2011, *Entomologist's Gazette* **62**: 35–68

Ovipositing, egg-batch formation and embryonic development in burnet moths (*Zygaena* Fabricius, 1775) (Lepidoptera: Zygaenidae)

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Synopsis

Observations on egg deposition by burnet moths have shown that there are principal differences in ovipositing. The formation of regular batches (parquet-like clusters) is described for the first time. New data are provided for 'large batches consisting of several layers' and for 'small batches consisting of a single layer', while the unique way of ovipositing by *Z. brizae* ('singly-laid eggs') is also described for the first time.

With the exception of *Z. rosinae*, all investigated species place their eggs in a horizontal position, i.e. with the long axis parallel to the substrate. Moreover, there are reliable records of species within the *olivieri*-group, females of which were observed to place their eggs in a vertical position. The eggs of the remaining species are not only attached to the substrate but are deliberately pressed against it by the female's abdomen and, as a consequence, become deformed, thus producing a characteristic depression on the uppermost side of every egg. This pressure produces a deformation of the eggs that are at the moment of emergence still 'ovoid' but now become compounded together with other eggs into a hexagonal shape. The different shapes of egg batches are described and figured. All non-Palaearctic Zygaeninae deposit their eggs in mono-layered batches. This character is herein regarded as primitive within the genus *Zygaena*. The most complex order of egg clusters is found in regular batches of several layers with a pyramid-like upward projection, providing shapes that are only found in species of subgenus *Mesembrynus*.

The trigonometric relationships of the basic layer in regular batches are shown. Eggs are deposited in rows, starting at the periphery and going toward the centre, egg by egg; every new egg is staggered by half an egg-length. Thus a fishbone-like structure is produced, when one combines the lines or arrows that result from the sequence of oviposition.

As the shells of *Zygaena* eggs are translucent, the embryonic development from the moment of deposition to the moment of hatching can be observed and is described below. After deposition, the egg consists of two sections, one somewhat opaque, the other translucent. The location of these two phases is dependent on gravity, which is why the lighter section that is translucent moves to one pole in the majority of cases. The opaque part consists of the yolk sack in which the gametes from each parent meet and where the embryo develops. The yolk sack is usually proximate towards the mother and it is at this pole that the micropylar region is situated. After two-thirds of its development, usually after 6–7 days, the first pigmented structures become visible ('the two-dot stage'), the transparent section now being displaced. The entire space within the egg is occupied by the embryo. Hatching occurs at the upper side close to the micropylar region.

Zusammenfassung

Vergleichende Beobachtungen der Eiablage lassen einige grundsätzliche Unterschiede bei den Zygaenen erkennen. Die Bildung regelmäßiger „Eispiegel" mit parkettartig angeordneten Eiern wird erstmals für „große Gelege mit mehreren Lagen" und für „kleine, einlagige Gelege" detailliert beschrieben. Erstmals beschrieben wird auch das eigenartige Ablageverhalten von *Zygaena brizae*. Als einzige Zygaenenart legt sie ihre Eier einzeln oder in kleinen Gruppen ab, versteckt in den Filz auf der Blattunterseite der Raupennahrungspflanze.

Bis auf eine einzige Art (*Z. rosinae*) legten alle von uns untersuchten *Zygaena*-Arten die Eier horizontal liegend (die lange Achse parallel zur Substratoberfläche) ab. Darüber hinaus liegen uns aber auch zuverlässige Angaben für Arten der *olivieri*-Gruppe vor, die eine vertikale („stehende") Position der frisch gelegten Eier beschreiben. Eier werden nicht nur mittels einer klebrigen Substanz an das Substrat angeheftet, sondern vom Weibchen aktiv mit der Spitze des Abdomens angepresst, wodurch es ‚dorsal' zu einer sichtbaren Verformung der Eioberfläche kommt, die bisher ohne plausible Erklärung als „Delle" bekannt war. Dieser Druck führt zu einer Deformation der bei Ablage noch ‚ovoiden' Eier, die, wenn im Verbund mit anderen Eiern, nun eine hexagonale Form annehmen.

Die verschiedenen Formen unterschiedlicher Eispiegel werden beschrieben und abgebildet. Alle außer-paläarktischen Zygaeninae legen ihre Eier in einlagigen Eispiegeln ab, ein Merkmal, das für die Gattung *Zygaena* als primitiv erachtet wird. Als komplexeste Eiablagestruktur sind mehrlagige Eispiegel mit geordnetem Gitternetz und pyramidenartigem Aufriss anzusehen, wie sie nur in der Untergattung *Mesembrynus* vorkommen. Die trigonometrischen Verhältnisse in der basalen Lage regelmäßiger Eispiegel werden aufgezeigt. Eier werden in Reihen abgelegt, startend an der Peripherie, jedes folgende Ei um eine halbe Eilänge versetzt, bis zur Mitte hin, wodurch ein fischgrätenartiges Muster entsteht.

Die Schalen der Zygaeneneier sind sehr dünn und durchsichtig. Dadurch lässt sich die Entwicklung vom Moment der Eiablage bis zum Schlüpfen der Jungräupchen gut beobachten. Kurze Zeit nach der Ablage sind deutlich zwei unterschiedliche Flüssigkeitsphasen im Ei zu erkennen: eine milchigweiße und eine eher klare Flüssigkeit. Erstere ist der Dottersack, in dem die beiden Gameten verschmelzen und wo sich die Embryonalentwicklung abspielt. Die klare Flüssigkeit ist spezifisch leichter und formiert sich folglich am oberen Teil des Eies, meistens an einem der beiden Pole. Der Dottersack befindet sich bei Eiablage häufig am proximalen Ende („Mutterpol"), wo auch die Micropylarregion zu erkennen ist. Nach *ca* zwei Dritteln der Entwicklungsdauer, normalerweise nach 6–7 Tagen, werden die ersten Pigmentierungen sichtbar („Zwei-Punkt-Stadium"), die Flüssigkeit ist jetzt komplett „verschwunden". Der Embryo hat den gesamten Inhalt aufgenommen und füllt gegen Ende der Embryogenese das Ei vollständig aus; zuletzt sind aktive Fressbewegungen gut sichtbar. Das Schlüpfen aus dem Ei erfolgt auf derjenigen Polseite, wo sich die Micropylen befinden, also „mutterzugewandt"; meistens seitlich versetzt nach oben.

Key words: Lepidoptera, Zygaenidae, *Zygaena*, ovipositing, ovum, embryonic development, egg batch, natural hexagon.

Abbreviations

CV	used for chronological reference of cultures in captivity; it means 'Copula Versuch' or beginning of 'curriculum vitae', e.g. CV 070604 began with a copula on 4 June 2007.
hybr.	means hybrid between two taxa (species, subspecies) or populations.

Introduction

Intensive investigations on the phenomenon of embryonic cannibalism in burnet moths (Kia-Hofmann, 2008; Hofmann & Kia-Hofmann, 2010), conducted over the period from 2007–2009, have provided detailed observations on the specific strategies of ovipositing and the subsequent development of the embryos.

Observations on egg deposition

Gravid females of all *Zygaena* species oviposit during the day. Even the predominantly nocturnal species *Z. nocturna* Ebert, 1974, that starts to copulate after sunset was observed to lay its eggs exclusively during the warmth of the day, usually during the afternoon after the pair had separated (A. Hofmann, pers. obs.). The same behaviour has been observed for other partly or predominantly nocturnal species such as *Z. cuvieri* Boisduval, [1828], and *Z. manlia* Lederer, 1870; their nocturnal activity in the wild has been confirmed by records of males that are regularly attracted to light-traps.

All *Zygaena* species oviposit several times; moreover, as already mentioned, copulation usually takes place more than once, as has been ascertained by dissection of worn females in which up to four spermatophores have been observed (Hewer, 1934; Tremewan, 1985: 87; Fänger, 1986: 80). Only one species (*Z. brizae* (Esper, 1800)) deposits fertile (inseminated) eggs singly (Fig. 18). In all other Zygaeninae species this is exceptional and indicates infertility or disturbance of the female whilst ovipositing.

The shape of the egg batches of burnet moths is defined by the structure[1] (regular, irregular), the contour[2], the number of layers and the size (Figs 19–76). Moreover, it is dependent on the surface of the substrate. Batches of *Z. speciosa* Reiss, 1937, which were found under stones in the wild (Fig. 39), do not have such a symmetrical form and grid as those that were laid in captivity on other substrates (Fig. 40). With only a few exceptions, e.g. very small batches (Figs 54, 56), or those consisting of only two or three rows (Guenin, 1997: 333, fig. 5), the contours of batches are always asymmetrical ('irregular'), while in 'regular batches' symmetry in the inner structure ('grid') is to be found (see below). The slightest degree of order is reached in so-called 'irregular batches' (Figs 20–34) where neither contour nor structure suggest any symmetry. The highest degree of order is found in species where the females deposit pyramid-like batches consisting of several layers (Figs 70–74),

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[1] Structures arise by the addition of similar or equal elements, e.g. waves or grids.

