base. Membranes in between these two structures and the **bending cuticle** on the proximal margin of the costal vein base contribute to the formation of this gap which gains in size during the progressing of wing folding. This gap results in an increased mobility of the forewing. Thus the forewing can easily be moved backward whereas a fixed construction would be a hindrance.

In the work of SHARPLIN (1964) the rotation point is located between the second axillary sclerite and the radial bridge and in RHEUBEN & KAMMER (1987) above the third axillary sclerite. This couldn't be proved. It can be shown that the rotation point is located on the proximal end of the radial plate. The proximal end of the radial plate turns forward, the distal one backward. Subcostal and radial vein base which are connected to the radial plate by bending cuticles move as well. This special type of cuticle (SHARPLIN, 1963a) permits these structures high flexibility. At rest it can be noticed that a little part of the posterior margin of the subcostal vein base is covered by the radial plate and the radial vein base. A little part of the radial vein base itself is covered by the median and the cubital vein base.

Whereas in SHARPLIN (1964) the radial bridge moves backward and coveres completely the scale plate during wing folding, detailed studies demonstrated that the scale plate and the radial bridge nearly move.

The first axillary sclerite, the second axillary sclerite and even the posterior notal wing process which consists of large bending cuticle areas permitting high flexibility and mobility don't participate in wing folding.

The **axillary cord** is the proximal part of the posterior margin of the forewing and a highly important bending system of the **posterior notal wing process**. When the wings are folded, the **axillary cord** has to be shortened. If it would be a fixed construction, it would break during wing folding. But because of its extremely flexible and pliable structure, it forms a loop which is covered by the wing veins and can hardly be seen when the wing is folded. As a result the length of the **axillary cord** is reduced.

Fig. 1 and 2 next page: Schematic illustration of the forewing base structures and their positions when the wing is held horizontally over the body (Fig. 1) and when the wings are folded (Fig. 2).

A=anal vein; 1, 2, 3 AX=first, second and third axillary sclerite; AXC=axillary cord; C=costal vein; CU=cubital vein; HP=humeral plate; M=median vein; MP=median plate; MSC=mesoscutum; PN=posterior notal wing process; R=radial vein; RB=radial bridge; RP=radial plate; S=scale plate; SC=subcostal vein; SP=gap; T=tergopleuralmuscle.



Fig. 3 Two motion-diagrammes which demonstrate the movements of the various forewing base structures during the process of wing folding. The left one shows the situation when the wing is horizontally held over the body and the right one when the wing is folded.

3AX=third axillary sclerite; HP=humeral plate; MP=median plate; R=radial vein; RP=radial plate; S=scale plate; SC=subcostal vein.



Special formations of the forewing base structures within the investigated material

1. THE GENUS CATOCALA (FIG. 7-19)

Investigated species: Catocala elocata (ESPER, 1787 (1788), C. puerpera (GIORNA, 1791) and C. sponsa LINNAEUS, 1767).

- At rest the proximal part of the third axillary sclerite lies along the processus of the first axillary sclerite and the second axillary sclerite.
- Only the distal part of the posterior notal wing process is covered by the anal veins.
- The anterior margins of the radial plate and of the radial vein base form a straight line.

2. THE GENUS NOCTUA (FIG. 20-35)

Investigated species: Noctua fimbriata (SCHREBER, 1759) and N. pronuba (LINNAEUS, 1758).

- The third axillary sclerite lies upon the tip of the processus of the second axillary sclerite.
- The posterior part of the forewing completely covers the **posterior notal wing process**.
- Within the species *Noctua fimbriata* the anterior margins of the **radial plate** and the radial vein base do not form a continous line because in comparison to the **radial plate** the base of the radial vein is bent. The species *N. pronuba*, however, shows a straight line formed by the posterior margins of the **radial plate** and the radial vein base.

3. THE GENUS *PHYLLODES* (FIG. 36-42)

Investigaated species: Phyllodes imperialis DRUCE, 1888 and P. verhuellii VOLLENHOVEN, 1858.

