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Extension and Coiling of the lepidopterous Proboscis — a new Interpretation of the Blood-pressure Theory

by

HANS BÄNZIGER

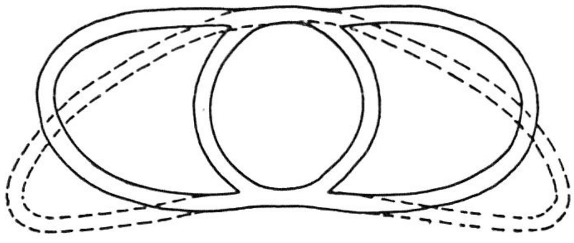
Abstract

In a series of experiments the theory claiming that the muscles inside the proboscis produce a dorsal transverse convexity, which finally would cause proboscis extension like in a steel measuring tape, and the theories explaining extension either by direct muscle contraction or by the proboscis' own elasticity, are shown to be not or only partially correct. Electric stimulation of these muscles proves that they cause full coiling (this is also true for the galeae under haemocoelic turgescence) ; elasticity keeps the proboscis in a loosely coiled shape. Extension is achieved by blood-pressure in the proboscis, proved by different experiments, as e.g. the forcibly reproduction of the movements of the blood-pumping stipes on anaesthetized or dead specimens.

Introduction

The mechanism of the extension and coiling of the lepidopterous proboscis has been the object of studies since the times of RÉAUMUR. The hypothesis or theories advanced since then have been reviewed in *extenso* by EASTHAM & EASSA (1955). The most important are : (i) extension as well as coiling are caused directly by two sets of muscles which lie in the galeae (RÉAUMUR, 1734 ; GERSTFELD, 1853 ; PORTIER, 1949). (ii) the muscles inside the galeae cause extension only, whereas coiling is due to the elastic properties of the proboscis' walls which return to their original resting shape after having been subjected to tension during the extension (SAVIGNY, 1816 ; KIRBACH, 1883 ; HERING, 1926 ; WEBER, 1933 ; PRADHAN & AREN, 1941 ; FORSTER, 1954 ; EIDMANN, 1970). (iii) extension is effected by elasticity and coiling by muscles (BURGESS, 1880 ; BREITENBACH, 1882 ; LAMEERE, 1938). (iv) the muscles inside the galeae cause coiling and extension is achieved by inflating the galeae with blood (SNODGRASS, 1935 ; SCHMITT, 1938 ; IMMS, 1947). (v) for extension the upper walls of the proboscis are bent transversally by the muscles to create a dorsal transverse convexity which finally causes extension in a way rather like that of a steel measuring tape, but with starting and resulting position reversed

(Fig. 1 and 2); the proboscis is coiled by elasticity due to a flexible bar situated in the upper wall of the proboscis (EASTHAM & EASSA, 1955; WIGGLESWORTH, 1964; SRIVASTAVA & BOGAWAT, 1969). The last theory is the only one which is supported by a number of experiments. SCHREMMER (1962) proposed a combined action of the mechanisms of theories (iv) and (v): Extension would be caused by both the dorsal transverse convexity and the blood pressure.



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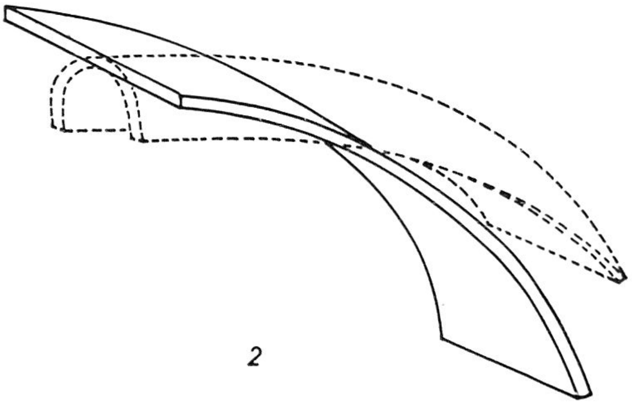

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Fig. 1. — Transverse section of the proboscis showing the supposed dorsal transverse convexity (broken line) which would lead to the extension of the proboscis (after EASTHAM & EASSA, 1955; diagrammatic).

Fig. 2. — Diagramm illustrating the effect of a transverse bending on a longitudinally curved elastic strip (after EASTHAM & EASSA).