[2] Contour describes the overall form (rhomboid, round etc.) and symmetry of the outline.

all of which clearly show a grid structure. In an ideal case the upward projection even tends toward a pyramidal shape (Fig. 70) and the horizontal projection to a rhomboid shape but, *de facto*, the contour in these batches becomes more irregular and a rhomboid or quadrangular contour may be only slightly indicated (or recognisable with some imagination).

Normally, eggs are laid in groups, predominantly in a regular cluster in which they are attached to each other. In regular clusters (Figs 40–76) the non-peripherally-placed eggs are horizontally surrounded by six other eggs that usually touch each other and, as a consequence, are slightly deformed (Figs 77, 78) into six-edged polygons. With such regular hexagons a flat surface can be covered parquet-like without gaps (Figs 77–79, 86–102) and that is why it often occurs in nature, human art or in engineering (e.g. honeycomb, basalt, architecture, spanner etc.).

Some Fabaceae-feeding species deposit 'irregular batches', a behaviour that is also known in species belonging to subgenus *Mesembrynus* (*Z. purpuralis* (Brünnich, 1763); *Z. fredi* Reiss, 1938), the majority of which live on Apiaceae; as the form and size of the batch varies depending on the surface of the substrate (Figs 20–26,) a thin leaf or a stem, for example, does not allow large regular batches. There are, however, species which predominantly deposit on host-plants with thin leaves (*Z. rosinae* Korb, 1903, *Z. olivieri* Boisduval, [1828], *Z. afghana* Moore, [1860], *Z. orana* Duponchel, 1835) and lay their eggs in small batches consisting of a regular grid (Figs 23, 54, 55) of two or three lines (e.g. Buntebarth, 2009: 91, figs 17, 21); others (*Z. fredi*) deposit small batches of predominantly irregular structure on the stems of the plant (Figs 20–23). However, even when the surface allows regular batches, some species (*Z. storaiae* Naumann, 1974, *Z. cocandica* Erschoff, 1874, *Z. sogdiana* Erschoff, 1874, *Z. trifolii* (Esper, 1783) etc.) 'cannot' oviposit the eggs in regular clusters (Figs 26–37).

Regularly shaped batches can consist of one or several layers, the bottom layer always being the largest and the number of eggs becoming progressively less from one layer to the other, the batch thus forming a pyramidal shape. The maximum number of layers that we have observed was seven in *Z. tamara* Christoph, 1889. Here are some examples:

Z. tamara (CV 070521,3): first batch of 7 layers (96, 88, 76, 67, 48, 29, 7)
Z. tamara (CV 070602): first batch of 5 layers (84, 70, 54, 41, 25)
Z. (?) *tamara* 'type *alborzina*': first batch of 4 layers (143, 116, 87, 62)
Z. hybr. *albormara* (CV 089515,1): first batch of 6 layers (126, 110, 103, 81, 39, 20).

Species of the *fausta*-group deposit their eggs in mono-layered batches of only one to two dozen eggs (Figs 13, 58–61). For *Z. fausta* (Linnaeus, 1767), Friedrich & Friedrich-Polo (2005: 129) counted an average of 11.3 eggs per batch. Others such as *Z. ephialtes* (Linnaeus, 1767), *Z. transalpina* (Esper, 1780), *Z. cambysea* Lederer, 1870, or *Z. loyselis* Oberthür, 1876, lay their eggs in mono-layered batches, too, but consistently in large numbers (Figs 66, 67). The number of eggs per batch can rise to 100 or more, an amount that is never found in *Z. fausta* or *Z. alluaudi* Oberthür, 1922. It is obvious that the behaviour of ovipositing (and consequently the general shape of the egg batch) is genetically fixed.

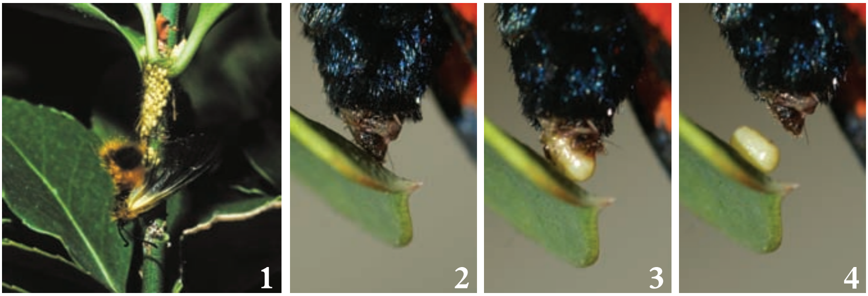
At the moment, the categorisation of 'regular cluster or batch' and 'irregular cluster or batch' is useful merely for practical purposes (e.g. descriptions), although intermediate clusters occur (Figs 30, 35–39). As long as no further comprehensive investigations concerning this behaviour, which should include the majority of species, have been undertaken, the phylogenetic value of this character remains unclear, as parallel development has obviously occurred. Moreover, even within one batch, the eggs that are laid last are often irregularly deposited.

However, this first comparative study allows some remarks to be made concerning the evolution of such characters. There can be no doubt for us that the single layer in an accurately arranged shape is the more primitive form in the genus *Zygaena*. Obviously only derived species (*Z. purpuralis*, *Z. brizae*, *Z. trifolii* etc.) have completely abandoned this behaviour, while regularities in the basic layer are even to be observed in these species. The most complicated shape consisting of a regular grid and several layers in a pyramidal form is found only in species of the subgenus *Mesembrynus* (Figs 68–74). Both 'types' of shapes are regarded as derived characters.

The majority of species belonging to the subgenera *Agrumenia* and *Zygaena* oviposit batches consisting of a single layer. The deposition of irregular batches has evolved (probably independently) in both subgenera. In some species-groups (*fausta*-group, *transalpina*-group, *loti*-group, *sarpedon*-group etc.) the shape of the batch is characteristic for all members. Consequently it provides evolutionary evidence and has to be regarded as an accomplishment of an ancestor.

All investigated Afrotropical (Figs 44–51) and Oriental Zygaeninae (Figs 41–43) oviposit horizontally laid eggs in regular (or almost regular) clusters consisting of one single layer. Only in *Praezygaena agria* (Distant, 1892) (Fig. 46) has the tendency for producing a second layer been noted. The shape and structure of *Reissita simonyi* (Rebel, 1899) (Fig. 41) is very *Zygaena*-like, a species in which the eggs are oviposited in a closed compound, thus producing the typical hexagonal shape of the eggs. The same structure is recognisable in *Orna nebulosa* (Guérin-Méneville, 1832) (Fig. 50), but the large shape, however, would be atypical for any *Zygaena* species. In *Epiorna* (Figs 44, 45), *Neurosymploca* (Figs 47–49), *Zutulba* (Fig. 51), *Praezygaena* (Fig. 46) and *Epizygaenella* (Fig. 42, 43), the distances between the single eggs are greater; often they even do not touch each other. Consequently the hexagonal contour is less developed (*Epiorna*) or not to be found. Strongly deviant is the green colour of eggs in *Zutulba* (Fig. 51). A unique behaviour within the Zygaeninae is that of *Pryeria sinica* Moore, 1877, a species that covers the eggs with abdominal setae (Figs 1, 19).

As the thin chorion is completely translucent, the coloration of the ovum of all *Zygaena* species depends on the colour of the yolk. It may be white, ivory, whitish, light grey, creamy or various shades of yellow, rarely orange. The eggs of high-mountain species (*Z. speciosa*, *Z. hindukuschi* Koch, 1937, *Z. persephone* Zerny, 1934, etc.) are significantly larger than those of lowland species. The



Figs 1–4. Ovipositing egg batches. 1, *Pryeria sinica*; female in ovipositing position with the head upside down and covering the eggs with abdominal setae (Japan: Kyoto, iv. 1984, ex photo archive C. M. Naumann). 2–4, *Zygaena alluaudi lamprotes*; ovipositing first egg (note in Fig. 3 that the egg is not deformed when exiting, but flattened when the female moves away in Fig. 4).

colour changes during embryonic development and always darkens towards the end of the egg phase (Figs 73, 74, 80, 81, 104, 105). The form of the ovum is ovoid with two poles and it is known as laterally flattened. The smooth surface lacks any prominent structure (Tarmann, 2004: 36) and is only inconspicuously 'gehämmert' [hammered like a piece of copper metalwork] (Döring, 1955: 119), a structure that is slightly visible in Figs 103 and 104. The micropylar region with its typical spiral rosette of polygons, which leads the spermatozoa to the pore through which they can penetrate into the interior of the egg, is barely visible with a binocular microscope and even SEM pictures (Eitschberger, 1991*b*: 280, 281, figs 1–4; Naumann, Tarmann & Tremewan, 1999: 17) show only a weak reticulate sculpture on the surface (Leigheb, Cameron-Curry & Balletto, 1998: 252). In contrast, the surface of the chorion of *Aglaope infausta* (Linnaeus, 1767) (Zygaenidae: Chalcosiinae) is strongly structured with a prominent reticulate pattern and irregular ribs that divide the polygons. The micropylar region is obvious (Eitschberger, 1991*a*: 277, figs 1, 2).