- The third axillary sclerite lies along the processus of the first axillary sclerite and the second axillary sclerite.
- Whereas in the species *Phyllodes imperialis* the **posterior notal wing process** is only half covered by the posterior part of the forewing, in the species *P. verhuellii* it is covered completely.
- The anterior margin of the radial plate and the radial vein base don't form a continous line, for the base of the radial vein is bent.

3.2. The process of hindwing folding

A general survey of the process of hindwing folding in the family Noctuidae (Fig. 4-6)

Within all four investigated species (*C. puerpera* (Fig. 43-45), *C. sponsa* (Fig. 46-49) and *Noctua* pronuba (Fig. 50-52)) the same course of hindwing folding could be noted although the two genus *Catocala* and *Noctua* are characterized by different resting positions. In the following part a general survey of this process shall be presented:

The tergopleuralmuscle which inserts on the third axillary sclerite contracts. As a result the proximal part of the sclerite is pulled forward, but not as much as it happens in the forewing. At rest the proximal part of this sclerite lies along the processus of the first axillary sclerite and the second axillary sclerite. The force of the muscle is transmitted to the rest of the hindwing by the cubital plates. The anal veins move to the body, are arched upwards and cover the axillary cord and the posterior notal wing process. On the whole, the hindwing is moved backward and put against the body.

The median plate and the median arm follow the movement of the third axillary sclerite and show a slight movement backward.

The area of the cubital veins is folded. Thus the second **cubital plate** rotates downwards and disappears on the ventral surface of the wing, trapped between the **median plate** and the subcostal vein base.

The subcostal vein base moves backward as well. At rest the proximal end forms the anterior part and the distal end the posterior part of this vein base.

The radial bridge nearly moves.

The first axillary sclerite and the second axillary sclerite are static structures which don't change their positions during wing folding.

As demonstrated in the forewing, the **axillary cord** is characterized by forming a loop when the wing is in the resting position. Due to its construction which hasn't yet been investigated satisfactorily the **axillary cord** is highly flexible in order to be able to cope with the mechanical forces arising during wing folding.

Fig. 4 Two motion-diagrammes which demonstrate the movements of the various hindwing base structures during the process of wing folding. The left one shows the situation when the wing is horizontally held over the body and the right one when the wing is folded.

3AX=third axillary sclerite; 2CP=second cubital plate; SCB=subcostal vein base.





Fig. 5 and 6 Schematic illustration of the hindwing base structures and their positions when the wings are held horizontally over the body (Fig. 5) and when the wings are folded (Fig. 6).

A=anal vein; 1, 2, 3 AX=first, second and third axillary sclerite; AXC=axillary cord; C=costal vein; 2CP=second cubital plate; CU=cubital vein; HP=humeral plate; M=median vein; MA=median arm MP=median plate; PN=posterior notal wing process; R=radial vein; RB=radial bridge; RP=radial plate; S=scale plate; SC=subcostal vein; SCB=subcostal vein base; T=tergopleuralmuscle.





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		PNM	IPR	RÄNDER DER I	R.PL. UND DER
3	AX	wird in der Ruhe den Flüge	position durch Ihinterteil	RADIALA[bilden in der	DERBASIS Ruheposition
liegt entlang der					kein●
Prozessus des 1AX	verdeckt den	ganz verdeckt	zum Teil	eine Linie	einheitliche
und des 2AX	Prozessus des 1AX		verdeckt		Linie
•			•	•	
	•	•			•
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	3. Ilegt entlang der Prozessus des 1AX und des 2AX	3AX liegt entlang der Prozessus des 1AX und des 2AX Prozessus des 1AX Prozessus des 1AX	SAX PNW SAX wird in der Ruhe liegt entlang der verdeckt den prozessus des 1AX Prozessus des 1AX und des 2AX Prozessus des 1AX 	PNWPR 3AX SINT SAX wird in der Ruheposition durch den Flügelhinterteil liegt entlang der Prozessus des 1AX ganz verdeckt und des 2AX Prozessus des 1AX ganz verdeckt 	PNWPR RANDER DER RADIALAI JAX wird in der Ruheposition durch den Flügelhinterteil RADIALAI Wird in der Ruheposition durch den Flügelhinterteil bilden in der Ilegt entlang der Prozessus des 1AX verdeckt den Prozessus des 1AX zum Teil verdeckt eine Linie

3.3. Tabule of the wing base data based on the investigations of the material

ZUSAMMENFASSUNG DER ERHOBENEN DATEN BEI DER FALTUNG DER VORDERFLÜGEL IN DIE RUHEPOSITION

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3.4. Photographic demonstration of the results

Fig. 7 Catocala elocata, δ , (France, NHMW), forewing base when the wings are horizontally held over the body.