However, KRISTENSEN (1968) discovered that no muscles are present in the proboscis of the primitive *Eriocrania*, whose proboscis, therefore, cannot be extended by the mechanism proposed by the theory of the dorsal transverse convexity. In 1969, in the course of a study on the piercing mechanism of fruit-piercing Noctuidae we observed several behavioural features which could not be explained by this theory either, and research was carried out to find a solution to the many conflicting theories. As these often were the result of only theoretical assumptions or speculations based on morphological data, and because experimental evidence is more convincing than theoretical calculations, it was felt that the present new analysis should be mainly experimental.

Material and methods

Since EASTHAM & EASSA (1955) used *Pieris brassicae* L., the same species was used as a test insect for a new approach to their findings. In addition, the Noctuids *Calpe thalictri* BKH. and *Scolyopteryx libatrix* L. were tested accordingly.

In order to obtain some information on the proboscis movements in other lepidopterous families a second series of tests, limited to the more fundamental experiments (i.e. 1a, b ; 4a ; 6a, b ; 8a) was made with the following species : *Agapetes galathea* L. (Satyridae), *Cyaniris semiargus* Rott. (Lycaenidae), *Adopaea silvester* Poda. (Hesperiidae), *Zygaena trifolii* Esp. (Zygaenidae), *Eilema depressa* Esp. (Arctiidae), *Ematurga atomaria* L. (Boarminae, Geometridae), *Geometra papilionaria* L. (Geometrinae, Geometridae), *Nomophila noctuella* Schiff. and *Sylepta ruralis* L. (Pyralidae).

General morphology of the mouth-parts

The mouth-parts of higher Lepidoptera are largely reduced with exception of the maxilla, i.e. cardo, stipes and galea. The morphology of the maxilla and its muscles has been studied in different species of the most important lepidopterous families by SCHMITT (1938), in *Pieris brassicae* L. by EASTHAM & EASSA (1955), in *Calpe thalictri* BKH. and *Scolyopteryx libatrix* L. by BÄNZIGER (1970). Therefore, only a generalized and concise review of the morphology will be given.

The cardo has no apparent function for the coiling and uncoiling movements. The very complicated shape of the stipes may be described as consisting of a cylindrical and a more or less flat part. The first has a slit-like aperture opening into the head cavity. The distal end of the stipes merges directly into the galea. SCHMITT (1938) found that the slit-like opening of the stipes can be closed like a valve by the stipital muscles and that by their action the cavity of the stipes is reduced in volume, thereby forcing the haemolymph into the galea thus causing extension of the proboscis. Extension through hydraulic pressure was already assumed by BERLESE (1909), but he took the saliva as the pressure fluid and the galeal trachea for a tubule into which the saliva should have been pumped to effect extension.

According to SCHMITT (1938) three stipital muscles are present in functional proboscides of higher Lepidoptera. The same has been reported for *P. brassicae* (EASTHAM & EASSA, 1955). In *C. thalictri* and *S. libatrix* on the other hand four muscles are attached to the stipes (BÄNZIGER, 1970). Two of them produce the blood-pressure, and two are responsible for the protracting and retracting movements of the galeae, one of the most important features in piercing.

The proboscis is formed by the two grooved galeae which enclose the food canal of the proboscis (Fig. 3). The galeae are held together dorsally and ventrally by two rows of interlocking processi (RÉAUMUR, 1734 ; BREITENBACH, 1882 ; EASTHAM & EASSA, 1955). The inner walls of the galeae, i.e. the lining of the food canal, consist of exocuticula, the outer walls of endocuticula with annuli of exocuticula embedded in them. This combination of relatively soft endocuticula and stiffer exocuticula gives the proboscis the suppleness necessary for coiling and at the same time a certain degree of stability. In the upper wall of the food canal of each galea lies, after EASTHAM & EASSA (1955), an exocuticular bar which in their view is responsible for the elastic coiling of the proboscis. The wall of the food canal is penetrated by a number of sensilla, first observed by KIRBACH (1883). EASTHAM & EASSA (1955) noted a great number of glands situated in a row in the upper angle of the haemocoel. They are connected with the exterior by a duct which terminates between the processi of the linkage. They possibly serve to seal up and to lubricate the processi of the linkage (EASTHAM & EASSA, 1955).

