9

Metamorphosis in Images: Insect Transformation from the End of the Seventeenth to the Beginning of the Nineteenth Century

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The English anatomist and discoverer of the circulatory system, William Harvey (1578–1657), was the first person to make a distinction between metamorphosis and epigenesis as two distinct forms of development in Nature. Whereas in epigenesis, the organic forms are created *de novo* successively one after the other, Harvey postulated that they are generated simultaneously during metamorphosis, like a seal impressing its structure on the mouldable material:

> In the generation by metamorphosis forms are created as if by the impression of a seal, or, as if they were adjusted in a mould; intruth the whole material is transformed. But an animal which is created by epigenesis attracts, prepares, elaborates, and makes use of the material, all at the same time; the process of formation and growth are simultaneous.
>
> (Harvey 1965: 335)

Harvey's studies of insect metamorphosis, which were intended to form part of his *Exercitationes de generatione animalium*, were lost during his lifetime (Harvey 1965: 481f.). Whilst his theory of epigenesis was repeatedly discussed, his concept of metamorphosis has so far received little attention (Pagel 1967; Keele 1965; Ruestow 1985: 229–31; Gasking 1967: 16–36; Roger 1963: 112–21). The same applies to the history of insect metamorphosis in the seventeenth and eighteenth centuries or later which remains scarcely studied to this day or restricted largely to individual authors (Ogilvie 2014; Reynolds 2019; Hansen 1907: 173–219; for a short historical comment see Kirby and Spence [1815] 1858: 31–41; an eclectic collection remains with Heselhaus 1953).[1]

In this chapter, I shall look at the development of the concept of insect metamorphosis from the end of the seventeenth to the beginning of the nineteenth century.[2] This time frame has not been chosen at random. On the one hand, it was Harvey's work which was instrumental in introducing the concept of metamorphosis into scientific research. From the end of the seventeenth through the eighteenth century, metamorphosis was regarded as a specific developmental form of the insect group. It was not until the beginning of the nineteenth century that it was recognized as an epigenetic developmental process and part of the newly emerging embryology. On the other hand, microscopy plays a decisive role in the study of metamorphosis during this epoch. The use of the microscope was widespread from the second half of the seventeenth and in the eighteenth century. However, the wealth of different microscopes, individual preparation techniques, methods of observation and, not least of all, highly diverse means of graphic depiction ensured that microscopy remained a heterogeneous research tool until the nineteenth century (Ruestow 1996; Fournier 1996; Wilson 1995). The history of ideas about metamorphosis provides an excellent example for this development.

I shall concentrate here on those researchers who attempted to understand insect metamorphosis with the aid of microanatomy, which merits a special place in the study of the transformation of insects. On the one hand, microscopic anatomy opened up the insect world to scientific research in the seventeenth and eighteenth centuries. By examining the interior of these animals with lenses and microscopes, it was possible to gain totally new insights into their transformation. Whereas insects were considered unworthy of anatomical research at the beginning of the seventeenth century, they became increasingly the focus of interest among physico-theologians who argued that precisely the lowest forms of life were testament to the greatness of God's divine work. On the other hand, microscopic observation raised the question of the role of pictorial representation in a special way. A look at the history of insect research shows that it evolved a rich iconographic tradition from the very outset.[3] Virtually all the major works of natural history published since the seventeenth century have appeared with numerous illustrations.[4] Working with the microscope required new strategies for visualization to an even greater degree. How could the image produced through the lens be transferred to paper? By what means could extremely tiny, complex, dense and malleable structures such as those found in insects be depicted? An even more difficult issue to resolve was how to capture pictorially the transformation of shape which metamorphosis entailed? What exactly changed during observation and how could a picture reflect the entire process of transformation?

In the following, I shall examine the works of three scientists who were active at different phases of the chosen epoch: Jan Swammerdam (1637–80), Pierre Lyonet (1706–89) and Johann Moritz David Herold (1790–1862). One reason for this selection is the fact that the studies by these three were the most elaborate on insect metamorphosis during this period. At the same time, they represent different historical eras: Swammerdam was among the first to deploy the microscope systematically towards the end of the seventeenth century, yet his work was shaped by a mechanistic world view. Lyonet's work, by contrast, is already characterized from the mid eighteenth century by efforts to liberate the living world from the traditional anatomical viewpoint and apprehend its inherent dynamics of development and transformation. Finally, at the beginning of the nineteenth century, Herold was working at a time when biology was becoming emancipated as an independent life science.

Studying their work, I argue that those researchers developed an understanding of metamorphosis through the work with their hand and pencil. I maintain that, up to the beginning of the nineteenth century, the history of insect metamorphosis cannot be written without taking account of the visual representation of metamorphosis. Conceiving metamorphosis meant not only explaining the various stages of transformation but demanded above all the *visualization* of these transformations. I shall show how each of the three authors struggled with the question of how to adequately depict metamorphosis. For them, pictures were an integral element of their work and argumentation. They were tools with which they played and experimented by trying out new techniques of drawing and composing pictures that enabled them to record the changes in an insect's life and thus render them visible.

This does not mean that pictures played the same role for Swammerdam, Lyonet and Herold. On the contrary, all three worked in very different contexts and held quite different views on the extent to which microscopic examination and its depiction were linked with one another. I intend to show, however, that the detailed analysis of how they worked with images and depicted metamorphosis opens up a novel view of the history of insect metamorphosis between 1670 and 1820.

Metamorphosis as a microanatomical drama in the work of Jan Swammerdam

Although predestined by his father to pursue a theological career, Jan Swammerdam turned his attention to science. Throughout his life, however, he remained torn in his scientific work between meticulous, scientific empiricism, on the one hand, and profound piety, on the other hand.[5] This tension was only mitigated by the fact that Swammerdam justified his devotion to insects with his belief that his scientific study of the allegedly lowest forms of animal life brought him closest to God's divine purpose (Swammerdam 1752: 301). In 1669, he published his anatomical studies on the metamorphosis of insects, the *Historia insectorum generalis, ofte*, *Algemeene verhandeling van de bloedeloose dirkens*. In his *Bybel der natuure*, which Hermann Boerhaave published in 1737–38 after a delay of 50 years, he extended his research through the use of the microscope. The subject of both works is the metamorphosis of a long series of insects. Swammerdam compares his studies to the cleaning of a painting:

> Because the true nature of the transformation of these tiny creatures is like a beautiful painting which, having become stained and dirty over time, does not display the true quality of the images it contains but something quite different; and we must […] consequently restore its original lustre by removing the surface impurities.
> (Swammerdam 1752: 2, translation added)

If metamorphosis is thus a painting which needs cleaning in order to perceive it, what role do the 53 elaborate and finely engraved copper plates play which the *Bybel der natuure* contains and which were based on Swammerdam's own drawings?[6] What idea of metamorphosis does Swammerdam conceive in his pictures?

On the action of the anatomist and the nature of transformation

Swammerdam devoted the major part of his pictures to the anatomy of insects, their interior revealed under the lens or with the naked eye, the fine structure of their bodies, their tissues and isolated organs which he displayed both as an illustrator in his drawings and as an anatomist on the dissecting table. But there are also the plates depicting metamorphosis (Figure 9.1A–D). In these plates, Swammerdam shows the 'treatment of the history' of an animal, recounts its 'changes' or its 'slow growth' (Swammerdam 1752, Plate XXXIV, 393; Plate ILIII: 400; Plate XXXVIII: 396; Plate ILVI: 404). Readers are already forewarned in the introduction:

> No one should take exception to the word change or transformation nor let themselves be misled into error. I remind the reader at the very beginning and beseech him to take note that, both here and in the following, I mean by these terms nothing other than a slow and natural growth of the limbs and wish to be understood thus.
> (Swammerdam 1752: 2, translation added)[7]

Swammerdam's concept of development evidently corresponds here to the preformationist thinking of his time, whereby all parts of the future organism already