The internal and external structure of the female genitalia, the production of the eggs and the translocation of spermatozoa are described at length by Fänger (1986), Bode & Naumann (1988), Fänger & Naumann (1988; 1993) and Naumann, Tarmann & Tremewan (1999: 33–38). Before the egg reaches the oviductus communis, it is fertilised in the infundibulum and then passes two secretory glands before it exits lengthways via the ooporus, aided by abdominal ring-muscles with wave-like movements of the last abdominal segments (Figs 2–4). Consequently the first pole that is visible is distal to the female's abdomen and will be called the posterior part of the ovum (Fig. 5).

In contrast to Rhopalocera and Noctuoidea, in which the females place the eggs upright, the majority of Macrolepidoptera species place their eggs horizontally (Chapman, 1896), 'in the flat form, the axis runs parallel to the substrate', as described by Scoble (1992: 105). All Oriental and Afrotropical

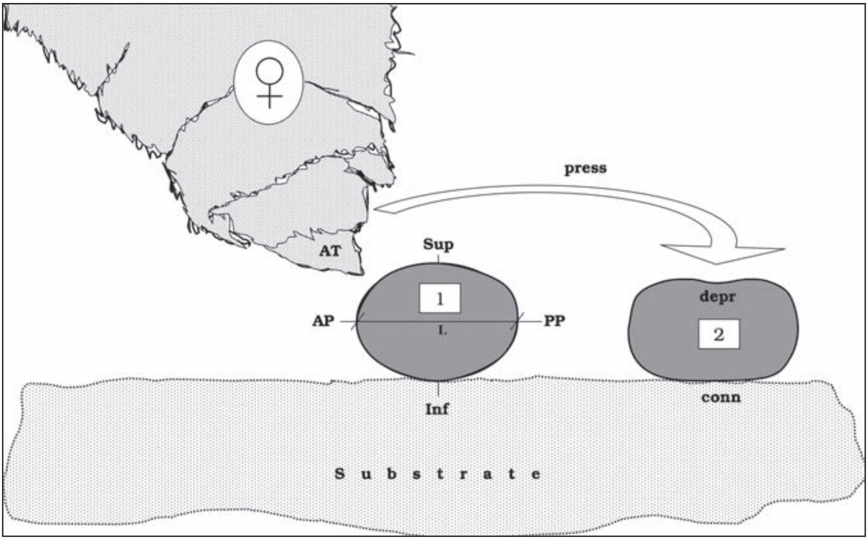


Fig. 5. Descriptive terms used to describe ovum in relation to the ovipositing female (schematic). 1, freshly laid egg before actively pressed by female. 2, egg after having been pressed by the female. **AP** – anterior pole, proximal pole; **AT** – abdominal tip of female with papillae anales; **conn** – lower connection to substrate after pressure has been applied by female; **depr** – upper depression of ovum after pressure has been applied; **Inf** – lower part, 'ventral' part; **L** – length of ovum measured from AT to PP; **press** – direction of pressure from female; **PP** – posterior pole, distal pole; **Sup** – upper part, 'dorsal' part.

Zygaeninae (*Orna*, *Epiorna*, *Neurosymploca*, *Zutulba*, *Praezygaena*, *Epizygaenella*, *Reissita*) and, with only one exception (*Z. rosinae;* Fig. 55), all Palaearctic Zygaeninae that we have investigated deposit their eggs in such a way; the same is to be said for all investigated Procridinae. This is in contrast to observations by Tremewan (1970: 75) and Buntebarth (2009: 90), both of whom record that *Z. olivieri* was observed to place its eggs in a vertical position. These records from Çorum (central Turkey) and Achalziche (western Georgia) can be confirmed by a further observation by Tremewan (pers. obs.) for a population of this species in Turkey (Hazar Gölü vic.), so that there can be no doubt that at least *Z. olivieri* places its eggs vertically, 'the transparent pole being uppermost' (Tremewan, 1970: 75). Efetov (1996: 27, fig. 1) has figured a batch of eggs from Crimea of a closely related species, viz. *Z. sedi* Fabricius, 1787, in which some of the eggs seem to be lying flat, others standing and slightly overlapping. At Gardaneh Avaj (Iran), a female of *Z. rosinae* was observed ovipositing on the upperside of a leaf (Fig. 55) of a pinkish flowering Fabaceae (probably a *Hedysarum* sp.). The batch consisted of two rows each of which contained four eggs all of which were laid in an upright position. It is noteworthy that these three species belong to a non-monophyletic group that is characterised by its green cocoons.

Further investigations should show if there is variation in this behaviour, whether it occurs in other species, if it is species specific, or if related species (*Z. fraxini* Ménétriés, 1832, *Z. separata* Staudinger, 1887, *Z. formosa* Herrich-Schäffer, 1852, *Z. sedi*, *Z. haberhaueri* Lederer, 1870, *Z. chirazica* Reiss, 1938, *Z. tenhagenova* Hofmann, 2005, *Z. naumanni* Hille & Keil, 2000) oviposit in the same way. If this should prove to be the case it could be of phylogenetic importance. Scoble (1992: 106) emphasizes that the position does not indicate a phylogenetic basis in the division of the order, because both kinds may occur within the same family (Hinton, 1981), for example in Geometridae and even within the same genus, as in *Sterrha* Hübner (i.e. *Idaea* Treitschke) and *Biston* Leach. According to Scoble (1992: 106), 'upright' and 'flat' may be of use as descriptive terms.

During the process of ovipositing, the pliable egg passes in a symmetrical ovoid form through the papillae anales (Figs 2, 3, 5, 11). Immediately after deposition the upper (superior, 'dorsal') part of the freshly laid egg that is opposite to the substrate, i.e. the 'top' of the horizontally placed egg, is already flattened (Figs 4, 5) or dented (Figs 13), while both poles and both sides (if not in direct contact to another egg) remain rounded. This slightly rectangular form (Fig. 4) is made by the female as part of the ovipositing process (Figs 6–12). Immediately after deposition, each egg is actively pressed (Figs 11, 12) against the substrate for a short moment by the tip of the immediately closed straight papillae anales in order to attach the egg more strongly to the substrate. This accidental deformation ('press-in') of its upper and lower side becomes equalised by lateral expansions on both sides ('press-out'). Then the deformed egg almost closes the gap between itself and the neighbouring eggs; in this compound they acquire a typical hexagonal shape. This not only occurs in the genus *Zygaena* but is also seen in *Reissita simonyi* (Naumann & Edelmann, 1985: 499, fig. 34) and *Orna nebulosa* (Fig. 50).

The females often sit upside down (i.e. with their venter uppermost) with their legs holding the leaf on which the eggs are placed, such a position easily allowing the female to press the egg with the tip of the abdomen (Figs 7–10). A round or oval form would only contact the substrate at a very small point of the chorion (Fig. 3) and masses of adhesive would be needed to attach each egg securely. This may be negligible when eggs are laid singly or in smaller numbers, but it becomes essential when some hundreds of eggs have to be attached. After deforming the shape of the pliable egg-shell, the egg has extensive contact with the substrate (cf. Figs 3–5) to which it is attached by a secretion from the female glandulae sebaceae. Moreover, the eggs are coated with a sticky proteinaceous secretion derived from Petersen's gland. However, these secretions alone would not be strong enough to attach the eggs to the substrate (mostly on the underside) and of course it is more economic not to have further secretions, which is why additional physical pressure from the female seems to be needed. This behaviour is genetically fixed and has been observed to take place by all investigated species of the Zygaeninae genera *Zygaena*, *Reissita*, *Epizygaenella*, *Praezygaena*, *Orna*, *Epiorna*, *Neurosymploca* and *Zutulba*. Moreover, similar 'depressions' in freshly deposited eggs of Indo-Australian (Tothill, Taylor & Payne, 1930: 79; Tarmann, 2004: 37) and

Palaearctic species of the subfamily Procridinae (Ebert & Lussi, 1994: 166, 182; Guenin, 1997: 404, 422; Keil, 1998: 118; Weidemann & Köhler, 1996: 491) might indicate that the same behaviour occurs in these groups.

During their short lifetime, females of some species (*Z. alluaudi, Z. fausta*) deposit more than two dozen batches of eggs with the number of eggs per batch remaining low and varying from two to less than 30 eggs per batch (Hofmann, 1994: 238; Friedrich & Friedrich-Polo, 2005); other species, such as *Z. tamara*, do not deposit more than two to four batches, the first of which can comprise 400 eggs or more (T. & A. Hofmann, pers. obs.).