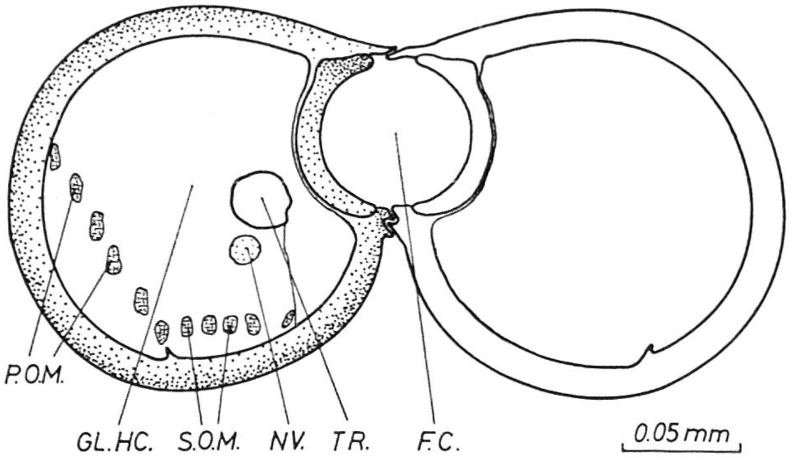

Fig. 3. — Transverse section of the proboscis of *Calpe thalictri*. F.C. = food canal; GL.HC. = galea haemocoel ; NV. = nerve ; P.O.M. = primary oblique muscle; S.O.M. = secondary oblique muscle ; TR. = trachea (after BÄNZIGER, 1970).

Each galea of *C. thalictri* has two sets of muscles which occur throughout the whole length of the proboscis (Figs. 3 ; 4a, b). The muscles of the first set, the primary oblique muscles after EASTHAM & EASSA (1955), are oriented in a proximal-distal manner from the dorso-ventral wall to the medio-ventral wall. The second set, the secondary oblique muscles, is oriented in a proximal-distal manner from the inner part of the ventral wall to the middle of the ventral wall. In *P. brassicae* only a few secondary oblique muscles are found in a very restricted area causing there the "knee-bend" described by EASTHAM & EASSA (1955).

C. thalictri, *S. libatrix* and to a much lesser degree *P. brassicae*, can uncoil their proboscis more than to full extension, so that the proboscis is turned upwards and backwards. This movement, called hyper-uncoiling (Fig. 6), is an interesting feature which will be of help for the understanding of the proboscis' extension mechanism.

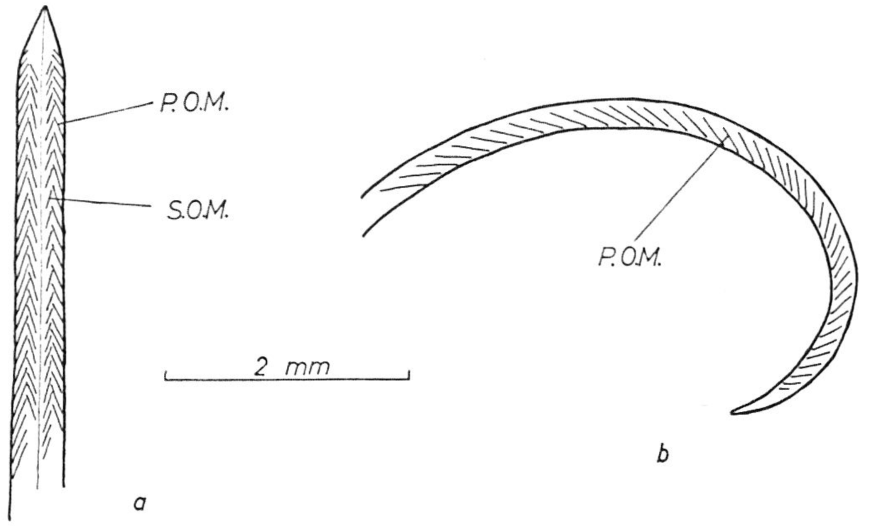

Fig. 4. — Longitudinal sections of median and distal region of the proboscis of *C. thalictri* showing the galea musculature *a*) from above and *b*) from the side. P.O.M. = primary oblique muscle ; S.O.M. = secondary oblique muscle (after BÄNZIGER, 1970).

Unlike *P. brassicae*, the Noctuids *C. thalictri* and *S. libatrix* can curve their proboscis laterally, a faculty which is important for the piercing of fruits (BÄNZIGER, 1969, 1970).

Experiments on extension and coiling of the proboscis

The following experiments were made in order to test the different theories on the extension and the coiling of the proboscis.