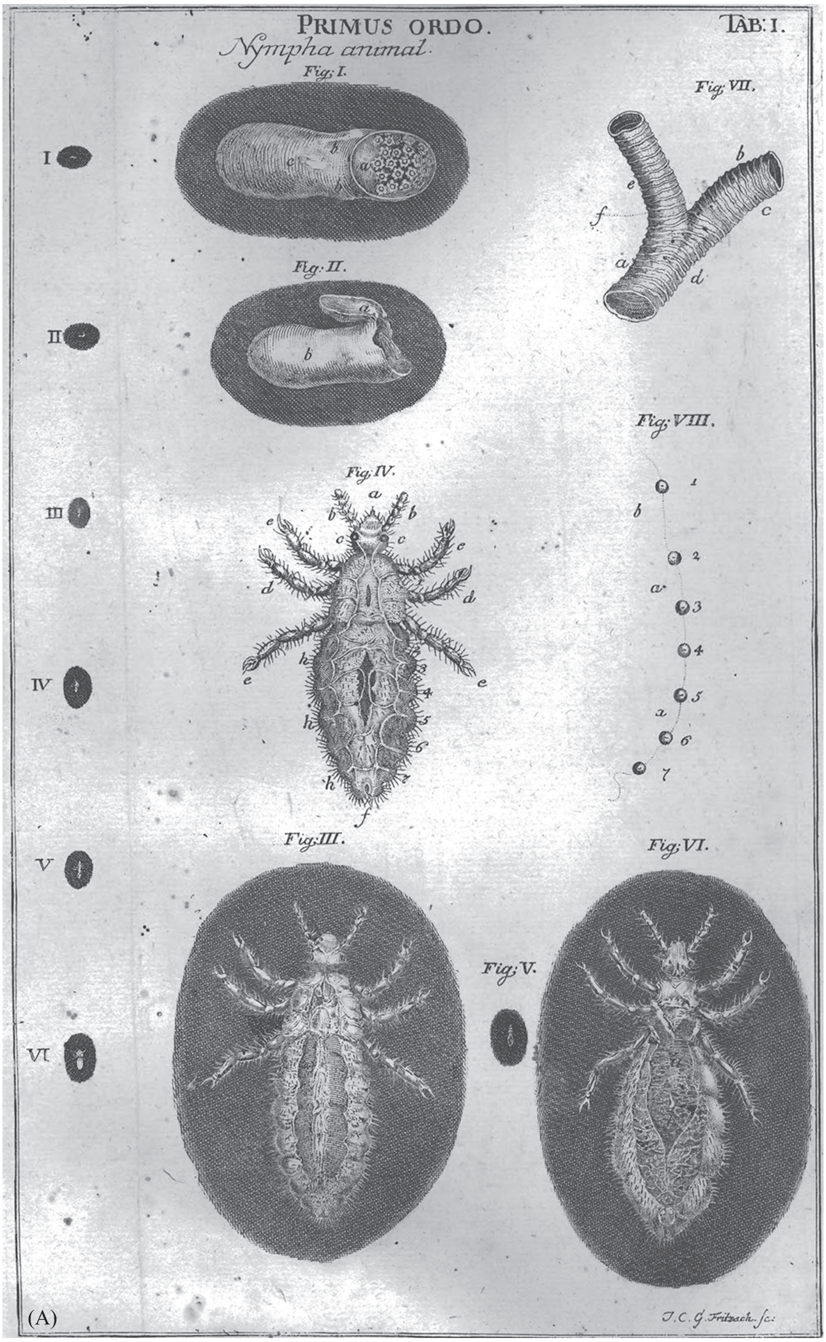
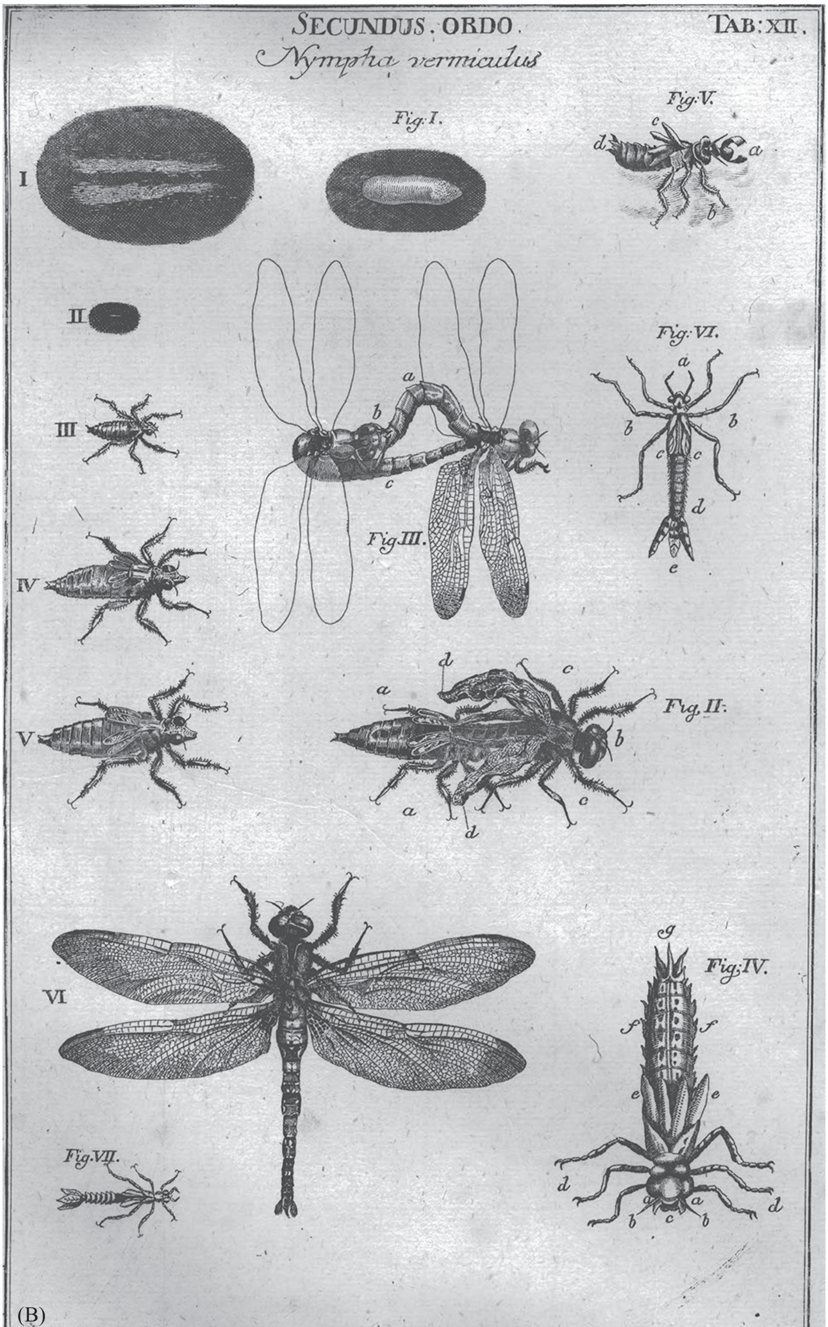


FIGURE 9.1A–D: The four classes of metamorphosis according to Swammerdam (1752: Plates I, XII, XVI and XXXVIII).



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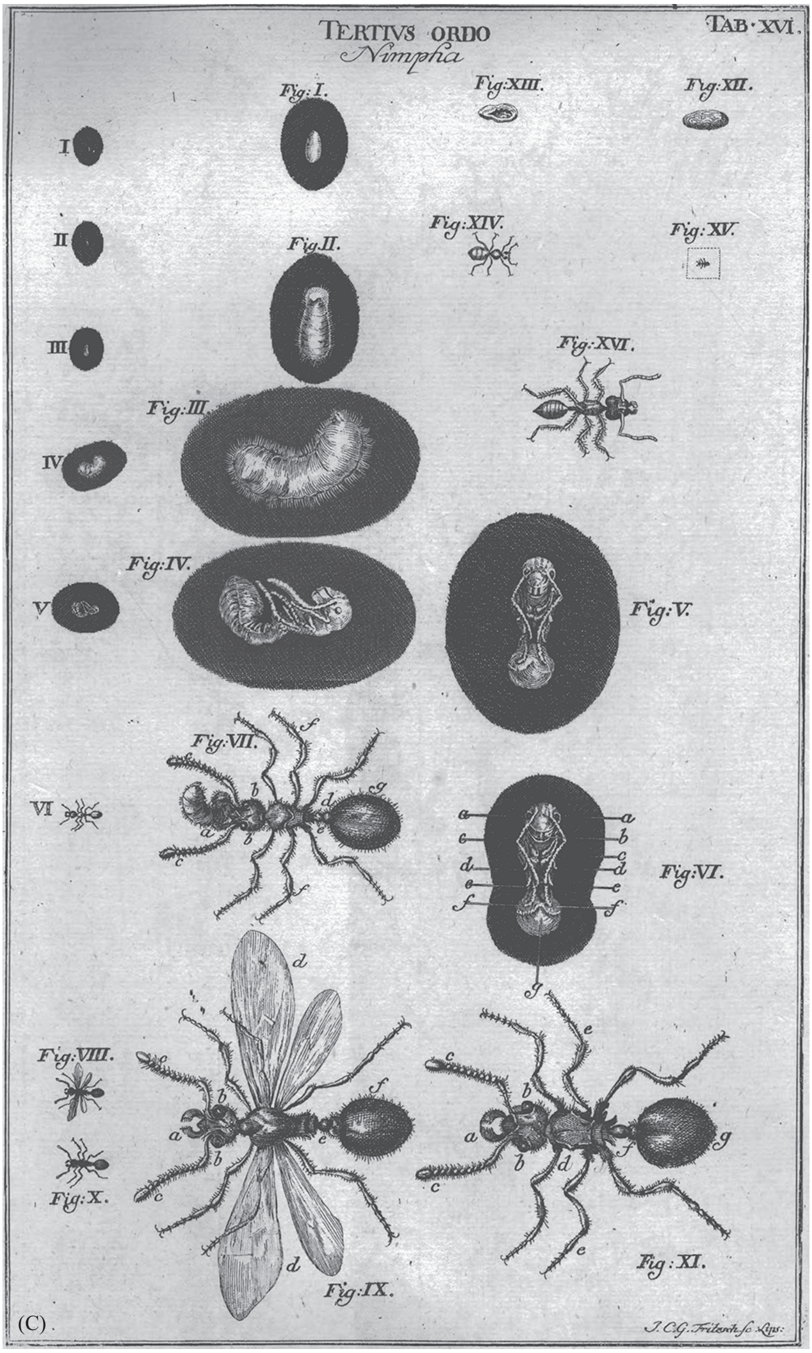

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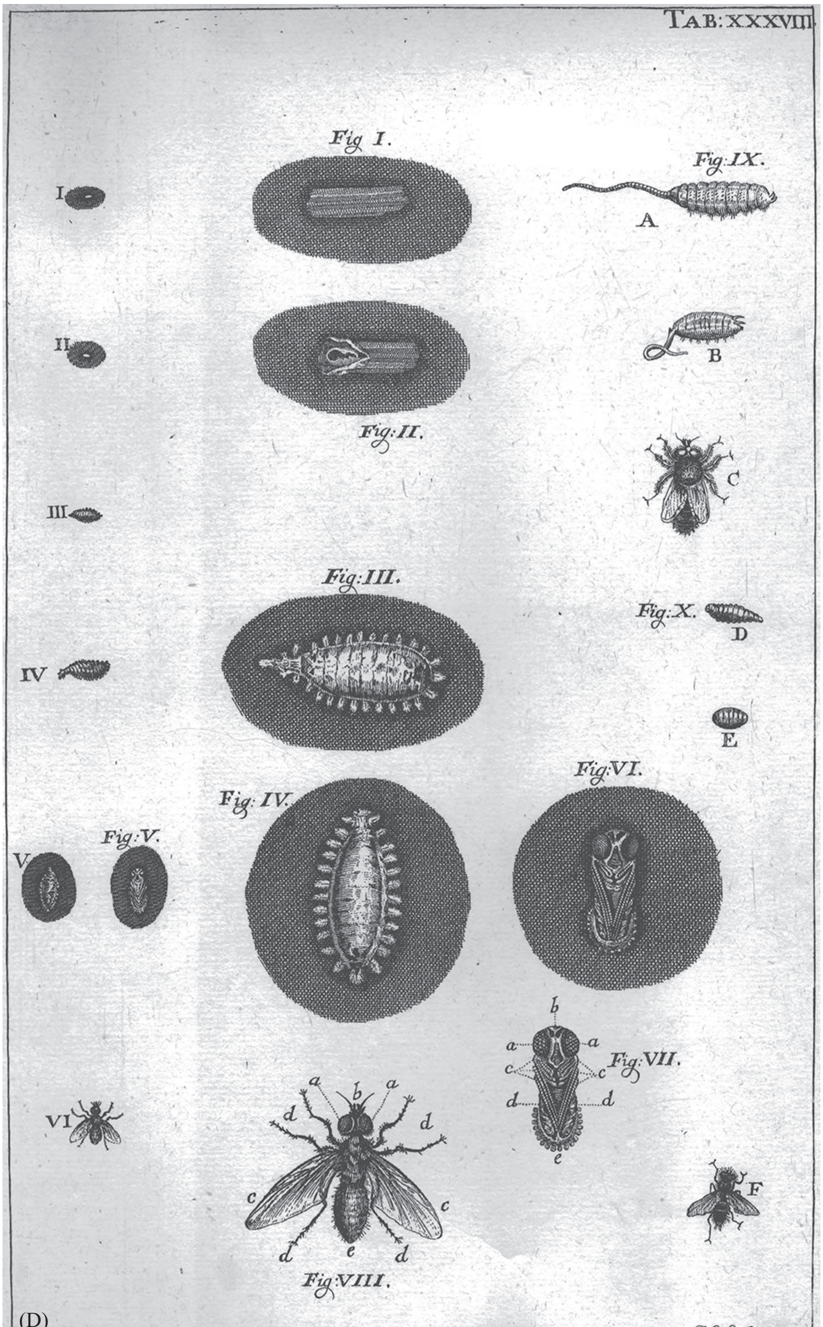