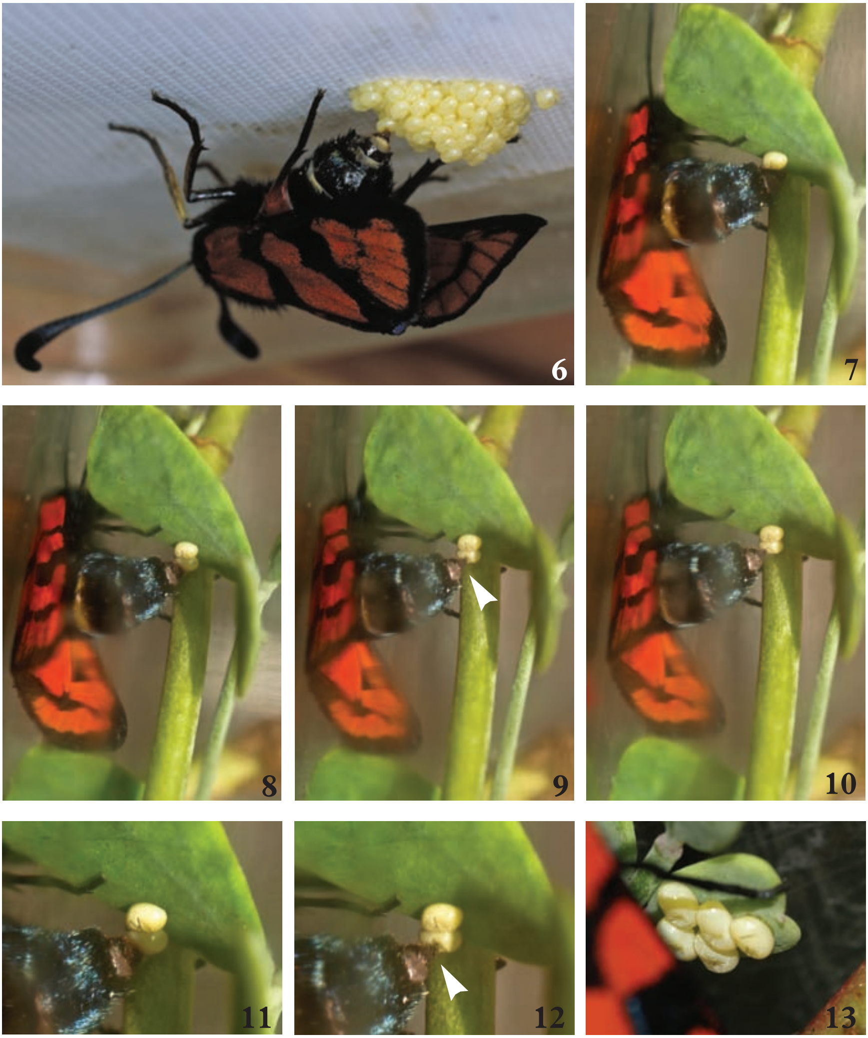
The number of eggs per batch is higher in the first batches that are laid and without further copulation they decrease rapidly in size. A female of *Z. dorycnii araratica* Staudinger, 1871 (CV 090522) separated after 21 h in copula at 13.00 h the next day and started ovipositing that day. The first batch (23.v.) consisted of 67 eggs; on 24.v. two batches with 69 and 25 eggs were noted. On the third day 52 eggs were deposited (25.v.), while 15 and 21 eggs comprised the batches on 26.v.2009. Only 11 eggs were laid on the sixth day and the last batch was laid on 28.v.2009 (13 eggs), bringing the number of eggs laid by a single female of *Z. dorycnii araratica* to 273 within six days.

The maximum number of eggs deposited by a single female of *Z. tamara* that had paired twice and which were counted exactly by us is 682; the first batch consisted of 274 eggs (CV 070602), the second was laid after the second copula and consisted of 408 eggs (CV 070604).

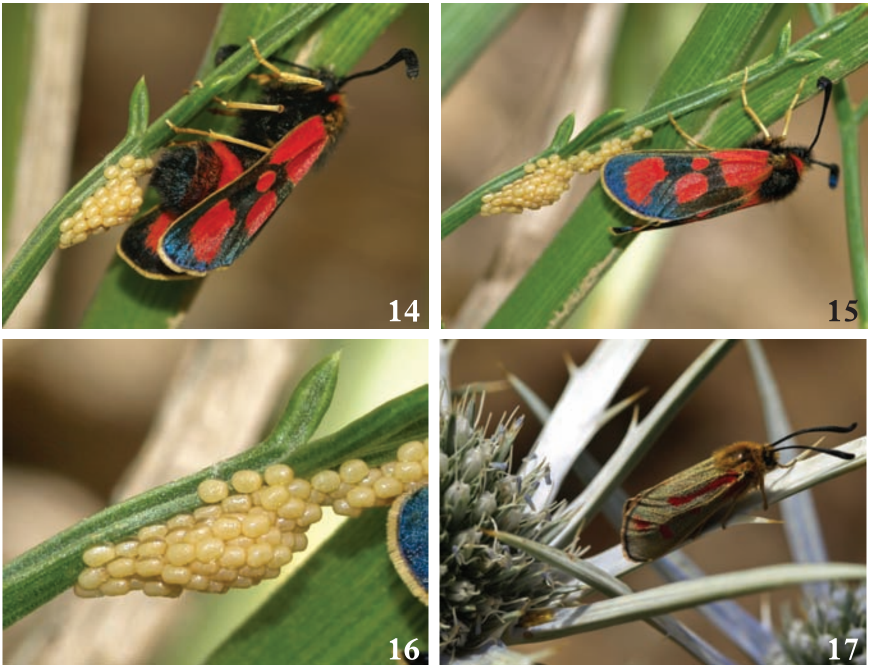
The behaviour of females during egg laying, which produces the characteristic batches of eggs, is genetically fixed. This has to be concluded by the fact that the form of egg batches is a species-specific character, e.g. females of *Z. trifolii* and *Z. filipendulae* (Linnaeus, 1758) always lay irregularly shaped batches, whereas those of *Z. fausta* and *Z. alluaudi* deposit small, regular batches consisting of 6–25 eggs that are always placed in a single layer; *Z. tamara* produces regular batches of several layers (step-pyramid-like construction) consisting of some hundreds of eggs. Within a species, the size and form of the batch varies, depending on the number of eggs that have already been laid by the female, the variable form and size of the substrate (stem or leaf, narrow or broad leaves etc.); moreover, in the wild, females may be influenced by temperature, wind and rain or might even be disturbed by predators or any movement or contact. However, the variability of batches is only within a certain range and *Z. filipendulae* will never lay regular batches as accurately as *Z. lonicerae* (Scheven, 1777) (Lane, 1962: 11); *Z. erythrus* (Hübner, [1806]) will never produce batches like those of *Z. trifolii*.

It is of interest to note that there are differences even within closely related species. While *Z. lonicerae* produces regular, single-layered batches, its sibling species *Z. trifolii* lays its eggs in a batch where no symmetry is apparent. The same can be said for *Z. purpuralis* (irregular batch) and *Z. erythrus*. There is no known species that exhibits such variation infraspecifically, e.g. different batches between lowland and high-mountain populations or between those occurring in far-distant localities.

The search for the right substrate and site on which to oviposit seems to be by optical orientation and often randomly chosen; the movement of antennae



Figs 6–13. Ovipositing of egg batches and deformation of freshly laid eggs. 6, *Z. tamara* subsp. (Iran: Alborz; ex CV 070527,1) depositing large batch of several layers and just pressing the last laid egg with the tip of the abdomen. 7–12, *Zygaena alluaudi lamprotes*; female ovipositing and immediately deforming the freshly laid egg by pressing the abdominal tip on the upper lateral part of the ovum. A well-visible depression remains on the surface, while the lower part becomes closer to the substrate (Morocco: Haut Atlas, Tizi n'Test N, vic. Idni, 1,700–1,800 m). 13, small batch of single layer, typical for *Z. alluaudi lamprotes*; the depression on each egg is recognisable.



Figs 14–17. *Zygaena* females ovipositing egg batches in the wild. 14–16, *Z. haematina* ovipositing large batch of irregular shape on the larval host-plant (*Prangos* sp.) (in Fig. 16 note the translucent area is not at one pole but at the lateral part of ovum that is in the upper position); Iran: Prov. Esfahan, Fereydun Shahr S., Sibak SE., Kuh-e Sibak, 3,100–3,300 m, 21.vi. 2009. 17, *Z. aurata* female with freshly deposited eggs, protected under the spiny leaves of the flower head of *Eryngium* sp., (Morocco, Haut Atlas, Marrakech S., Jebel Oukaïmeden, Tizi n'ou Addi, 2,800 m, 13.vii. 2008).

and contacting the substrate with the abdominal tip are seemingly part of the identification and acceptance. High-mountain species (*Z. cacuminum* Christoph, 1877; *Z. speciosa*; *Z. alpherakyi* Sheljuzhko, 1936; *Z. pamira* Sheljuzhko, 1919; *Z. exulans* (Hohenwarth, 1792); Z. *persephone*; *Z. anthyllidis* Boisduval, [1828]) very often lay their eggs on the underside of stones of medium size (Figs 34–39; Tremewan, 1989: 16, fig. 3; Tremewan & Naumann, 1998: 109, fig. 4; Hofmann, 2000: 345, figs 1, 2; Naumann, 2003: 367; Hofmann & Kia-Hofmann, 2008: 39, fig. 8), thus showing that olfactory orientation can be excluded in these cases. In the wild, ovipositing on 'wrong' substrates, i.e. often on plants growing close to the host-plant, is well known in *Z. filipendulae* and *Z. lonicerae* (Tremewan, 1985: 86; Hofmann, 1994: 315, 323) and in other European species. In captivity many – probably the majority – of gravid females will lay their eggs on the wall or bottom of their cages instead of on the host-plants that have been provided.