Extension

1. *a)* With the aid of a stereomicroscope one may often observe how Lepidoptera during recovery from anaesthesia try to extend and coil their proboscis. Each stretching is accompanied by an oblique lateral movement of the stipes towards the gena. This is the externally visible pumping action of the stipes which forces the blood into the galea.

b) With the aid of forceps it is possible to imitate this movement and reproduce the same effect on anaesthetized or freshly killed specimens. Each time the stipes is forced sideways the proboscis extends more or less fully. If a specimen is submerged in water for one day or more it is possible to inflate the proboscis gradually by moving the stipes to and fro until it is hyper-uncoiled (Fig. 6). Probably some pressure or swelling effect due to the prolonged submersion prevents the reflux of the blood or impedes the opening of the stipital valve once the external pressure on the stipes is released.

2. If the proboscis of a living specimen is cut off near the base, a little drop of haemolymph can be seen flowing out from the stump of the proboscis at each lateral movement of the stipes. The same can be observed on a freshly killed specimen whose stipes is moved sideways by forceps.

3. A finely drawn out glass cannula was introduced into the base of the galea. By injecting ringer solution any degree of uncoiling, including hyper-uncoiling, could be readily achieved.

4. *a)* Squeezing of the proboscis results in extension of the part located distally from the squeezing point. This happens independently of whether the proboscis is still *in situ* or has been cut off from the insect. The squeezing both diminishes the lumen of the galea and impedes the reflux of the haemolymph.

   b) A dead proboscis whose oblique muscles do not contract when under the influence of electric impulses shows the same reaction.

5. *a)* If in a living moth the proboscis is cut across or the galea is punctured the proboscis can no more extend and blood can be seen to flow out from the wound. The same happens when on such proboscis the experiment 1b is made. In the case where the terminal part of the proboscis is cut, it may extend for a moment as the blood only slowly can escape from such a minute leak and because the terminal part of the galeal haemocoel is filled up nearly completely by the oblique muscles (EASTHAM & EASSA, 1955).

   b) The same is true for proboscides so operated which have been cut off at the base and tested as in experiments 4a and b.

   c) The same happens if the pressure chamber of the stipes is punctured. This has already been demonstrated by EASTHAM & EASSA (1955) but was in contrast to the findings of PRADHAN & AREN (1941) with *Danaida chrysippus* L. Since the latter checked the ability to extend the proboscis of treated specimen only after a long interval, it is well possible that the wounds had been sealed up in the meantime. Another possibility to explain their result lies in the assumption that they punctured only the flat part of the stipes, thus leaving the tubular part with the pressure chamber intact.

Coiling

6. *a)* The proboscis of a *P. brassicae* at rest has 4½ coils (Fig. 5b), that of the two moths 2½. If the insects are anaesthetized, generally the proboscis keeps this coiling degree.

   b) However, if in one of these species the proboscis is gently uncoiled or loosened the proboscis always assumes a loosely coiled shape of 2½ coils in *P. brassicae* (Fig. 5a) and one only in the two moths.

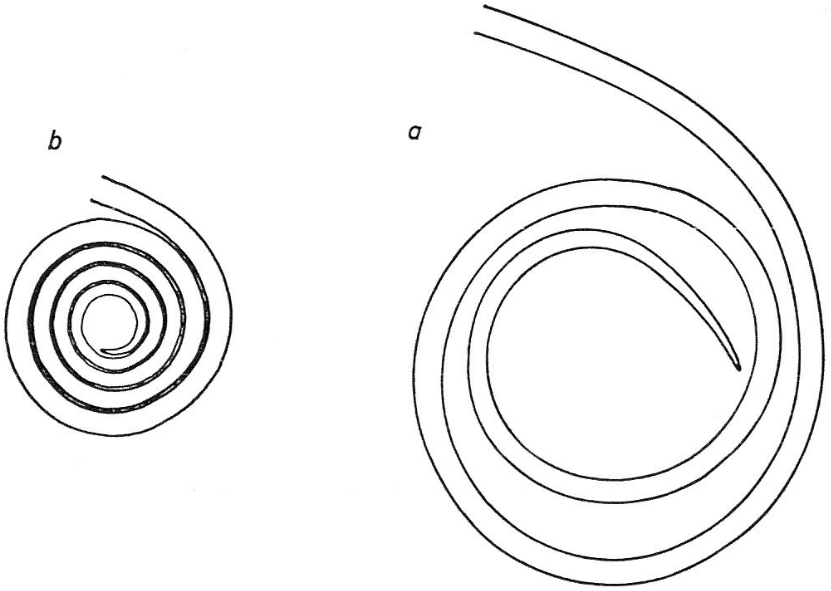

Fig. 5. — Proboscis of *Pieris brassicae a)* loosely coiled and *b)* fully coiled.