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exist in miniature in the germ cell and merely become larger and visible in the course of development (Roger 1963; Gasking 1967). The same also applies to metamorphosis. Through his work, Swammerdam wants to show that larva, pupa and imago are *one and the same* animal. What happens during metamorphosis is thus merely a

> sprouting, growing, shooting or expanding of a worm or a caterpillar. [...] The worm or the caterpillar do not in fact transform into a pupa but become a pupa due to the growth of their limbs. In the same way, the pupa does not subsequently transform into a winged animal but the very same worm and the very same caterpillar, having taken on the form of a pupa by shedding its skin, becomes a winged animal out of the pupa.
>
> (Swammerdam 1753: 3, translation added)

Swammerdam's research thus has a firm aim from the outset: to make the given visible, reveal the hidden and enlarge the miniature under the microscope. As a result, he faces a special challenge: he must show that caterpillar, larva and imago, which patently differ considerably from one another, are nevertheless similar in each phase of the transformation. The plates on metamorphosis provide a particular body of evidence (Figure 9.1A–D).

In the four plates, Swammerdam classifies the insects according to the completeness of the metamorphosis they are undergoing. The first class covers those insects which are not subject to any further metamorphosis after hatching from eggs, such as lice and fleas. The second group consists of insects whose larvae only differ from the adult imago in that their wings still have to grow or unfurl (e.g. dragonflies). The third class comprises insects which undergo a full metamorphosis, i.e. they first transform into a larva before subsequently entering a pupal stage (like ants) and only then emerge as an adult imago. Swammerdam's fourth and final group, a differentiation from the third, includes animals like beetles, flies and moths which undergo a complete metamorphosis but, unlike the third group, no longer shed their skin (Swammerdam 1752: 17f., 89–93, 115–20, 246–54).[8]

The third class of full metamorphosis includes the butterfly, to which Swammerdam devotes one of the most remarkable plates in the entire book. It not only assembles all the stages of transformation on a single copper plate like those for the individual classes. Plate XXXVII (Figure 9.2) rather stands out because Swammerdam *demonstrates* metamorphosis here in this picture. The picture is the enactment of how he single-handedly transforms the caterpillar into a butterfly, from one developmental stage to the next, under experimental conditions. 'As an encore, I thus want to describe the manner in which a butterfly is embedded in a caterpillar'

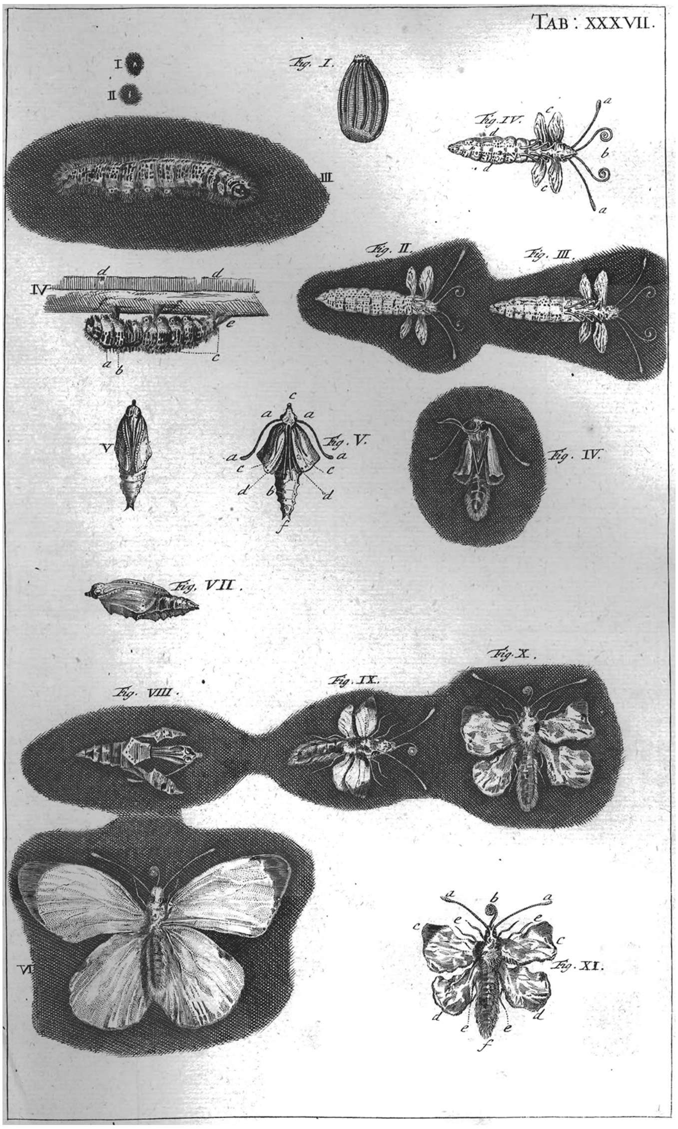


FIGURE 9.2: The metamorphosis of the butterfly in Swammerdam (1752: Plate XXXVII).

(Swammerdam 1752: 241). Put another way: 'At the same time, I shall show that all the little animals presented on this copper Plate XXXVII are one and the same little animal which is merely hidden in various shapes' (Swammerdam 1752: 243).

The illustration shows individual figures spread over the copper plate, some of which are depicted as positive and others as negative.[9] The latter stand out particularly against the black background with which the objects contrast. In addition to this optical sub-division of the copper plate, there is a second differentiation through the added letters and numbers: solitary Roman numerals denote the insect 'in life', whilst numerals with the adjunct 'Fig.' designate the animal in its 'outline'. As a rule, that is its anatomical duplication, enlarged through the magnifying glass (Swammerdam 1752: 245, 29f.). The vertical arrangement of illustrations I to IV thus shows the various stages of the butterfly from egg to imago in life size: (I) shows the 'butterfly in the shape of a caterpillar wrapped in its first coat, wherein it is called an egg', (II) the empty 'little skin' after emerging, (III) the caterpillar or 'the butterfly dressed in the shape of the caterpillar', (IV) the caterpillar shortly before moulting, (V) the pupa and (VI) finally the completed butterfly (Swammerdam 1752: Plate XXXVII: 395f.). In addition to the vertical arrangement, the plate also has a horizontal sight line. Illustration IV develops from left to right into Figures II to IV (Figure 9.3).

In Figs. II, III and IV (Figure 9.3), Swammerdam shows the 'butterfly as it is drawn out of the coat of the caterpillar displayed at No. IV' (Swammerdam 1752: 396). The sequence of figures from left to right thus follows the movement of dissection, the extraction of the butterfly from its shell, the caterpillar. This movement is captured again pictorially in the lower part of the plate, in the sequence of Figs. VIII–X (Figure 9.4).

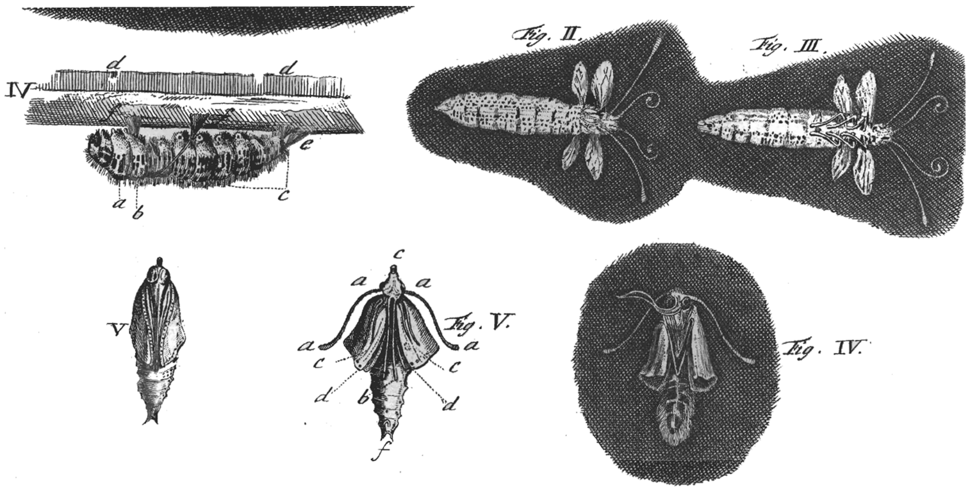


FIGURE 9.3: The sequence of figures II to IV shows how the butterfly can be 'extracted' from the caterpillar according to Swammerdam (1752: detail from Plate XXXVII: IV, VI; Figs. II, III, IV and V).

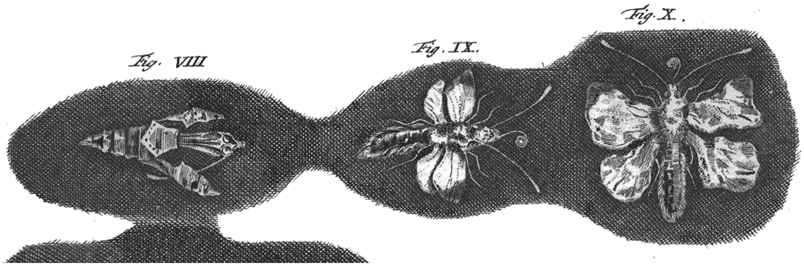


FIGURE 9.4: The emergence of the image from the pupa (Swammerdam 1752: detail from Plate XXXVII: Figs. VIII, IX and X).