Fig. 8 Catocala elocata, δ , (France, NHMW), forewing base moved backward, position 1.

Fig. 9 Catocala elocata, &, (France, NHMW), forewing at rest.







Fig. 10 *Catocala puerpera* (Poland, NHMW), forewing base when the wings are horizontally held over the body.

Fig. 11 *Catocala puerpera* (Poland, NHMW), forewing base moved backward, position 1.

Fig. 12 Catocala puerpera (Poland, NHMW), forewing base in the resting position.

Fig. 13 Catocala puerpera (Italy, NHMW), position of the humeral plate when the forewing is in the resting position.









Fig. 14 Catocala sponsa, &, (NHMW), forewing base when the wings are horizontally held over the body.

Fig. 15 Catocala sponsa, &, (NHMW), forewing base moved backward, position 1.

Fig. 16 Catocala sponsa, δ , (NHMW), forewing base when the the wing is at rest.







Fig. 17 Catocala sponsa, \mathcal{S} , (Austria inferior, NHMW), humeral plate when the forewings are horizontally held over the body.

Fig 18 Catocala sponsa, δ , (Austria inferior, NHMW), humeral plate when the forewings are moved backward, position 1.

Fig. 19 Catocala sponsa, \mathcal{S} , (Austria inferior, NHMW), humeral plate when the forewings are in the resting position

Fig. 20 *Noctua fimbriata* (NHMW), forewing base when the wings are horizontally held over the body.

Fig. 21 Noctua fimbriata (NHMW), forewing base when the wings are moved backward, position 1.

Fig. 22 *Noctua fimbriata* (NHMW), forewing base when the wings are moved backward, position 2.













Fig. 23 Noctua fimbriata (NHMW), forewing base when the wings are moved backward, position 3.

Fig. 24 Noctua fimbriata (NHMW), forewing base when the wings are at rest.

Fig. 25 Noctua fimbriata (NHMW), humeral plate when the forewings are horizontally held over the body.

Fig. 26 *Noctua fimbriata* (NHMW), **humeral** plate when the forewings are moved backward, position 1.

Fig. 27 Noctua fimbriata (NHMW), humeral plate when the forewings are moved backward, position 2.

Fig. 28 Noctua fimbriata (NHMW), humeral plate when the forewings are at rest.













Fig. 29 Noctua pronuba, \mathcal{J} , (Austria inferior, NHMW), forewing base when the wings are horizontally held over the body.

Fig. 30 Noctua pronuba, \mathcal{S} , (Austria inferior, NHMW), forewing base when the wings are moved backward, position 1.

Fig. 31 Noctua pronuba, δ , (Austria inferior, NHMW), forewing base when the wings are moved backward, position 2.

Fig. 32 *Noctua pronuba* (Austria inferior, NHMW), forewing base when the wings are moved backward, position 3.

Fig. 33 Noctua pronuba, δ , (Austria inferior, NHMW), forewing base when the wings are in the resting position.

Fig. 34 *Noctua pronuba,* δ , (Austria inferior, NHMW), forewing base when the wings are at rest.













Fig. 35 Noctua pronuba, δ , (Austria inferior, NHMW), forewing base when the wings are in the resting position. The axillary cord forms a loop. A=anal veins; AC=axillary cord; 3AX= third axillary sclerite; PN=posterior notal wing process; TH=thorax.

Fig. 36 *Phyllodes imperialis*, \mathcal{P} , (NHMW), forewing base when the wings are horizontally held over the body.