A female of *Z. fausta* (Germany, Schwäbische Alb, Schelklingen vic., 10.viii.2000) was observed for some minutes flying slowly close to the ground and apparently 'searching' for its larval host-plant. The flight can be described as more skipping/bouncing and several plants were briefly touched. When a small plant of *Coronilla coronata* L. was haphazardly found after half a dozen trials, the female crept onto the underside of the leaf; while both antennae were moving alternately up and down, it touched the plant several times with the tip of its abdomen and then started ovipositing. The female deliberately (without disturbance) finished after nine minutes and then flew away. During this time a precisely arranged, single-layered batch consisting of 14 eggs was deposited, thus 39 seconds on average was required to deposit each egg.

In large batches the ovipositing rate can be higher. Within three hours (14.29–17.30 h) a female of *Z. tamara* (CV 070521,3) laid a batch of seven layers consisting of exactly 411 eggs. Here the female needed on average 26 sec. per egg. The same rate was noted in another female of *Z. tamara* (CV 080429,2), which laid an extremely large batch consisting of 538 eggs from 12.25–16.22 h. In the laboratory we closely observed the behaviour of ovipositing by two species belonging to two different subgenera, viz. *Z. alluaudi*, which is placed in the subgenus *Agrumenia* and is endemic to Morocco, its larva feeding on plants of the genus *Coronilla* (Fabaceae), and the Irano-Anatolian *Z. tamara* (subgenus *Mesembrynus*) that feeds on *Eryngium* spp. (Apiaceae).

Singly-laid eggs (Fig. 18)

Zygaena brizae is a species that has a disjunct areal with one small refuge in south-west France and a distribution extending from Austria and the Czech Republic to the southern Balkans, Turkey and Lebanon. Further east it reaches the western part of Iran, is well known from the Caucasus region and extends northwards to the vicinity of Orenburg (Russia). Although widely distributed, with colonies in Austria and France, the preimaginal biology of *Z. brizae* is only poorly known and the species has never been reared ab ovo. The fully-grown larva from southern France is figured by Dujardin (1977: front cover) and from Crimea by Efetov & Tarmann (2004: 302, fig. 3), by Efetov (2005: pl. 25 fig. 4) and by Freina & Witt (2001: 523, fig. 14), while Larsen (1980: 105) provides a description based on adult larvae from Lebanon. In July 2009, at several sites in the Caucasian part of Georgia, we had the opportunity of doing fieldwork that involved this species and were able to observe its manner of ovipositing.

Some biological peculiarities make *Z. brizae* fairly unique. The larvae live on Asteraceae, feeding on different species of *Cirsium*, *Onopordum*, *Jurinea* and *Carduus*. The freshly hatched larvae from Georgia (Adzharia, Akhalzikhe 40–45 km W., Goderzis Pass E., 1,650–1,750 m; Borjomi W., Abastumani N., Zekari Pass S., 1,500–1,700 m) are completely un-pigmented, with all the setae white and even the basal rings where the setae arise from the integument are un-pigmented. In contrast to all other burnet species, the female obviously does not oviposit in clusters but lays the eggs singly or in small groups of 2–4 eggs. The majority, however, were laid singly on the underside of the leaves of the host-plant. Moreover, the eggs are not deposited on the surface as with all other *Zygaena* species, but were inserted into the pubescence (tomentum) that is characteristic of the underside of the leaves of many *Cirsium* species; thus the eggs are concealed and almost invisible to the observer. Even with this knowledge and after having observed a female with curved abdomen hanging onto the underside of a leaf, the eggs were fairly difficult to find. This might be one reason why there are no recorded observations of ovipositing by this species. Even without having disturbed a female in such a position, it does not remain for very long (less than 2 min.) on one leaf, then changing to another, while other *Zygaena* species can sit from 15 minutes up to three hours in order to oviposit at the same site.

This behaviour is not to be regarded as a primitive character but as a specific adaptation to an unusual host-plant. A comparison with all other species of the genus and with the outgroup clearly shows that it is a derived character (autapomorphy) of *Z. brizae*.

'Irregular batches'[3] (Figs 20–34)

Several species (*Z. haematina* Kollar, 1849, *Z. purpuralis*, *Z. exulans*, *Z. filipendulae*, *Z. trifolii* etc.) are known to deposit their eggs in clumps of irregular structure. A basic grid and definable layers are not recognisable or are only rudimentary (e.g. for *Z. filipendulae*, see Hofmann, 1994: 315). Egg batches of *Z. fredi* that were found in the wild at several sites in Iran (Alborz and Zagros mountain ranges) were attached as clumps around the stem of the host-plant or irregularly deposited on the thin leaves of *Bupleurum exaltatum* M. Bieb.

Phylogenetically this behaviour is most likely a derivation of regular batches, as regular structures are at least rudimentarily observed in most of the species that are known to deposit irregular batches. While *Z. trifolii* in Europe deposits its eggs in clumps without any degree of order (e.g. Tremewan, 1985: 110), the batches of populations of this species from North Africa show more or less a basic grid. Some regularity is expected to be found even in such batches (number of eggs, size, height etc.). However, the irregular form of egg depositing is here only mentioned for the sake of completeness, as it is not a subject of the present work.

Small batch of single layer (Figs 7–13, 23, 54–63)

In contrast to *Z. tamara*, females of *Z. fausta* and *Z. alluaudi* start laying eggs on the same day that the copula has separated (Table 1). For example, on 26 October 2008, a female of *Z. alluaudi lamprotes* Dujardin, 1973 (CV 091024), was observed searching for a suitable position; the couple had started to copulate at around 16.00 h on 25 October and separated on the following day at 12.35 h. At 12.40 h, room temperature 19–20°C, her antennae were moving up and down and within five minutes she began probing with the tip of her abdomen the surface of the leaves of *Coronilla valentina* L. that had been provided, on the stem of which the copula had taken place for more than 20

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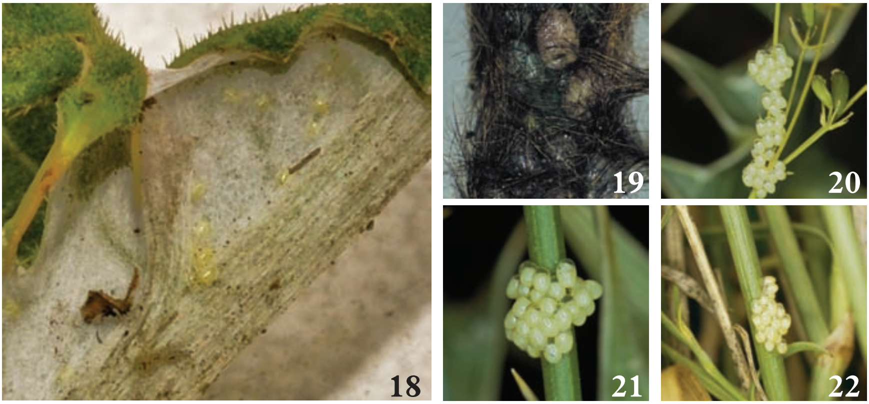
[3] It would be more correct to call it 'batch of irregular structure' in contrast to 'batch of regular structure'; however, the term 'irregular batch' or 'irregularly shaped batch' is used in the literature (e.g. Tremewan, 1985: 86) and there is no confusion with any other term.



Figs 18–22. Different shapes of egg batches within the Zygaeninae. 18, singly-laid eggs by *Z. brizae adsharica* (Georgia, Borjomi W., Abastumani N., Zekari Pass S., 1,500–1,600 m, 22.vii. 2009). 19, *Pryeria sinica* (Japan: Kyoto, iv. 1984, ex archive C. M. Naumann), abdominal setae covering the eggs. 20–22, batches of irregular structure (I): *Z. fredi* subsp. (Iran, Prov. Tehran, Tehran NNW., Kendevan region, Azadbar vic., 2,900 m, 5.viii. 2005).

hours. The female did not even move further than some centimetres. The reason for the probing may be identification of the substrate but further probing after oviposition of the first eggs remains unclear. Re-identification of host-plant, searching for an earlier batch of eggs and application of adhesive are possible but not very probable explanations. Why should the female, after having laid the first eggs, identify the surface several times before laying further eggs? To search for another batch on a small leaf is not really convincing, as it could be very close to the next. The eggs are already covered with a sticky substance before exiting the ooporus; is more adhesive needed at the base? At 12.45 h, the female was in a position on the underside of a leaf with her dorsum facing downwards and started ovipositing. At 13.16 h, she had finished ovipositing and changed place; two batches, each of which consisted of 5 eggs (Fig. 13) were deposited within 31 minutes; at 13.25–13.45 h the next batch was laid and consisted of five eggs (*ca* 3 min./egg). With the central heating switched on, the room temperature increased to 22° C; the female started ovipositing again and on the side of the plastic box (Figs 7–12) a batch of six