This time the sequence of pictures shows the imago emerging from the pupa. The series begins with the empty pupa which the insect has left. This is followed by the freshly emerged animal. Finally, we see the butterfly whose wings are slowly unfolding.

The picture composition suggests that the two processes represented are a qualitatively comparable procedure: the sequence of three figures each is arranged in parallel, develops from left to right and the presentation on a black background (with the exception of No. IV, which nevertheless largely corresponds to No. 3 above it) optically reinforces the linear chain of the images. In fact, the natural process of emergence at the end of the butterfly's metamorphosis is represented in the second case whilst the artificial 'extraction' of the butterfly from the caterpillar by the anatomist is in the first case. That this is by no means a comparably natural act is clear from a more precise description of Swammerdam's procedure which has made this 'extraction' possible:

> In order now to prove irrefutably that the butterfly is present within the skin of the caterpillar, one may now use the following technique. One takes an adult caterpillar, ties it to a fine thread and immerses it several times in boiling hot water, but withdrawing it rapidly each time. The caterpillar's outer skin will then peel off from the inner which surrounds the butterfly.
>
> (Swammerdam 1752: 242, translation added)

Swammerdam was indeed one of the most skilful microanatomists of his time (Ruestow 1996; Bodenheimer 1928: 342–65). Hermann Boerhaave portrays Swammerdam's tools in his introduction to the *Bibel der Natur*. He describes his examination table with its 'brass arms', 'which could be turned, raised and lowered as one wished', his 'incredibly fine and sharp scissors', 'knives, lancets and stillettoes, which were so small that he had to sharpen them under a magnifying glass', as well as the 'little tubes' as fine as hairs with which Swammerdam injected 'dyed liquids' and 'inflated' the insect body (Swammerdam 1752: X, XI, also 9, 17).[10] Swammerdam preserved the insects prepared in this way, 'frozen' so to speak in each stage of its development and built up an immense collection:

> I also possess some worms and caterpillars, different gold pupae and some worms which are half caterpillars and half gold pupae. I can thus also demonstrate after life how the butterflies lie in miniature in their last skin [...], with all their colours [...]. Furthermore, [I] keep the antennae, intestines, stomachs and mouthparts of the butterflies.
>
> (Swammerdam 1752: 220, translation added)

Boerhaave reports how Swammerdam staged the metamorphosis of the insects as a drama with the aid of this collection:

> With such skill, intelligence and tools [...], he finally brought things so far that, as often as he wished, he could visually demonstrate the nature of the enshrouding and development of the transforming bodies of the little creatures. He could at will transform the caterpillar into a pupa, accelerate, stop, interrupt and steer its moulting. What he saw, he claimed and what he claimed he manifestly proved.
>
> (Swammerdam 1752: X, translation added)

Metamorphosis is here the result of anatomical dissection and preparation.[11] Anatomy not only allowed the examination to be separated from the natural development process. On the contrary, it created a completely new observer situation that could be updated, repeated and reversed at any time. The researcher rather than the insect becomes the actor and Swammerdam announces: 'Yes I can, if I wish, transform a caterpillar into a gold pupa' (Swammerdam 1752: 9, also 17). Plate XXXVIII (Fig. 9.2) shows this kind of transformation: it equates the anatomical act of dissection with the natural act of metamorphosis. Here the anatomist becomes the imitator of Nature who can himself produce metamorphosis via anatomy and thus prove the continuity between the various stages. Swammerdam achieves this impression on the plate by linking the horizontal and vertical sightlines with one another. From top to bottom, the picture sequence I–VI reveals the development from egg to adult butterfly. The respective connection of these stages then results from looking right, to the anatomical 'outline'. The viewer reads in a zigzag pattern, as it were: he links the natural order of the individual insect stages with one another via the anatomical dissection. Correspondingly, anatomy appears as the natural explanation for metamorphosis in the illustrations. However, the picture which Swammerdam draws here of metamorphosis is the picture of a non-transformation. It presupposes that in each individual stage 'the shape of the future animal and its limbs can be perceived', i.e. that the individual organs and structures are always recognizably similar (Swammerdam 1752: 4). Swammerdam's depiction is based on the similarity, the comparability of what has been observed, in order to optically equate the violently extracted and naturally emerged body. But a transformation whereby completely new structures are created, new forms evolve or existing ones are replaced, also requires other representational techniques to elaborate the continuity of the body beyond mere similarities. In other words: that 'very beautiful painting' with which Swammerdam earlier compared metamorphosis not only had to be cleaned. Ways and means to paint it had to be found first.

The perfect picture. Pierre Lyonet's anatomy of the caterpillar

The *Traité anatomique de la chenille qui ronge le bois de saule* from 1762 is one of the most significant works on insect microanatomy in the eighteenth century. Here too, pictures are of central importance.[12] Pierre Lyonet was predestined for such a work since he had trained not only as a draughtsman but also as a copper plate engraver. He was first a pupil of the portrait painter Carel de Moor. Through his acquaintance with the painter Hendrick van Limborch, Lyonet became a member of the guild Confrérie Pictura of The Hague in 1733. There he also learned drawing from a model and cast under Jan van Gool. His first encounter with engraving was in the 1740s. Trembley reports in his *Mémoires* that Lyonet began copper plate engraving after just one visit to Jan Wandelaar (1690–1759), who created the famous engravings for Albinus' anatomy (Trembley 1744: VIII).[13]

Before Lyonet became famous with his own *Traité*, he had already made a name for himself as an artist. In 1742, he published the French translation of Friedrich Christian Lesser's *Insecto-Theologia*, which had appeared in German without illustrations in 1738. He not only published the work with his own additions but made drawings which he had engraved in copper by Jakob van der Schley. The first work with Lyonet's own engravings was Abraham Trembley's *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce,* which appeared in Leiden in 1744. He produced all the drawings for the plates, however, only engraved the last eight plates himself. Lyonet also made three engravings for Johann Nathanael Lieberkühn's *Dissertatio anatomico-physiologica* (1745).[14] He planned a detailed anatomical study of the willow caterpillar, for which he abandoned a natural history of the insects of The Hague he had already started, because he considered this topic 'sufficiently difficult to leave the field free for me' (Lyonet 1762: IV). Lyonet began his dissections in 1745. Initially, he only made drawings of them. It was not until 1757, after a hiatus of six years during which he served the Dutch government as a decipherer of diplomatic correspondence, that he resumed the work and needed two years to complete the copper plates (Seters 1962: 67–71).[15]

Metamorphosis as inner transformation

The treatise on the anatomy of the caterpillar was only the first and 'least' of a total of three planned tracts: a second and third on the anatomy of the pupa and the butterfly were supposed to follow (De Haan and Lyonet 1832: I). Lyonet's work remained unfinished and some of his preliminary works were only published posthumously in 1832. The crucial point is that his project was not aimed at an anatomical description of the caterpillar solely for the sake of its anatomy but rather at 'following the successive interior changes which the pepper-and-salt moth undergoes whilst preparing to become a chrysalis and during its pupal state to transform into that of the winged insect' (De Haan and Lyonet 1832: I). Lyonet is already departing here from the preformationist theory without yet adopting a clear alternative position. Instead he seeks a solution through the pictures.

Although Lyonet was unable to complete the project, he had taken his studies so far that he had recognized metamorphosis as a process of dramatic transformations inside the caterpillar: a series of 'admirable and almost universal changes which the entire interior organisation of the caterpillar undergoes in order to become a butterfly' (De Haan and Lyonet 1832: 544). Lyonet's approach is to break down the transformation as such into a series of distinguishable subprocesses. He differentiates between six central transformations in total. The most conspicuous is first 'the complete transformation of the caterpillar's exterior form' (De Haan and Lyonet 1832: 544). Second, he observed 'the dissolution of more than four thousand muscles which dissolve within a few days during the metamorphosis' (De Haan and Lyonet 1832: 544f.) Then comes third 'the dissolution of two external sheaths' of the bronchia (De Haan and Lyonet 1832: 545). Fourth, Lyonet mentions the changes to the nervous system, where most of the nerves disappear as they lose their function and the remaining nerves receive new tasks (De Haan and Lyonet 1832: 545). The fifth change concerns 'the production through intussusception of an innumerable quantity of channelled scales with three edges' (De Haan and Lyonet 1832: 546). The sixth change is also the most remarkable: 'the production of close to twenty-one thousand telescopes' which form the butterfly's compound eye and take the place of the caterpillar's twelve eyes which were constructed in a completely different manner (De Haan and Lyonet 1832: 546).

For Lyonet, pictures are the pivotal element for understanding metamorphosis. He stresses that there is so far no work 'whose illustrations, which do not make up the least essential part, are suited to satisfy the eyes that are so little illuminated about these kinds of objects' (De Haan and Lyonet 1832: I). Although unable to finish his illustrations on metamorphosis, Lyonet developed a pictorial language in his *Traité anatomique* which fulfils all the requirements to represent metamorphosis in a novel manner. The precision of representation which Lyonet strove for in his treatise pursued not only the ideal of a mathematical exactness (Stafford 1996: 254) but also the approach that the changes during metamorphosis could only be followed if one succeeded in representing the internal structures of the caterpillar as a fabric of miniature, connected and coordinated units. Only when this interior topography is precisely recorded will it be possible also to comprehend the many small changes that lead to structures changing their position, breaking loose from old connections and entering into new ones as a complete internal transformation. In order to achieve this precision, Lyonet utilizes a series of new picture techniques.