Fig. 37 Phyllodes imperialis, 9, (NHMW), forewing base when the wings are in the resting position.



Fig. 38 *Phyllodes verhuellii* (Java, NHMW), forewing base when the wings are horizontally held over the body.

Fig. 39 *Phyllodes verhuellii* (Java, NHMW), forewing base when the wings are moved backward, position 1.

Fig. 40 *Phyllodes verhuellii* (Java, NHMW), forewing base when the wings are moved backward, position 2.

Fig. 41 *Phyllodes verhuellii* (Java, NHMW), forewing base when the wings are moved backward, position 3.

Fig. 42 Phyllodes verhuellii (Java, NHMW), forewing base when the wings are in the resting position.













Fig. 43 Catocala puerpera, δ , (Vienna, NHMW), hindwing when the wings are horizontally held over the body.

Fig. 44 Catocala puerpera, δ , (Vienna, NHMW), hindwing when the wings are moved backward, position 1.

Fig. 45 *Catocala puerpera*, \mathcal{F} , (Vienna, NHMW), hindwing when the wings are at rest.







Fig. 46 Catocala sponsa, \mathcal{P} , (Vienna, NHMW), hindwing when the wings are horizontally held over the body.

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Fig. 47 Catocala sponsa, \mathfrak{P} , (Vienna, NHMW), hindwing when the wings are moved backward, position 1.

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Fig. 48 Catocala sponsa, \mathcal{P} , (Vienna, NHMW), hindwing when the wings are moved backward, position 2.

Fig. 49 Catocala sponsa, \mathfrak{P} , (Vienna, NHMW), hindwings at rest.









Fig. 50 Noctua pronuba, \mathcal{F} , (NHMW), hindwing when the wings are moved backward, position 1.

Fig. 51 Noctua pronuba, δ , (NHMW), hindwing when the wings are at rest.

Fig. 52 Noctua pronuba, \mathcal{E} , (NHMW), hindwing when the wings are at rest.







4. Conclusion

4.1. Forewing folding

The third axillary sclerite, the humeral plate, the radial plate, the radial and subcostal vein bases and the axiallary cord turned out to be the central elements in forewing folding. For the first time, the process of forewing folding has been documented and analysed step by step. Due to its construction the axillary cord permits high flexibility by forming a loop during wing folding. Additionally, the humeral plate guarantees the anterior part of the wing high mobility. The rotation point is located at the proximal end of the radial plate. The first axillary sclerite, the second axillary sclerite and the posterior notal wing process do not participate in wing folding. The numerous bending cuticle-areas of the wing base result in an extraordinary flexibility and mobility of the wing and ensure that the sclerotized elements do not break because of the various mechanical forces they are exposed to during wing folding.

The wing is a "high-capacity-system". It consists of a very complex arrangement of membranes, ligaments, slerites and muscles which permit a multitude of movements. During wing folding the wing has to cope with high tensions. If the wing only consisted of cuticular and slerotized structures, it would break under the influence of the different mechanical demands. Membranous and special morphologically developped structures help to compensate these tensions. The peculiar construction of the **posterior notal wing process** - especially the large **bending cuticle** areas - have lead to the conclusion that this **notal wing process** may play a central role in compensating these tensions. But as it could be proved, the **posterior notal wing process** does not participate in wing folding. Therefore the **posterior notal wing process** may function as a "tension-compensating-system".

4.2. Hindwing folding

This paper succeeded for the first time in presenting the process of hindwing folding. The functions of the various wing base structures were carefully investigated and photographically documented.

As it could be demonstrated in a detailed way, the third axillary sclerite, the second cubital plate, the subcostal vein base and the axillary cord play a central role in the process of hindwing folding. In the hindwing the cubital plates take over the function of the median plates of the forewing. They transmit the movement of the third axillary sclerite to the rest of the wing. The subcostal vein base of the hindwing is characterized by the same mobility and flexibility as the radial plate of the forewing. The first axillary sclerite and the second axillary sclerite don't participate in wing folding and therefore don't change their position. They are static elements of the hindwing base. The construction of the axillary cord guarantees high mobility to the hindwing as well as to the forewing.

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