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Figs 23–34. Different shapes of egg batches within the Zygaeninae. Batches of irregular structure (II): 23, *Z. fredi fredi* (Iran: Prov. Fars, Eqlid SSE., Kuh-e Bol, Darre Zard Ab, 2,800–2950 m, 12.vi. 2009). 24, *Z. rubricollis nasukmiri* (Afghanistan: Prov. Panjshir, Astanah NE., Cheshmeh Gardaneh, 2,900–3,050 m, 10.vii. 2007). 25, *Z. haematina* (Iran: Kuh-e Dena, Sisakht vic., vii.1995, *photo* C. M. Naumann). 26, *Z. cocandica cocandica* (Kirgistan: Western Alai mts, Sokh valley, Sary Talaa, 1,900–2,000 m, 14.vii. 1992, *photo* C. M. Naumann). 27, *Z. sogdiana* (Kirgistan: 18 km N. Ala Buka, 1,500–1,600 m, 23.vii. 1993, *photo* C. M. Naumann). 28, *Z. sogdiana tschimganica* (Uzbekistan: Tshimgan reg., 4.v.1997). 29, *Z. storaiae flaugeri* (Afghanistan: Prov. Kabul, Kuh-e Paghman, Kotale Kotandar S., 3,600, 26.vii.2007). 30, *Z. haematina* (Iran: Prov. Esfahan, Fereydun Shahr S., Sibak SE., Kuh-e


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Sibak, 3,100–3,300 m, 21.vi. 2009). 31, *Z. minos* (Germany: Baden-Württemberg, Fridingen vic., 4.vii.1993). 32, *Z. filipendulae* (ex Germany: Baden-Württemberg, Deggendorf, Brotjackenriegel vic., 830 m, 3.vi. 2009). 33, *Z. trifolii mideltica* (ex Morocco: Haut Atlas, Imilchil NE., Tizi n'Tirhadouine, E-Seite, 2,500 m). 34, *Z. alpherakyi* (Dagestan: Caucasus or., SSE. Akhty, vic. Kurush, 2,900–3,200 m, 22.vii. 1996, *photo* C. M. Naumann).

Table 1. Results of duration of copulae, ovipositing and size of egg batches of investigated species of burnet moths (*Zygaena*) cultured from 2007–2009.

Species/hybrid[1]	Origin	Duration of copula[2]	Start of ovipositing after copula[3]	Number of batches[4]	Number of eggs per batch
Z. tamara	CV 070604	24	96	1	408
Z. tamara	CV 070602	20	6	1	274
***Z. tamara* (‘type *alborzina*’)**	CV 070524	18	96	1	> 400
***Z. tamara* (‘type *alborzina*’)**	CV 080503,1	18	120	1	> 300
***Z. tamara* (‘type *alborzina*’)**	CV 080503,2	19	72	2	> 150, > 150
Z.* hybr. *albormara	CV 070521,3	19	48	1	411
Z.* hybr. *albormara	CV 080429,1	44	96	1	> 200
Z.* hybr. *albormara	CV 080515,1	24	6	1	479
Z.* hybr. *nocturzina	CV 070521,3	21	72	1	313
Z.* hybr. *manlivieri	CV 090509	19	24	1	> 300
Z. manlia	CV 090507	17	24	2	> 250
Z. hindukuschi	CV 080502,2	2	24	1	136
Z. speciosa	CV 070521,1	18	6	5	21, 28, 27, 32, 40
Z. speciosa	CV 070527,3	18	6	3	29, 33, 43
Z. trifolii (Morocco)	CV 090517,1	24	2	1	242
Z. trifolii (Morocco)	CV 090518	20	2	1	154
Z. filipendulae	CV 080428	19	6	2	99, 70
Z. filipendulae	CV 090531	24	6	9	4, 6, 8, 12, 14, 22, 23, 24, 32
Z. dorycnii araratica	CV 090522	19	2	8	11, 13, 15, 21, 25,52, 67, 69
Z. alluaudi	CV 081006	18	6	18	2, 2, 2, 3, 3, 5, 5, 6, 6, 6, 6, 7, 8, 9, 11, 12, 12, 17
Z. alluaudi	CV 081008	20	1	11	2, 3, 4, 8, 9, 9, 10, 10, 19
Z. alluaudi	CV 081011,1	19	1	20	2, 3, 5, 5, 5, 6, 6, 7, 8, 8, 9, 10, 10, 10, 11, 11, 13, 13, 15, 20

Z. alluaudi	CV 081011,2	20	6	20	2, 2, 2, 2, 3, 5, 6, 6, 7, 7, 7, 7, 8, 8, 8, 8, 8, 8, 9, 10, 12, 12, 13, 13, 15, 18, 19
Z. alluaudi	CV 081024	21	1	4	5, 5, 6, 8 [fem. died]
Z. alluaudi	CV 081103,1	20	6	14	2, 3, 5, 5, 6, 6, 7, 8, 9, 11, 12, 13, 15, 23
Z. alluaudi	CV 090426	16	1	9	2, 6, 6, 6, 7, 11, 13, 15, 16,
Z.* hybr. *tremeaudi	CV 081103,2	19	1	8	3, 4, 5, 5, 8, 11, 12, 14

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[1] A more detailed article (A. Hofmann & W. G. Tremewan, in prep.) will deal with hybridisation experiments 1989–2009. Here only some copulae with reference to the subject concerned are mentioned.

[2] Duration of copula (in hours); this time span is minimal as the beginning was not recorded precisely. After noon the boxes were normally controlled every two hours followed by a control that was made during the night and again in the early morning until the partners had separated.

[3] Start of ovipositing after the copula had separated; 1 = within the first hour; 6 = the same afternoon; 24 = the following day; 48 = two days later; 72 = three days later etc.)

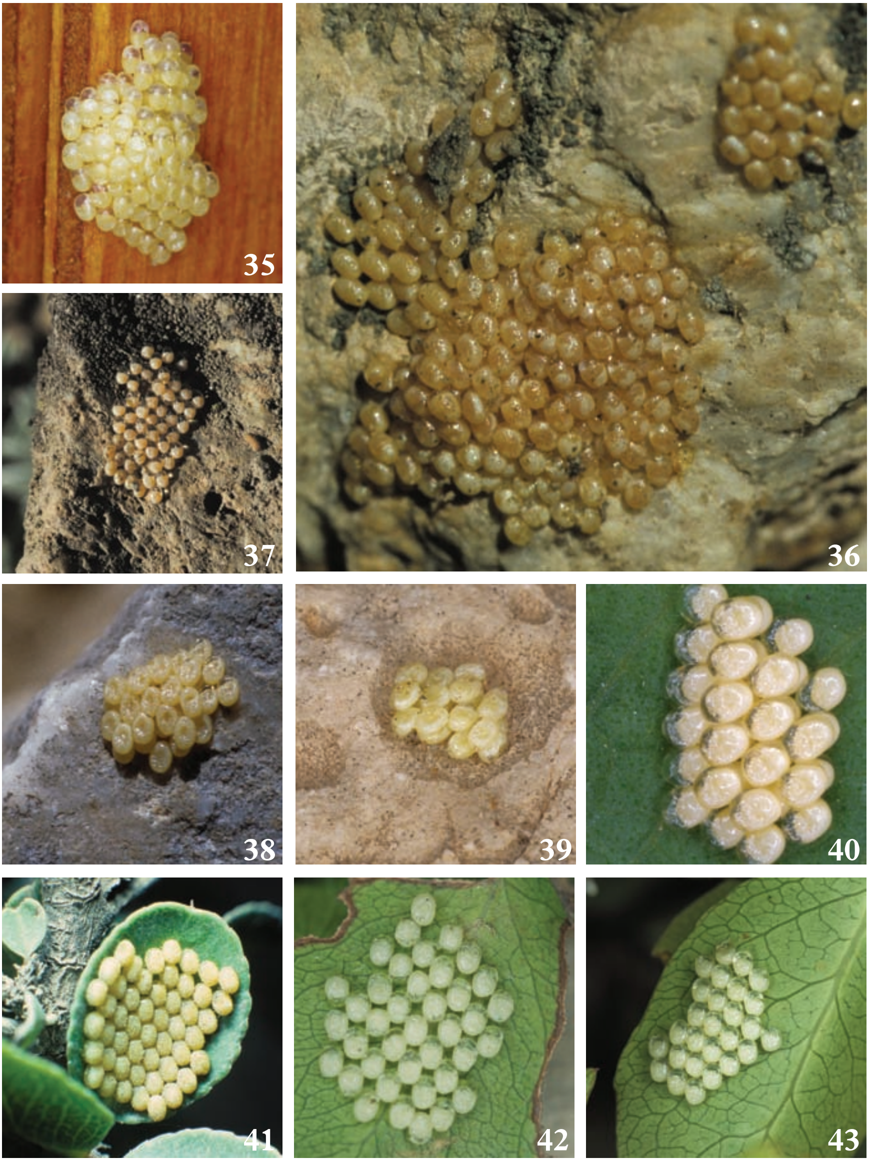
[4] Number of batches that were laid during the first two days or before the female began to call again (usually after 3–4 days).

eggs was deposited within 12 min. (*ca* 2 min./egg). On the first day the female laid five batches comprising 48 eggs. Comparable data were obtained for three further females of *Z. alluaudi lamprotes* and for the hybrid from *Z. tremewani* Hofmann & Reiss, 1983 × *Z. alluaudi lamprotes* (CV 081103,2).