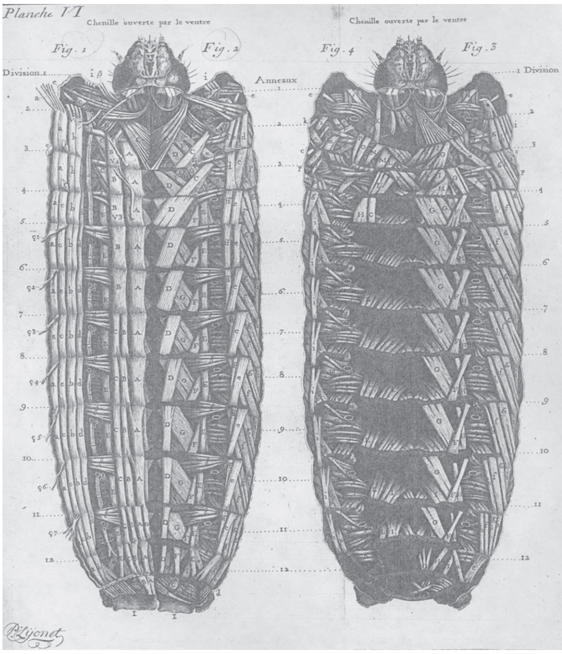
On the location of seeing: The *lignes idéales*

Lyonet strove for the perfect picture – the picture in which everything was visible, which recorded every vessel, every trachea and every individual muscle inside the caterpillar. The picture shown by previous research, including that by Swammerdam, Réaumur, Malpighi and de Geer, was merely 'extremely simple figures and largely formless' (Lyonet 1762: XXI) and nothing more than 'the work of daubers' (Letter to Réaumur, quoted in Hublard 1910: 65). Lyonet demanded more of himself: 'I have taken exactness to such a point […] I do not believe I could have taken it any further than I have done' (Lyonet 1762: VII). He himself calculated what that meant: 228 muscles of the head, 1647 of the body, 2186 of the intestinal tract, a total of 4061, minus those counted twice, making 4041 muscles alone for which he was supposed to find space in his pictures – not to mention all the other structures inside the caterpillar (Lyonet 1762: 584).

This interior complexity posed a representational problem for Lyonet. Naming all the individual structures was out of the question: 'that would have been crazy. Ten thousand names would not have sufficed. It would have required a dictionary to find them' (Lyonet 1762: VII). Apart from some important, recurring structures which receive a name, the others are therefore identified with 'letters, marks or numbers' (Lyonet 1762: VIII). But the letters and numbers do not guarantee a clear location and allocation to the respective structures depicted. A vestige of imprecision remains in the reciprocal reference between picture and letter – a practice adopted in the early days of anatomy. Lyonet solves this problem: he invents a genuinely graphic element, the *lignes idéales*. These lines form a kind of topographic mesh which Lyonet places over the illustrations. They function like those numbers, letters or other marks. But rather than being beside the picture, they are an intrinsic part of it: they designate the place where the eye must search within the picture. Unlike linguistic terms, the *lignes idéales* are not completely arbitrary. On the one hand, they are notional, imagined lines; on the other hand, Nature itself – for example, in the segments of the insect's body – has suggested them: 'It appears as if Nature itself had taken care to provide them and secure them in all types of caterpillar with markings which are usually very easy to recognise' (Lyonet 1762: 21).

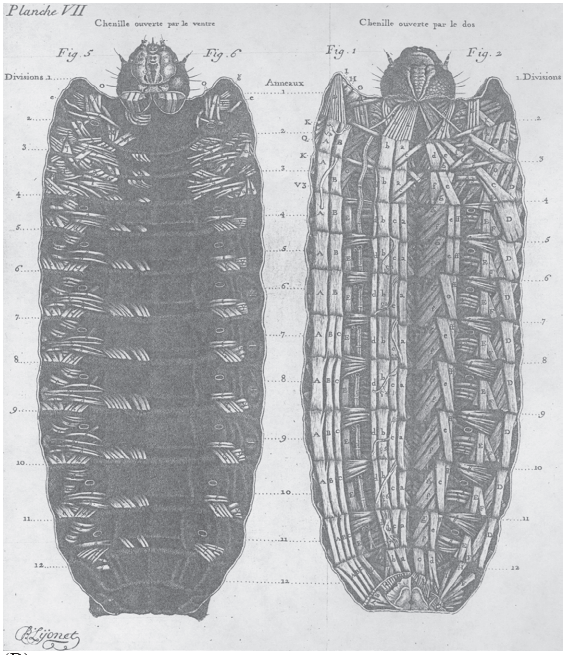
The *lignes idéales* thus form a mesh of vertical and horizontal lines which are partly selected at random and partly follow the natural segmentation or vessels of the insect's body (Figure 9.5A–C). In this way, eight lines form a grid of 104 fields altogether, in which each structure within the caterpillar can be precisely pinpointed:

> The eight longitudinal lines […] together with the twelve transversal lines, which I have called divisions, split the caterpillar, including the head, into 104 parts and provide, thus planned, a comfortable means to designate the places about which one wishes to speak and to locate them without the aid of any letter.
>
> (Lyonet 1762: Chapters 2 and 25, translation added)

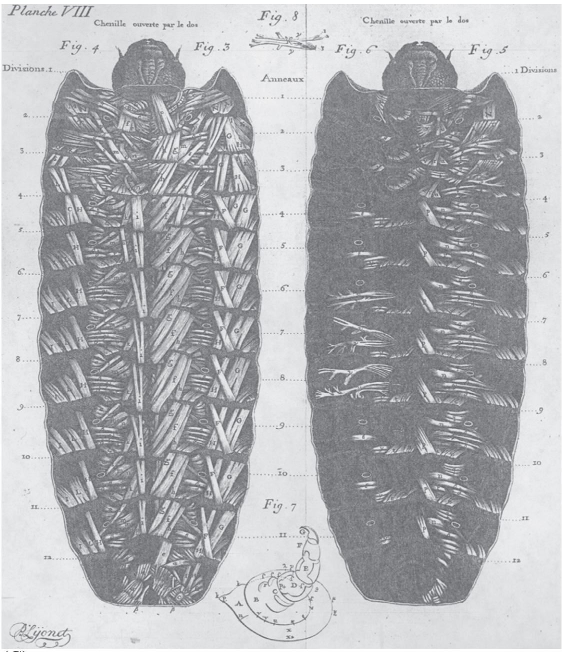


(A)

FIGURE 9.5A–C: The anatomy of the muscles of the caterpillar of the pepper-and-salt moth (Lyonet 1762: Plates VI, VII and VIII).



(B)



(C)

FIGURE 9.5A–C: The anatomy of the muscles of the caterpillar of the pepper-and-salt moth (Lyonet 1762: Plates VI, VII and VIII).

The individual structures are quasi duplicated by the grid of the ideal lines – they are represented both as tissue and in the coordinate system of the lines. What is depicted and its description are overlaid, as it were, and pictorially merged. That has a central consequence for Lyonet's further course of action: the *lignes idéales* are a key means of dissolving the body into layers. Each structure is present in the picture even when it is absent; it has its place beyond its current representation. Another graphic procedure which serves this purpose is to depict each of the caterpillar's various tissues using a different engraving technique. Lyonet thus represents the caterpillar's fat with dots known as stippling, the muscles with linear hatching and the bronchia with transverse arches (Lyonet 1762: X).

The muscles provide an example of the specific effect this has on the pictures (Figure 9.5A–C). Due to their uniform linear hatching, Plates VI, VII and VIII are highlighted 'at a glance' as a coherent unit and delineated from the other plates (Lyonet 1762: VIII).

The sequence of Plates VI–VIII is devoted to the caterpillar's muscles. Each plate shows two caterpillar bodies. A total of six, equal in size and with the same tissue hatching, are placed side by side against a white background. On closer examination, it becomes apparent that although they are iconographically very similar, the internal structure of the caterpillar bodies varies. Only the muscles are depicted with linear hatching; all other organ structures are blanked out. However, this act of reduction only creates the prerequisite for the new complexity which Lyonet strove to achieve in the plates. Above the six caterpillar bodies, a line of text explains 'caterpillar opened from the stomach side' or 'caterpillar opened from the back side'. Thus the first three figures (cf. both figures on Plate VI and the left figure on Plate VII) show the opened caterpillar from the stomach side, the following three figures (cf. the right figure on Plate VII and both on Plate VIII) give a back view. In addition to the change from front to back view, another peculiar differentiation between these views becomes apparent: each individual depiction of the opened caterpillar is divided once again down its longitudinal axis into two parts, which Lyonet calls 'figures'. The front and back views are thus each subdivided into six figures. Instead of six caterpillar bodies, the observer is presented with twelve half-figures, or more precisely two times six. What initially seems like an interior view of six opened caterpillars is actually a composite: what one sees on the plate is not *one* prepared caterpillar body but two, which are merged into a single body along the *ligne supérieure*. What appears pictorially as a single entity is de facto a dissection sequence: one half of the caterpillar shows the muscles at a moment of anatomical dissection, the second shows the subsequent step of the dissection which now reveals the layer of muscle which was still hidden by the first. Lyonet writes the following:

> The muscles which appear fully uncovered in one figure have been removed in the following figure in order to show the muscles they covered. As a result, one sees new letters designating the new muscles each time in the first to the sixth figure: and if one sees the same letter on the same ring in two figures, then that is the certain marking of the same muscle which has not yet been removed.
>
> (Lyonet 1762: 'Explication des Figures', Plates VI, VII and VIII: 39, also 114, translation added)

The pictures are a kind of in-depth preserved specimen and pursue the exposure of ever newer structures as they penetrate deeper into the body. But even more they are a pictorial record of the dissection process. They permit a dynamic view of the specimen. As the gaze wanders to and fro between the halves, it establishes relations between the muscles and permits it to follow how the topography changes during the dissection. The once anatomically rigid body is here taken further into a structure of potential options. The view into the depth of the caterpillar thus at the same time opens up the pictorial space for the temporal development of structures during metamorphosis.[16]

Lyonet is convinced by the layout of his pictures: 'solely with the aid of such figures, incidentally, can one produce an accurate idea of the things' (Lyonet 1762: XXI). At the same time, he is aware of the disturbing nature of his pictures. He knows they 'do not resemble at all' the pictures of traditional anatomy (Lyonet 1762: XXI).[17] Indeed, Lyonet brought anatomy into a new pictorial form: first, he created a form where the animal was dissected but did not fall to pieces. In Lyonet's work, the viewed object does not dissolve under the anatomist's knife, so to speak, and disintegrate into the individual parts of a unit which is no longer coherent. On the contrary, the integrity of the caterpillar remains preserved. Regardless of the ever deeper penetration of the insect's muscle and tissue layers, the body continues to exist as a whole. Although dead and dismembered, the picture shows the caterpillar's intact form. Second, this new form brought the anatomist's procedure into the picture itself: the picture both conceals and exposes the anatomical act at the same time. The individual steps of the dissection become visible across the three plates, whilst the viewer's gaze repeatedly reassembles the various levels and thus remains directed at the animal's overall unity.