   c) When recovering from anaesthesia the insects try to coil the proboscis completely to 4½ and 2½ coils respectively. However, the proboscis soon uncoils slowly to the former 2½ (viz. 1) coils until the next coiling attempt is made. One also may notice spasmodic coiling movements of the proboscis. Only after complete recovery are the insects able to coil their proboscis completely and keep it fully coiled.

7. *a)* If a proboscis is cut from a living adult in its extended state during the food uptake the proboscis assumes the loosely coiled shape.

   b) The same happens with a proboscis cut in its fully coiled position from a resting specimen.

8\. *a)* A cut proboscis, loosely coiled, suddendly coils fully when touched by electrodes (1 V, AC of 50 cycles, 8 or more µA in distilled water) and re-uncoils to the previous state when the electric current is interrupted.

b) Proboscides under pressure in a more or less fully extended state react similarly. If in feeding specimens the reflux of blood from the extended galeae is prevented by a ligature at the base of the proboscis it stays extended. Under the influence of electric impulses the proboscis starts coiling as expected. However, coiling is only partially achieved, since coiling increases the blood-pressure which counteracts the coiling movement. After interruption of the electric current the proboscis extends again.

9\. The nerve supply of the oblique muscles was cut inside the galea, about 5 mm distally from the base. There is little doubt that in this operation the nerve supply of the blood-pressure producing muscles has not been cut. The ramification of the nerve supply of these muscles lies probably in front of or less probably within the stipes, but surely not in the galea. If the ramification were to lie within the galea two nerve cords should be visible in the transverse section of the galea ; this is not the case. Result : in those cases where the specimens did recover sufficiently from the operation, the proboscis could be extended more or less completely, whereas complete coiling failed to occur. The difficulty of extending the proboscis in the operated specimens is probably a consequence of the severity of the operation. Also, it was especially difficult to seal the galea tightly enough against the force of the blood-pressure.

10\. *a)* Maceration of a fresh or dead, loosely coiled proboscis in 10% KOH causes complete coiling.

b) Maceration of a proboscis in water causes more or less complete extension after a few days. The failure to react to electric stimuli shows that the muscles of such proboscides are dead.

c) If a proboscis as in 10b is placed for a few minutes in 10% KOH, it coils quickly. The same occurs if it is put into a saturated solution of NaCl.

d) If brought back in water the proboscis extends again.

e) Drying causes extreme coiling if not even shrinkage.

11\. *a)* When a ringer solution for *P. brassicae* larvae (NOVÁK, 1960) is used, the proboscis retained, also after the death of the muscles, its loosely coiled shape ($2\frac{1}{2}$ coils) for two days, after which it uncoiled almost imperceptibly.

b) Similar results were obtained with proboscides placed in the adult's haemolymph.

c) The loosely coiled shape of the proboscis resulted also after the muscles were poisoned with iodoacetic acid (death controlled by electric stimulation).

12. The upper wall of the galea with the elastic bar was stripped off from the lower wall. When placed in ringer solution, the upper half assumed a loosely coiled shape, but coiled up fully when placed in KOH.

The experiments 10 to 12 show that coiling and uncoiling of a dead proboscis are osmotic reactions resulting from the galea's peculiar structure. The bar consists of exocuticula, whereas the rest of the proboscis is made of endocuticula and annuli of exocuticula. The cuticula can shrink and swell depending on whether water is removed or added (RICHARDS, 1951). Swelling can be influenced by pH, salts and other factors (KATZ, 1933). FRAENKEL & RUDALL (1947) had shown that the endocuticula undergoes far greater dilatations or contractions in the plane of the surface than the exocuticula. Therefore, when put for not too long a time in a solution of KOH or NaCl (or if dried in the air) the upper wall containing the exocuticular bar shrinks much less than the lower consisting mainly of endocuticula and the result is coiling. The contrary is achieved when water is added, since then the upper wall swells less than the lower.

The maximal extension which can be attained by the mechanism of the principle of the transverse convexity would be a straight state. With the blood-pressure mechanism, on the other hand, the proboscis can be hyper-uncoiled (Fig. 6, experiments 1b and 3), because of the asymmetrical longitudinal elasticity of the galea due to the relatively stiff bar and the more elastic lower wall, which can become longer than the bar on account of the blood-pressure.