The egg deposition started to form the typical V-shape after the first three eggs (Figs 82–85) were laid, then 'egg 4' was normally placed above 'egg 1', the contour now being rhomboid. However, in one case a female varied and deposited 'egg 4' not in the middle but beside 'egg 3'. In any case the typical grid remained. All batches were mono-layered, the number of eggs varying only from 2–23 eggs.

Large batch consisting of a single layer (Figs 41–53, 64–67)

Like non-Palaearctic Zygaeninae species, *Z. loti* ([Denis & Schiffermüller], 1775), *Z. transalpina*, *Z. cambysea* and others oviposit their eggs in mono-layered batches of regular structure. The number of eggs can be up to 100 or more. Occasionally single eggs are deposited on top of this first layer but without forming a second layer (Hofmann, 1994: 293). The contour is irregular, close to quadrangular, sometimes longitudinal or rounded. The inner structure of a mono-layered batch is always of a regularly formed grid that is described below (under pyramidal batch of several layers).



Figs 35–43. Different shapes of egg batches within the Zygaeninae. 35–40, batches of high-mountain species attached to stones: 35, *Z. hindukuschi* (ex Afghanistan: Prov. Panjshir, Astanah N., Shava NW., Hausak, 3,300 m, ex CV 080502,2). 36, 37, *Z. pamira* (Tadjikistan: Pamir, Turumtaikul Lake, 4,300 m, 17. viii.2000, *photo* C. M. Naumann). 38, *Z. cacuminum* (Iran: Prov. Mazandaran, Sharud W., Shah Kuh, Shah Kuh-e-Pa'in S., 2,900 m, 20.vii.1999).

Small batch consisting of two layers (Figs 38–40, 76)

The batches of a couple of species vary between single layered and two or even more layers. At Dorahun (Iran, central Zagros, 1,900–2,100 m, 15.vi.2009), 55 batches of eggs of *Z. seitzi* were found and counted in the wild. The number of eggs per batch varied from 25 to more than 200. The majority of batches (*ca* 60%) were double layered with 40 to 70 eggs per batch, while some were of a single layer (25%) or three layers (20 %). The largest consisted of four layers and contained more than 200 eggs. The density of egg batches at this site was so high that on the underside of the leaves of the larval host-plant (*Eryngium billardieri* Delar.) sometimes three (in one case even four) batches could be found (Fig. 76). Egg batches of *Z. speciosa* vary between two and four dozen eggs. A female (CV 070527,3) started ovipositing with a fairly irregular cluster of 43 eggs. The next two batches were more regular and pyramidal; one consisted of 29 eggs (15, 12, 3), the other consisted of 33 eggs (22, 11).

Pyramidal batch of several layers (Figs 68–75)

Zygaena tamara is a polymorphic species with alternate, contrasting coloration of red or yellow on the fore- and hindwings (Naumann, 1987; Hofmann & Tremewan, 2003). Like some females of *Z. nocturna*, the majority of those of *Z. tamara* do not oviposit on the same day after the copula has separated and they very often sit for three or more days before starting (Table 1). Such behaviour has been observed over a period of several years in individuals from different localities and consisting of different phenotypes in Iran (Kordestan (yellow/red), Zanjan (red/red), Ardabil (yellow/red), Mazandaran (red/red) and Qazvin (red/red)). Moreover, the same behaviour was observed in hybrids between *Z. tamara* (yellow/red) and *Z. tamara* (type '*alborzina*')[4](red/red).

It seems to be independent of whether the females were fed with a solution of sugar and water or offered nectar plants. Probably the long period of time between the transfer of spermatozoa and ovipositing has something to do with the enormous number of eggs and their production in the ovarioles. Compared with other species, the first batch laid by *Z. tamara* always contains some hundreds of eggs. However, our observations in the wild do not always conform to this behaviour when the females are in captivity. While some wild-caught females did not lay eggs for a day or two, others began ovipositing the same day that they were placed in the breeding boxes. However, one could not be sure whether these females had already waited or had already laid eggs, as females from copulae obtained in the wild could be from a second mating.

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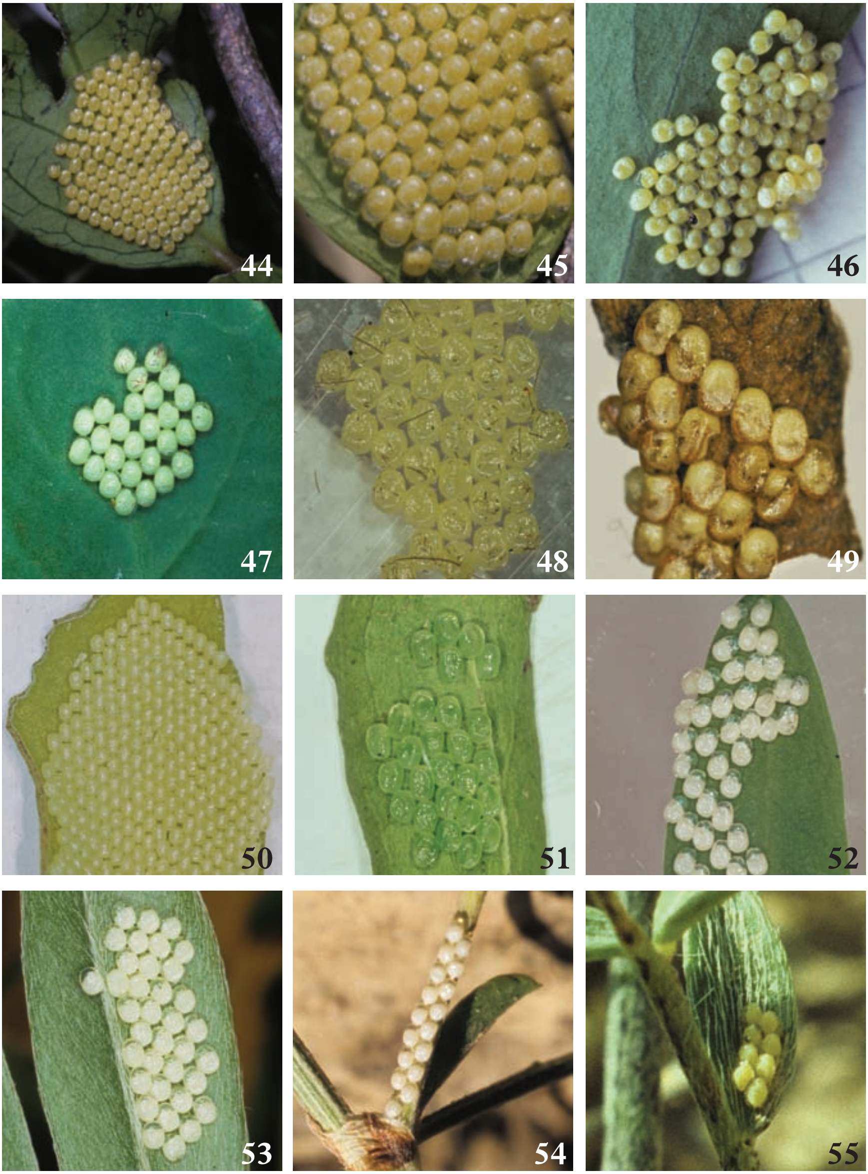
[4] The taxonomic status of these undescribed populations occurring on the north side of the Reshteh-ye Alborz (Iran) is unclear.

39, *Z. speciosa* (Iran: Prov. Tehran, Pass Dizin-Shemshak, Kuh-e Dizin, 3,500–3,600, 10.vii. 2006). 40, *Z. speciosa* (Iran: Prov. Tehran, Tehran N., Kuh-e Tochal, 3,600–3,800 m, ex CV 070521,1). 41–43, Mono-layered batches of non-Palaearctic Zygaeninae (I): 41, *R. simonyi* (Yemen: Dj. Masnah, iii.1980, *photo* C. M. Naumann). 42, 43, *E. cashmirensis* (Pakistan: Islamabad, Margalla Hills, Daman-e-Koh, iv.1997, *photo* C. M. Naumann).



Figs 44–55. Different shapes of egg batches within the Zygaeninae. 44–51, mono-layered batches of non-Palaearctic Zygaeninae (II): 44, 45, *E. abessynica* (Ethiopia: Goha Tsyon, x.1990, *photo* C. M. Naumann). 46, *P. agria* (South Africa: Pietersburg, vii.1985, *photo* C. M. Naumann). 47, *Neurosymploca* sp. (South Africa: Blinkwater stream, xii.1984, *photo* C. M. Naumann). 48, *Neurosymploca* sp. (South Africa: Tygerberg, i.1984, *photo* C. M. Naumann).

Examples of the procedure of egg depositing will be described here from a F_2 hybrid female of *Z.* hybr. *albormara* (CV 080429,2)[5] that was more than 44 h in copula with a male of the same origin. However, this long duration was extraordinary, as it normally lasts for 18–22 h.