By merging the figures into an apparently single insect body (instead of representing them as two separate halves), Lyonet blends anatomical analysis and intactness together. In contrast to Swammerdam, Lyonet's plates represent the attempt to capture the dynamics of a process in pictures. The sequence of pictures, the graphic dissolution of the body into layers through the *lignes idéales*, the isolation of a single structure using the hatching technique: all these are pictorial instruments which provided the basis for representing metamorphosis. Whereas Swammerdam still wanted to 'clean' the finished painting of metamorphosis which was 'sullied' by false ideas about an actual transformation, Lyonet tried to understand this transformation. The 'drawing pencil' was supposed to lay the foundations for being able to draw the 'admirable changes' by 'sketching with a steady hand the details of an insect's interior parts before and after its transformation, following it from one form to the next in its passage' (Lyonet 1762: XVII). Lyonet's approach was initially not adopted by others. It was not until 50 years later that a German natural scientist began a study which resembled Lyonet's intentions in many respects.

From picture to picture series: Johann Moritz David Herold's Developmental History of Butterflies

Johann Moritz David Herold's *Entwickelungsgeschichte der Schmetterlinge* (*Developmental History of Butterflies*) appeared in 1815. Despite the emergence of biology as an independent science of living things and the establishment of the epigenetic concept of development, knowledge about the processes inside insects during metamorphosis was still very scant. Herold felt that what Swammerdam and Lyonet had furnished was 'really just a fraction' since they had 'noted almost nothing at all about the changes which occur within the organisation during the transformation of caterpillars into pupae and these into butterflies' (Herold 1815: IIIf.).

Johann Moritz David Herold is a largely unknown figure in the history of science. His brother-in-law, Ernst August Daniel Bartels, professor for anatomy and obstetrics in Helmstedt, had a substantial influence on Herold's career. After starting medical studies at the University of Jena in 1806, Herold switched the following year to Helmstedt where his brother-in-law taught him. In 1809, he was appointed prosector working for the anatomist Johann Friedrich Meckel the Younger (1781–1833) at the University of Halle. In 1811, Herold moved to Marburg where he continued his scientific career until his death. In recognition of his work on the developmental history of butterflies, Marburg University made him an associate professor of medicine in 1816. Herold became a full professor of medicine in 1822, then finally professor for natural history and director of Marburg's zoological institute in 1824. Instructed by Meckel in the dissection of lower animals, insects remained Herold's real passion right up to his death. After completing work on the developmental history of butterflies, he planned a developmental history of invertebrates. With the first part of *Studies on the History of the Formation of Invertebrate Animals in the Egg* (1824) devoted to spiders, Herold provided the first work on the embryology of spiders. A sequel to this work appeared posthumously as part of Herold's literary estate, published by Arnold Gerstenacker in three parts in 1835, 1838 and 1876 under the title *Studies on the History of the Formation of Invertebrate Animals in the Egg. On the Generation of Insects in the Egg.* Although Herold made a major contribution to the embryology of lower animals with these works, their significance for the history of science has not been properly recognized to this day.[18]

However, the *Developmental History of Butterflies* from 1815 can be regarded as Herold's main work, in which he adopted completely new methods of studying his objects. The caterpillar of the large cabbage white butterfly (*Papilio brassica L.*) was the focus of his attention. He restricted himself to studying the caterpillar, disregarding the embryonal stage due to the small size of the eggs and the associated difficulty of observing them. In 1811, he had made the discovery that within the caterpillar it was already possible to distinguish the gender-specific predisposition for the future reproductive organs (Herold 1815: V). Based on this discovery, Herold formulated a new concept for the transformation of insects: he represented the caterpillar's metamorphosis by concentrating on the genesis of a single structure, namely the reproductive organs. To this end, Herold used a new pictorial representation of metamorphosis: the picture series.

The picture series

Developmental History of Butterflies contains a total of 33 coloured copper plates. The pictures were drawn by Herold himself and engraved by Jakob Samuel Walwert (1750–1815), a draughtsman, copper plate engraver and miniature painter from Nuremberg (Schwemmer 1974: 53).

Lyonet's work was dominated by the ideal of the wealth of detail in the picture which reproduced the complexity of the insect's interior in a dense drawing. Herold chose the exact opposite procedure: he emptied the individual picture but instead multiplied the number of pictures. Thirteen plates show the transformation of the male reproductive organs and fifteen the female (Figure 9.6A–O). In the book, plates of the male and female reproductive organs are bound alternately one after the other. This juxtaposition made it possible to reveal the differences in the male and female development which Herold was the first to recognize and which he considered his key discovery. But the pictorial arrangement of the plates permitted another quite different order, namely to track the caterpillar's 'type of development' (Herold 1815: 12). In order to follow the emergence of the female reproductive organs, the viewer should stick to the sequence of the plates 'Tab. XXI, Tab. XXIII, Tab. XXV, Tab. XXVII, Tab. XXIX, Tab. XXX' (Herold 1815: 12). So instead of looking at the plates alternately, the viewer should only observe the plates of the male or the female caterpillar respectively.

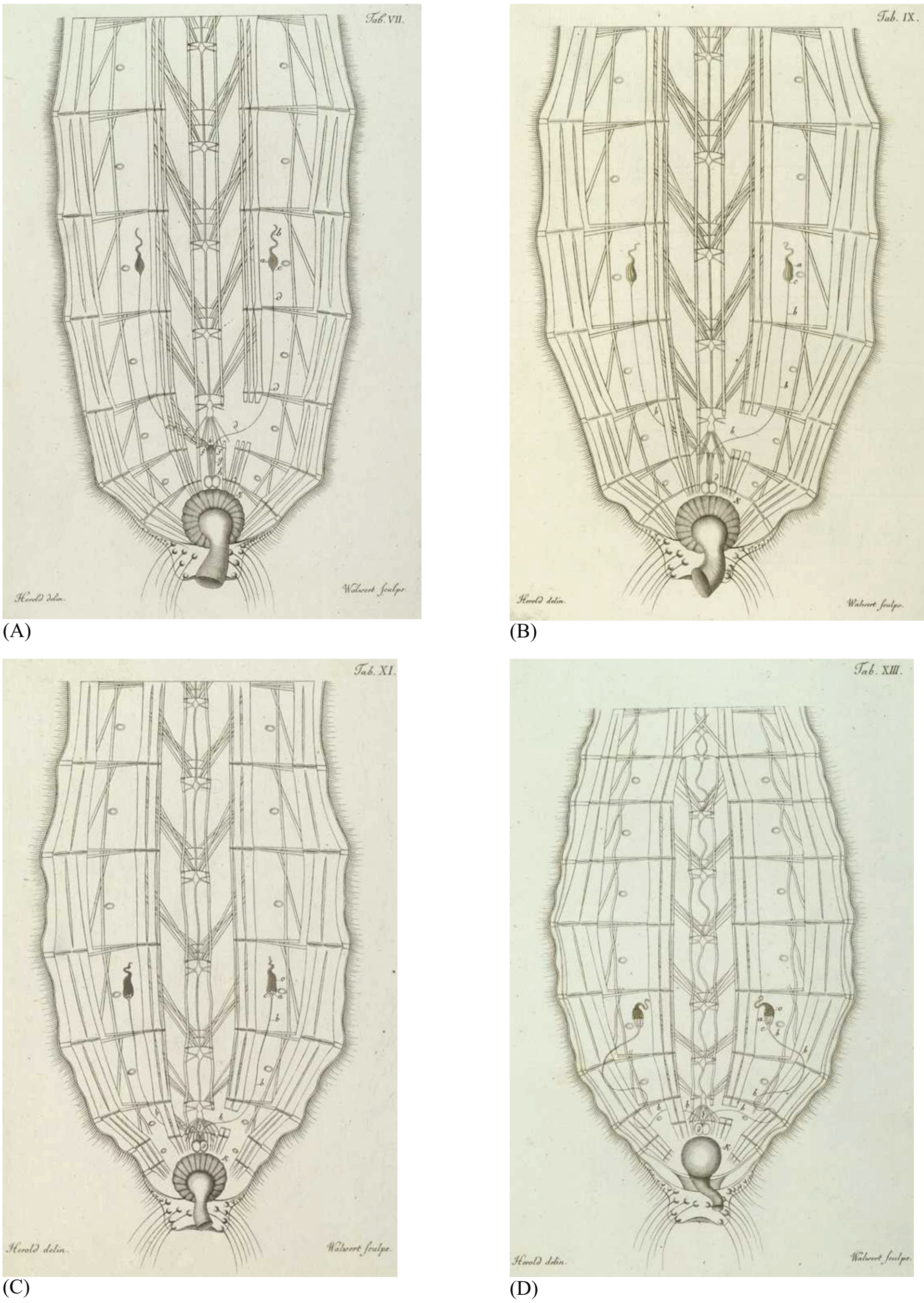
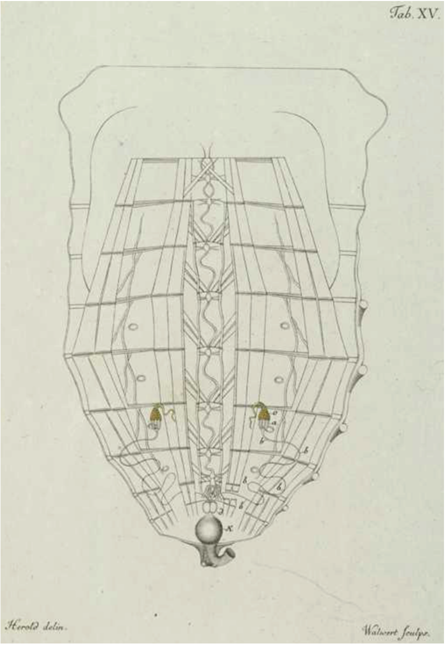
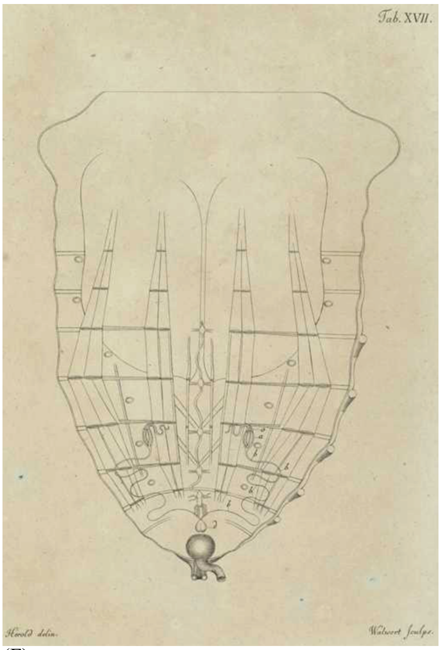