Comparing the experiments made with the species of the more limited series of tests and those made with the three main test species, no qualitative difference was noticed (it is obvious that quantitative differences, in the number of the proboscis' coils and the intensity of the reactions, were found). Further, it is not essential for the achievement of the extension, whether the experiments 5 and 10 are carried out on a single galea or on the proboscis as a whole organ.

Discussion

The first three theories ((i) oblique muscles cause both extension and coiling ; (ii) oblique muscles cause extension, elasticity full coiling ; (iii) the contrary of (ii)) explain incorrectly the mechanism of extension since they claim that it is either caused by the oblique muscles or is the result of elasticity (both refuted by the experiments 1 to 5, 7 to 9, 11 and 12). The explanation of the coiling mechanism is in all theories partially correct, as it is achieved mainly by muscle action and to a lesser extent by elasticity (experiments 7, 8, 11 and 12).

Since the theory of the dorsal transverse convexity is supported by a number of experiments and reflections (EASTHAM & EASSA, 1955), these should be analysed first before the theory itself will be examined.

1. EASTHAM & EASSA state (p. 31) that SCHMITT (1938) thought that the haemolymph was forced from the *head* into the proboscis through a slit-like opening in the stipes. To reject this and with it the blood-pressure theory they punctured the head of *P. brassicae*, thus impeding the building up of a high blood-pressure in the head. Since they found the butterflies still able to extend the proboscis, they apparently rejected the blood-pressure theory. However, nowhere does SCHMITT (1938) claim that the blood is forced from the *head* into the proboscis. He clearly states (pp. 8, 26 and Fig. 4) that the pressure is built up in the *stipes*, and that blood is forced from the *stipes* into the galeae. The experiment, therefore, does not undermine in the least the validity of the blood-pressure theory. One wonders whether EASTHAM & EASSA were not simply misled by the earlier false interpretation of SCHMITT's theory by IMMS (1947).

2. Since EASTHAM & EASSA thought that the primary oblique muscles cause extension, it was necessary to explain coiling by another mechanism, and elasticity remained the only possible one. To test whether a proboscis on which no muscles act does coil or extend, EASTHAM & EASSA employed KOH maceration ; they found that the proboscis coiled up completely. However, KOH does not only destroy muscles, it also causes the cuticle to shrink unequally, which results in the coiling of the proboscis, as demonstrated by experiments 10 to 12. After correct elimination of the oblique muscles, i.e. without affecting the galea walls physically or chemically as in experiment 11, the proboscis is not fully coiled but loosely (Fig. 5a and b). However, after the theory of EASTHAM & EASSA, the proboscis without functioning muscles should coil up completely.

3. EASTHAM & EASSA tried to localize the agent of the elastic coiling movement by stripping off the lower galea wall from the upper in which they found the rod which they called the elastic bar. Whereas the lower wall assumed a loose shape, the upper one containing the rod coiled up fully. However, the experiments 10 and 12 show that this was only possible if EASTHAM & EASSA dried the operated parts or put them in KOH to eliminate a possible action of the muscles. If so, EASTHAM & EASSA were again misled by an artifact.

4. EASTHAM & EASSA carried out an experiment which they thought would prove that the proboscis extension is brought about by the

oblique muscles. They cut the nerve supply of these muscles between the suboesophageal ganglion and its entrance into the stipes. After this operation they found that the galea could no longer be extended and that it remained loosely coiled. But the argument that the failure of the proboscis to extend was due to the failure of the oblique muscles to work, is not valid, since it has not been proved that by this operation the nerve supply for the muscles producing the pressure in the stipes was still intact. The failure of the pressure producing muscles would likewise prevent the proboscis to extend. The experiment 9 shows that the proboscis can be extended after the nerve supply of the oblique muscles is cut. Furthermore, as complete coiling failed to occur, the experiment is a further proof that not elasticity, but the oblique muscles assure complete coiling.

Thus the experiments supporting the theory of the dorsal transverse convexity are not valid. This does not imply that the theory itself is not correct, but after consideration of the following arguments it seems to us that also the theory must be rejected :

1) The presumed agent of the supposed dorsal transverse convexity, the oblique muscles, in reality cause coiling. This is true also for the galeae under haemocoelic turgescence.