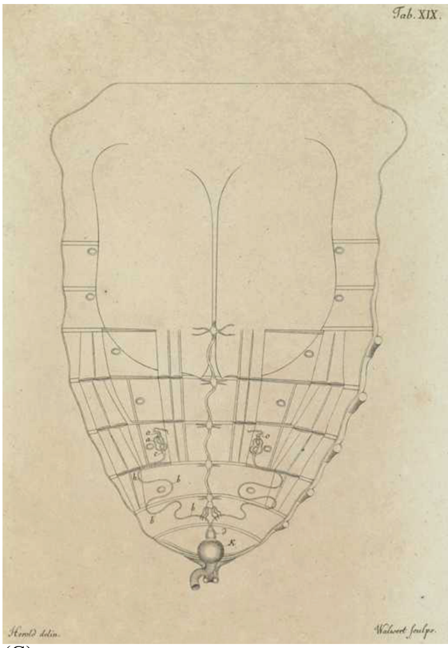
FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



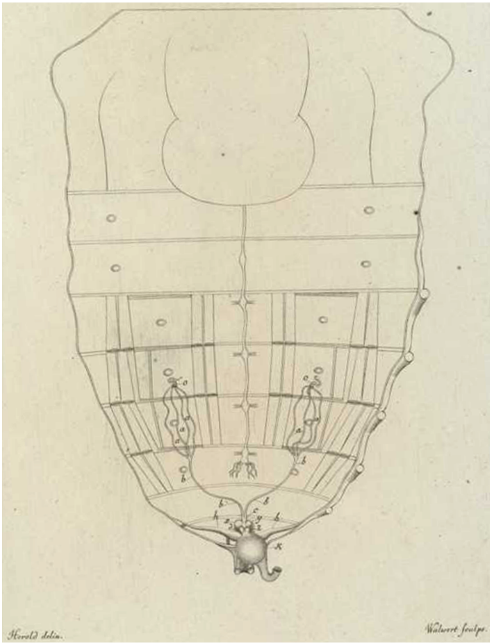
(E)



(F)

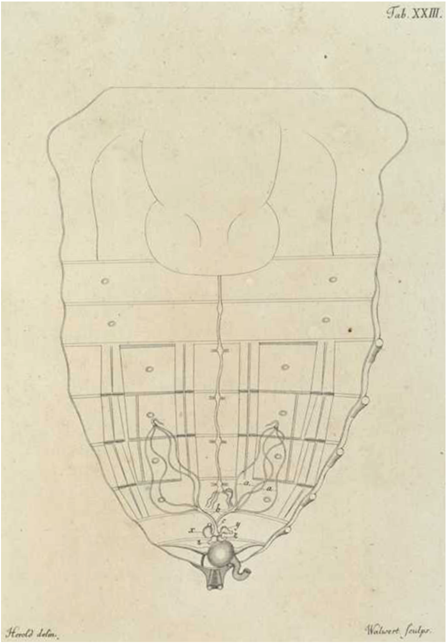


(G)

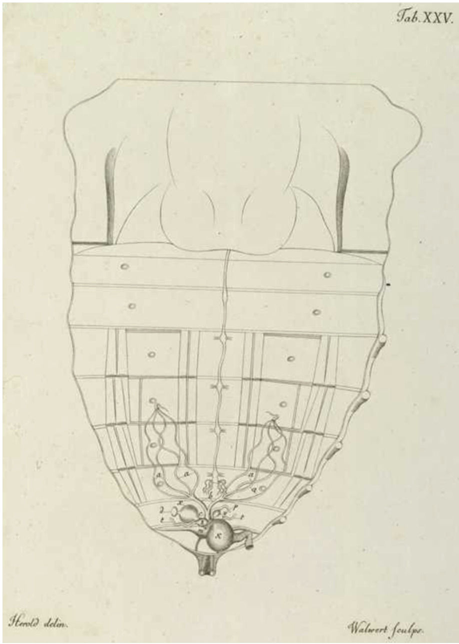


(H)

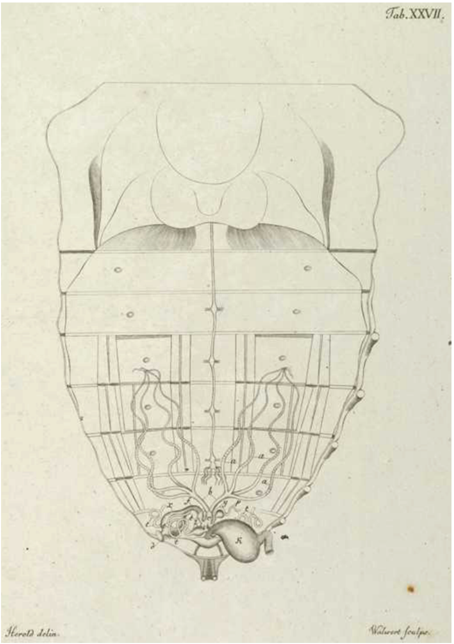
FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



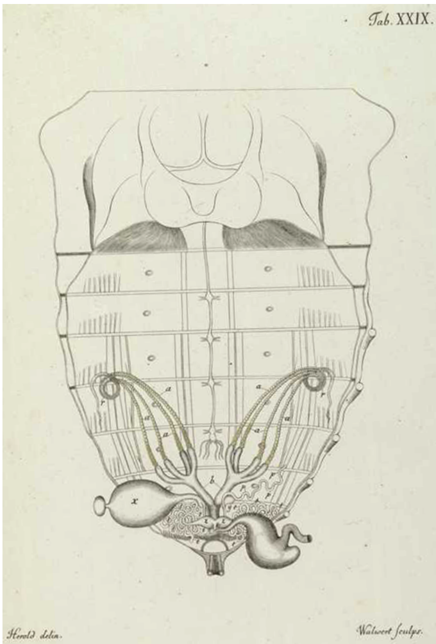
(I)



(J)

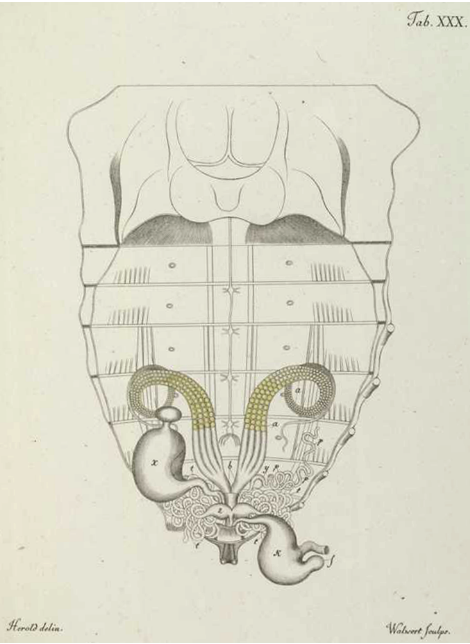


(K)

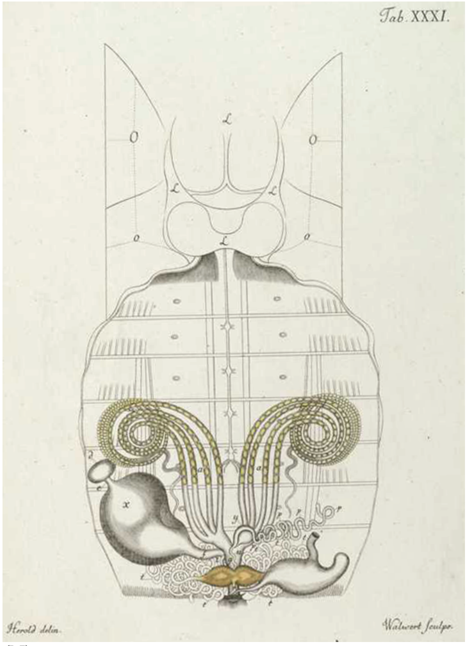


(L)

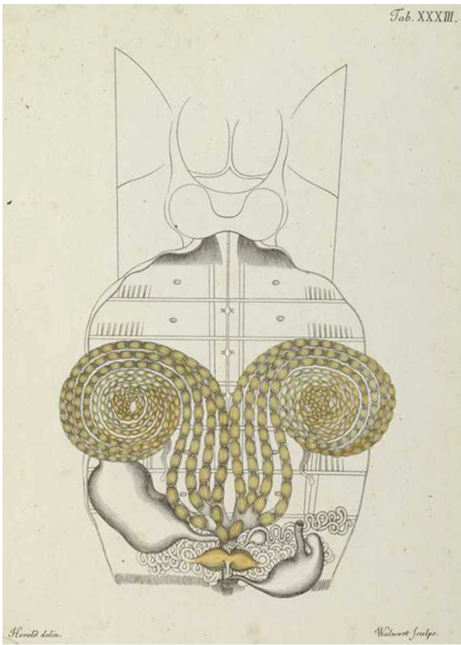
FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



(M)



(N)



(O)

FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).

The design of the plates makes this visual elaboration of the transformation possible: the selection and the concentration of the pictorial elements are their outstanding characteristic. First, the use of colour (which we also encounter again in Baer's *Developmental History* of 1828) guarantees maximum attention. The caterpillar's male reproductive organs are highlighted in red, the female reproductive organs in yellow: more precisely, the change in their appearance and their migration within the caterpillar's body during metamorphosis. In addition to the colour highlighting, a further central feature of the pictures is the separation of foreground and background: all the tissues not involved in the metamorphosis, which make up the larva's body, are merely drawn schematically. As a result, the action in the plate's foreground is completely detached from events in the background. Finally, there is also the multiplication of the pictures. Isolating an individual organ with the aid of these different pictorial means makes it possible to follow the trail of the changes from one picture to the next. Taken together, the series of pictures evokes the impression of the continuous development of two small red dots into the complex organic structure of the reproductive organs. Herold deliberately employs colour highlighting, the combination of schematic and detailed views, the separation of foreground and background as well as the isolation of a single structure in order to give centre stage to the continuous changes of the reproductive organs.

Metamorphosis as epigenetic development

The reproductive organs were central to understanding the transformation since 'apart from the ability to reproduce […] the little caterpillar is equipped to perform all the functions of an insect' (Herold 1815: 4). That is to say, the reproductive organs were the only ones which the insect possessed and the caterpillar did not. Herold observed not only how the later reproductive organs emerged from rudiments but also how they changed their location in the course of metamorphosis by migrating further and further down in the caterpillar's body. He thus showed that metamorphosis is an epigenetic transformation. The formation of the reproductive organs from rudiments as well as their migration during development represented a twofold argument for their successive new creation since they meant that the organs were not already present but even replaced other structures whose position they took in the course of development.

Epigenetic development and serial pictures

Swammerdam had still 'extracted' the butterfly from the caterpillar. He had designed a complicated pictorial composition in order to demonstrate the connection between the individual stages on the basis of similar forms. When we come to Herold, however, caterpillars and butterflies no longer have the slightest structural similarity:

> This strange animal, formed out of the egg's liquid and consisting of the stated various parts, has not the slightest similarity with a butterfly. Through the peculiar nature of the organs, of which it is composed during its development, the butterfly is quite dissimilar to the state of its reproductive ability and it thus appears *in the shape of the caterpillar as an independent insect of a peculiar kind*.
>
> (Herold 1815: 4, original emphasis, translation added)

The caterpillar and the butterfly were here two completely different animals. Although they were connected with one another, their connection no longer consisted in having identical structures but a connection through development. Whilst the similarity of structures could be easily depicted and – as in Swammerdam's work – provided an obvious argument for the conformity of the animals, representing a development connection, in which the starting and end points look fundamentally different, required the use of new pictorial means. In Herold's work, this new pictorial technique was the picture series.

The transformation itself was highlighted for the first time in this serial representation. Development was no longer constituted in a single picture but in the relation between the pictures. Organic change was now something which could not be observed itself but which could only be manifested as a series of pictures: the transformation occurred in the pictures as well as between them. Only the sequence of pictures, the interchange of space and representation, fullness and emptiness, depicted and non-depicted, constituted development. It was the sum of changes across the series of pictures which evoked the impression of a continuous progression. But not only development appeared in the picture series. It was more than a mere technique for visual representation. It was a new way of thinking which made it possible not just to depict development connections but first and foremost to conceptualize them.

At virtually the same time as Herold's work, Christian Heinrich Pander's *Contributions to the Developmental History of the Chicken in the Egg* appeared in 1817 and then Karl Ernst von Baer's epoch-making paper *On the Developmental History of Animals* in 1828, with which they laid new foundations for embryology. As with Herold, the serial sequencing of pictures was also key for the concept of epigenetic development in these two fundamental works (Wellmann 2017). The significance of Herold's *Developmental History of Butterflies* for metamorphosis teaching is comparable with the embryological works by Pander and Baer: the change of shape, which metamorphosis described, attained the character of epigenetic transformation. Instead of still designating two opposing forms of development as in Harvey's work, from now on metamorphosis and epigenesis both describe the gradual change of shape, the successive stages of a continuous transmutation in which the organic material repeatedly takes on a new form.

Whilst the picture in the series was constantly repeated, it was never identical to the next picture. Every aspect of the transformation was thus always based on what previously existed, which it continued, but also always changed as it took it forward. As a result, the picture series subjected the continuous change of the organic to a rule, namely the order of repetition and variation. Change therefore followed a rule which it continuously modified without, however, being able to completely break out of this rule. It was only in this alternation between repetition and variation that the concept of development became possible: as a link with the past, which it perpetuated and as a stride into the future, which it opened up. Metamorphosis hence became an epigenetic development and Harvey's distinction finally obsolete.

NOTES

1. From its origins in classical mythology to concepts of modern art, metamorphosis has had a broad impact on art, poetry and culture. Relating this cultural history context to the natural history discussion would be an attractive and rewarding project. For more on the cultural history, see Coelsch-Foisner and Schwarzbauer (2005), Gottwald and Klein (2005), Nicklas (2002), Lichtenstern (1990, 1992) and Barkan (1986).
2. This chapter is a slightly modified and abbreviated translation from the German Wellmann (2008), 'Die Metamorphose der Bilder. Die Verwandlung der Insekten und ihre Darstellung vom Ende des 17. bis zum Anfang des 19. Jahrhunderts', *NTM*, 16, pp. 183–211. Throughout the text, translations from the German and French original are the translator's.
3. Neither a modern history of entomology nor its iconography exist. The standard works, although primarily a collection of material and list of works are Bodenheimer (1928), Essig (1965); on contemporary computational visualization methods, Hall and Martin-Vega (2019); for a history of pests, see Cloudsley-Thompson (1976); and a social history of entomology in the nineteenth century, see England Clark (1995).
4. Thomas Muffet's *Theater of insects* was written towards the end of the sixteenth century. The edition of 1634 appeared with numerous, albeit simple woodcuts. Pictures were also present in the most important works of the seventeenth century. To name a few examples: Malpighi's *Dissertatio epistolica de bombyce* (1669) with the first anatomical depictions of insect larvae; Francesco Redi's main work *Esperienze intorno alla generazione degl'insetti* (1668) or Jan Goedart's *Metamorphosis naturalis insectorum* (1662–69, in Latin 1685). In the eighteenth century, works created in the tradition of physico-theology, such as Johann Leonhard Frisch's *Beschreibung von allerley Insecten in Teutschland* (1720–38) or the

French translation (1742) of Friedrich Christian Lesser's *Insecto-Theologia* were just as richly illustrated as Réaumur's fundamental work, *Mémoires pour servir à l'histoire des insectes* (1734–42). In addition, natural history painters turned their attention to insects at an early stage. The insect pictures by the Belgian painter Jacob Hoefnagel were created in the late sixteenth century. Maria Sibylla Merian, famous to this day for her pictures in the tradition of Dutch still life and flower painting, was active in the late seventeenth century. In Germany, Johann Rösel von Rosenhof und Wilhelm Friedrich Gleichen-Russworm, who worked in Nuremberg in the late eighteenth century, provided not only exact and diverse microscopic observations but also a colourful panorama of the insect world.

5. Swammerdam spent some years towards the end of his life in religious seclusion under the influence of Antionette Bourignon's spiritualist movement. The most important biographical source for Swammerdam is Boerhaave's introduction to the *Bybel der natuure*. The only major monograph on Swammerdam is by Schierbeck (1967); for an introduction also (Cobb 2000). Swammerdam has gained greater attention in the context of modern research into the history of microscopy, see Ruestow (1996, 1985), Wilson (1995), Fournier (1996: 62–72); for further context also, see Roger (1963) and Pinto-Correia (1997).
6. Ruestow places Swammerdam's pictures in the Dutch tradition of miniature painting and anatomy. Giglioni examines the relationship between seeing and microscope, not the connection between picture and metamorphosis, see Ruestow (1996: 132–45) and Giglioni (1998).
7. The terms used in the Latin original are 'mutatio', 'series mutationum' (Swammerdam 1737–38: 2, 3, 4, 6, 11, 18, 42); 'metamorphosis' (Swammerdam 1737–38: 4, 5, 6, 9, 18); also 'transformatio', 'transformatur' (Swammerdam 1737–38: 5, 6, 14, 20). The Dutch terms are 'verandering', 'vervormingen' and 'verwisselingen' (Swammerdam 1737–38: 3, 4, 5, 9, 14, 22).
8. Swammerdam's observation that insects undergo not just one type of metamorphosis as well as its description are still valid today. One basically differentiates between larval stages (development stages with temporary organs which are later shed) and juvenile or developmental forms. These are already largely similar to the adult imagines but do not yet possess any reproductive organs. They only materialise in the course of further moultings from which the imago then emerges. In some insect species there is additionally a pupal stage. If there is no such pupal stage, one speaks of an incomplete (hemimetabolous), otherwise a complete (holometabolous) transformation (in Swammerdam's work the second and third classes, respectively). Insects such as the louse and the flea without any transformation (only moultings after the embryonal stage) as in the case of Swammerdam's first class are designated analogously as ametabolous. This form of development occurs in particular when both larva and imago already populate the same habitat, as is the case e.g. with the locust, see Hüsing (1963).
9. Swammerdam depicted all naturally white insects against a black background and, by contrast, all naturally coloured against a white background, see Swammerdam (1752: 30). In Plates I, XVI and XXXVIII, an additional effect is achieved by representing all vertically arranged pictures as negatives (cf. here Figure 9.1A–D). As a result, they form a kind of gauge along the left picture axis.

10. The interventions of the anatomist are also represented on a few plates, for example in the form of putti (Plate XXIV, Fig. IV) or via the portrayal of the researcher's hands and hand movements (Plate IV, Fig. VIII, Plate XLIX, Figs. V, VI and VIII).
11. What Swammerdam presumably saw with the aid of his preparation techniques are cell clusters, today called imaginal structures or discs. These are subcutaneous invaginations which evolve into organs in the course of metamorphosis; see the current entomological description in Ursprung and Nöthiger (1972). However, these differ from the final shape of the organs so extensively that one cannot speak of rudiments, etc. in the sense of a morphological similarity as Swammerdam postulated.
12. Lyonet was a multi-talented person: lawyer, naturalist and microscopist, draughtsman and engraver; for a while, he also worked for the Dutch diplomatic service as a decipherer of secret correspondence. Furthermore, he assembled one of the most famous collections of shells in the eighteenth century as well as a considerable collection of paintings, see Lyonet (1796). Nevertheless, there is little modern research into Lyonet and his work with the exception of Scholten (2017) and Anthérieu-Yagbasan and Laulan (2021). To this day, the standard works of reference are Hublard (1910), Seters (1962) and Lyonet's anatomical dissections are treated by Cole (1951).
13. The copper plates of Lyonet's first engravings are still preserved in the National Museum in Leiden, see Seters (1962: 68).
14. For more on the copperplate engravings in other people's works, see Hublard (1910: 75–82) and Seters (1962: 65–70).
15. A second edition of the *Traité* appeared in 1762 at the initiative of Lyonet's friend, the physician Le Cat. Unlike the first edition, this also contains an explanation of the drawing boards and a letter to Le Cat in which Lyonet explains his instrument, his magnifying glasses and his anatomical dissections. There is also a plate engraved by Lyonet himself which depicts his instruments (Lyonet 1762: Lettre à Le Cat: 2).
16. This can also be shown by Lyonet's discussion of the anatomy of the head, but there is insufficient room to deal with this here.
17. Lyonet feels compelled to refute possible criticism even in the foreword to his work. On the one hand, he secures his representation on the side of Nature with reference to witnesses ('convaincus par leurs propres Yeux'). On the other hand, he argues on the side of Art that no human being could be as creative as Nature itself (Lyonet 1762: XXIf.).
18. For more on Herold's life, see Runge (1983); on Marburg University, Altpeter (1992); on Herold's work only, Balan (1979: 305–08).

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