2) The presumed agent for full coiling, the elasticity, in reality keeps the proboscis in a loosely coiled state.

3) Hyper-uncoiling (Fig. 6) of the proboscis would be impossible on the basis of the mechanical principle postulated for the theory of the dorsal transverse convexity (the same applies to steel tape model).

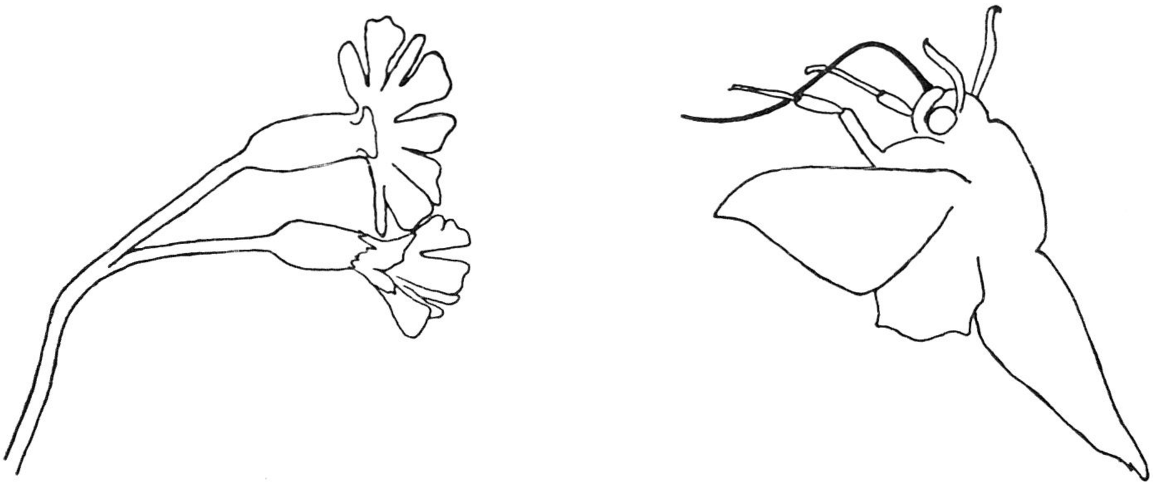

Fig. 6. — *Deilephila elpenor* (Sphingidae) flying to a pink. Note the pronounced hyper-uncoiled state of the distal half of the proboscis. (Drawn from a photograph by T. Angermayer.)

4) The mechanical principle of extension by the dorsal transverse convexity should operate also without pressure, exactly as it does in the steel tape model, but it has been proved that blood-pressure in the galeae is necessary for extension (experiment 5).

Furthermore : the dorsal transverse convexity actually taking place has never been seen or demonstrated directly. Unlike the steel tape, the ventral wall of the galea is longitudinally very elastic and therefore does not seem to be fitted to withstand the longitudinal stress arising from the dorsal transverse convexity. The mechanism of the dorsal transverse convexity has been assumed for the proboscis as a whole organ and a single galea should not or only very slightly be able to extend, as practically no convexity is then left. However, it has been shown that a single galea can be extended with the same ease as the linked galeae of the whole proboscis.

The blood-pressure theory is proved by experiments 1 to 12. In the theory by SNODGRASS (1935) and SCHMITT (1938) the blood-pressure is built up by inflating the galeae. Theoretically, however, the blood-pressure in the proboscis might only partially be the result of the blood pumped into it, and partially brought about by a reduction of the volume of the proboscis. If the oblique muscles by their contraction would flatten the galeae they might reduce the galea haemocoel. Because of the closure of the stipital valve, the blood, in the absence of an outlet, would force the proboscis to extend. Such a mechanism would allow very rapid extension of the proboscis without the need of a pumping apparatus. However, this mechanism is incompatible with the findings from the experiments 8 and 9. The proboscis, either under haemocoelic turgescence or in the loose state, always coils when the oblique muscles contract on electric stimulation and the proboscis can extend also after the nerve supply for the oblique muscles has been cut. In addition, the pumping mechanism has been demonstrated in the experiment 1 and 2. Besides this, it is not probable that the oblique muscles should permit extension as well as coiling.

Another variant of the blood-pressure theory could be the following : the blood-pressure would cause a dorsal transverse convexity which in its turn would lead to the extension of the proboscis. This variant would contain some of the principle of the mechanism of the dorsal convexity, but not the way it is brought about. However, the configuration of the outer wall of the galea, the great longitudinal elasticity of the lower wall, the fact that it is not essential for the extension whether only a single galea or the linked galeae are involved in the movement and the difficulty in explaining the hyper-uncoiling, seem all to rule out this variant.

It would have been desirable to know whether or not a proboscis in the extended state becomes dorsally convex because of muscle contraction, but we were unable to check this. The shape of the proboscis is so susceptible to the influence of different liquids, which would be needed for the preparation of sections, that it was thought too delicate an undertaking to ascertain the degree of so slight a convexity. Besides the danger of artifacts (experiment 10), there is the problem of how to fix the proboscis in the extended state. Hot Bouin, as used by EASTHAM & EASSA does not prevent the proboscis from coiling. Though certain means, like maintenance of pressure by applying a ligature at the base of the proboscis or pinning it flat can help, objections may be raised against these unnatural interventions. In any case, neither the occurrence of the dorsal convexity nor its failure to occur would contradict the blood-pressure theory.

Since complete coiling is assured by muscle contraction one may ask the question how the insect keeps the proboscis coiled when at rest. The experiment 6a makes it probable that the muscles are not needed to keep the proboscis fully coiled. Otherwise it would be expected to assume the loosely coiled shape in anaesthetized individuals. Because of the annuli of exocuticula the walls of the proboscis have transversal depressions and elevations and it is probable that the proboscis is kept coiled by the artrition between the annuli of the different coils which are in thight contact with each other. It is not excluded that the superficial tension of the secretion released by the many glands in the upper angle of the galeal haemocoel may support the tight contact of the coils. Moreover, it was often observed how accurately the proboscis is coiled up and that this action may be repeated many times, apparently until the coils "fit well". The palps may also assist a proper coiling and the keeping of the coils.

The coiling and uncoiling mechanism of the proboscis is probably not exactly the same in all Lepidoptera. In the primitive Eriocraniidae, for instance, the galeae are lacking the oblique muscles (KRISTENSEN, 1968). Therefore, coiling in this group cannot be realized by muscle action, but, evidently, by elasticity alone. However, preliminary experiments with Lepidoptera of 7 different families, other than Noctuidae and Pieridae, seem to indicate that the mechanisms involved during extension are likely to be fundamentally the same.

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Zusammenfassung

Die verschiedenen, sich zum Teil widersprechenden Theorien über den Mechanismus des Streckens und Einrollens des Schmetterlingsrüssels wurden neu analysiert und durch eine Anzahl Versuche an Vertretern verschiedener Schmetterlingsfamilien geprüft. Die Streckung des Rüssels geschieht durch Blutdruck in der Galea (Rüsselhälfte). Blut wird durch eine besondere Pumpe im Stipes in die Haemocoele der Galeae gepumpt. Durch künstliche Bewegung des Stipes betäubter oder toter Falter kann die Rüsselstreckung reproduziert werden. Ein Rüssel mit Leck kann nicht gestreckt werden, da das Blut aus der Öffnung entweicht. Die Theorie, nach welcher die Streckung die Folge einer Spannung ist, die durch die Querbiegung der dorsalen und ventralen Rüsselwände entstehen soll — einem Stahlmessband vergleichbar — wird widerlegt indem gezeigt wird, dass die Muskeln, die diese Querbiegung verursachen sollten, in Wirklichkeit den Rüssel einrollen (Demonstration durch elektrische Stimulierung, selbst für den speziellen Fall, wo die Galea unter Blutdruck steht). Die Eigenelastizität des Rüssels vermag diesen nur teilweise einzurollen (durch Vergiftung der Muskeln sowie Durchschneiden des diese Muskeln innervierenden Nerven gezeigt). Mazerieren in KOH oder Wasser beeinflusst aus physikalischen und chemischen Gründen die natürliche Rüsselform. Die dabei entstehenden Artefakte können als Ursache für die falsche Beurteilung der Eigenelastizität des Rüssels durch andere Autoren betrachtet werden.

Postscript

Since the correction of the proof a new, elongated triangular structure has been found on the rings of the proboscis of a number of moths. Owing to their shape, arrangement and dense distribution, the processi appear to be — at least in the species studied — the main agent for the keeping at rest of the coils of the proboscis (cf. p. 237) : the processi of adjacent coils intercept mutually or catch the rings of the opposite coil. Details will be given in an article on the biology of lachryphagous moths in S.E. Asia to appear soon in this journal.

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