The copula began on the afternoon of 29 April 2008 (copula found at 19.00 h) and lasted till 01.30 h on 1 May. Three days later (4.v.2008), at 12.25 h, the female started laying eggs while upside down on the translucent lid of the plastic box that also included the larval host-plant (Figs 77–81, 86–99). Egg laying was continuous, without any long break, and the duration of oviposition in a shady-sunny place was nearly 4 h (237 min). At 16.22 h, after having laid 532 eggs in one single, pyramidal batch consisting of four layers, the female stopped. The basal layer consisted of 197 eggs, the uppermost of 73, while 148 and 114 were in between. Consequently, an egg was laid on average every 27 seconds. However, during the first two hours when the female was continuously observed there were phases when an egg was deposited every 15 seconds.

After having deposited and actively pressed the first egg onto the substrate, the female of *Z. tamara* (like *Z. alluaudi*, see Figs 82–85) moves her abdomen to the lateral side of the egg but only goes about half the length of an egg down toward the posterior end of 'egg 1'. With the tip of the abdomen she touches the side of 'egg 1', as if she were controlling her position. The second egg is then laid beside the first, both now partially touching each other laterally. 'Egg 2' is placed in such a way that its posterior end is situated at the middle of the first egg. The next egg is then laid in the same manner but on the opposite side of 'egg 1'. If 'egg 3' is deposited exactly on the same position (just on the other side of 'egg 1'), all three together then forming a symmetrical 'V'-shape, the batch begins to form as a 'perfect' rhombus. The fourth egg is the first that touches another egg at its anterior pole, its posterior end to the anterior of 'egg 1', all four now producing a quadrangle of rhomboid shape, a pattern that will occur several times during the formation of the batch (Figs 77,78, 86, 89). From then on, rows of eggs were laid (Figs 86–91), each egg touching the previously laid one along the longitudinal side, but staggered by one step (= half an egg-length). The rows are deposited in an alternating manner, one on the left side, the next on the right side and so on. As the eggs are already in

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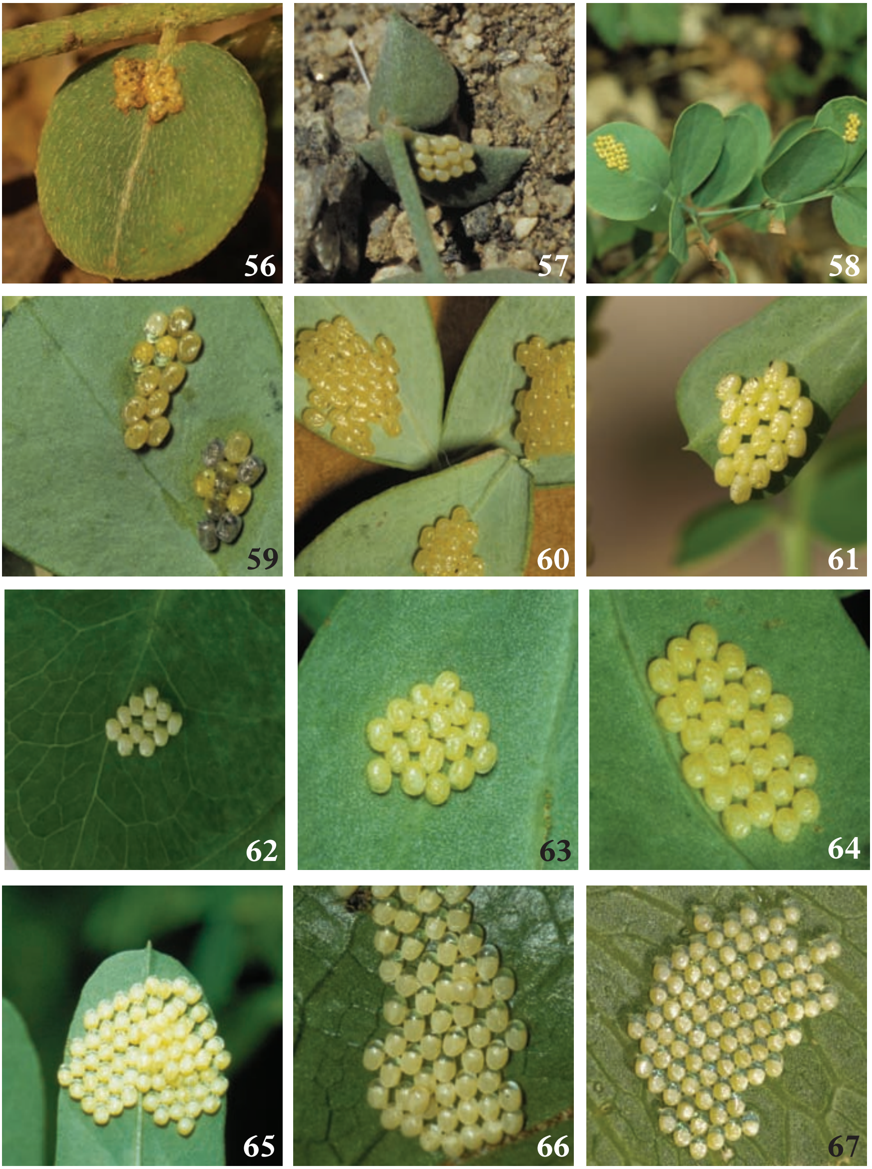
[5] Hybrid names are not given to a natural population, nor are they available in the sense of the *International Code of Zoological Nomenclature*. However, they are useful for laboratory work and especially during the breeding period. 'Albormara' is a combination of both parents. The taxonomic status of the male is unclear; it was found in the Alborz range while the female originated from a population of *Z. tamara* from Khalkhal (Iran).

49, *N. meterythra* (South Africa: Hogsback, ii.1986, *photo* C. M. Naumann). 50, *O. nebulosa* (South Africa: East London, iii.1984, *photo* C. M. Naumann). 51, *Z. ocellaris* (South Africa: Buffalo pass, 12 mls W. East London, *photo* C. M. Naumann). 52–55, batches of single layer (I): 52, *Z. armena* (vii.1984, *photo* C. M. Naumann). 53, *Z. loti* (Germany: Baden-Württemberg, Kaiserstuhl, Badberg). 54, *Z. christa* (Iran: Azarbayejan-e Sharqi, Tabriz NNW., Dugijan, Sultan Zangir Dagh, 3,100, 26.vii. 2006). 55, *Z. rosinae* (Iran: Prov. Hamadan, Hamadan NNE., Razan N., Gardaneh Avaj, 2,300–2,400, 19.vi.1998), eggs deposited in vertical position.



Figs 56–67. Different shapes of egg batches within the Zygaeninae. Batches forming a single layer (II): 56, *Z. beatrix metaxys* (Morocco: Haut Atlas, Imilchil, Lac Tislit vic., Auberge Tislit vic., 2,200–2,400 m, 3.vii.2008). 57, *Z. afghana* (Afghanistan: Prov. Herat, Herat NE., Karokh NE., Khajeh Chahar Shanbeh NE., 2,000 m, 18.vi.2006). 58, *Z. fausta suevica* (Germany: Baden-Württemberg, Schwäb. Alb, Schelklingen, Hartenbuch, 640 m, 3.viii.1991). 59, *Z. algira telealgira*, batch with parasitised eggs (ex Morocco: Haut Atlas,

contact with each other when deposited and are then pressed, the typical hexagonal shape of the surrounding eggs is thus produced (Fig. 78, marked).

Every row starts from the periphery and goes to the centre, egg by egg. The opposite way from the centre to the periphery was never observed. The 'central line' (Fig. 100) is fixed by the extension of egg 1 to egg 4. When the female moves with the abdomen to this 'centre', it lays the last egg in this line and then moves to the periphery of the other side, here starting a new line. Time after time the female moves forward a millimetre or so. If one connects by arrows or lines the eggs in the order that they were laid on the substrate, one obtains a fishbone-like arrangement (Figs 94, 97, 99) with the 'central line' forming the backbone from where the lines diagonally run to the periphery. In this way the grid structure of the batch is principally fixed; however, the contour and size is variable and is dependent on the point from where the female begins the diagonal rows. Until 'egg 16' was deposited, the symmetry remained perfect (Fig. 93), but then the female started the diagonal line (D7) with one egg displaced. Such displacements occur regularly and they are necessary as otherwise the shape would become too broad for the laying female and movements even during the deposition of one row would be the consequence. Therefore, in large batches the shape looses its quadrangular or rhomboid contour and becomes more longitudinal (Figs 79, 80).

The angle of the diagonal lines (Fig. 100) is determined by two variable factors: (1) the position where the second egg is deposited; and (2) by the relation of the length and breadth of the egg. This allows one to count the gradient of the diagonals ('fish-bones') and therefore the structure of the cluster by a simple trigonometric operation. We use the formula :

$\tan \beta = (L \times 1/x)/B$ and with the inverse function (**$\arctan \beta$**) we obtain the required angle (**β**).

(L) is the length and (B) is the breadth of the egg, while (1/x) describes the height of deposition of 'egg 2' compared with 'egg 1'; e.g. when 'egg 2' is deposited half a length higher than 'egg 1' we get $\tan \beta = \tfrac{1}{2}\, L/B$.

In *Z. alluaudi lamprotes* we measured the egg size of 1.1 mm (L) and 0.8 mm (B); 'egg 2' was approximately placed at the mid of 'egg 1', which gives us:

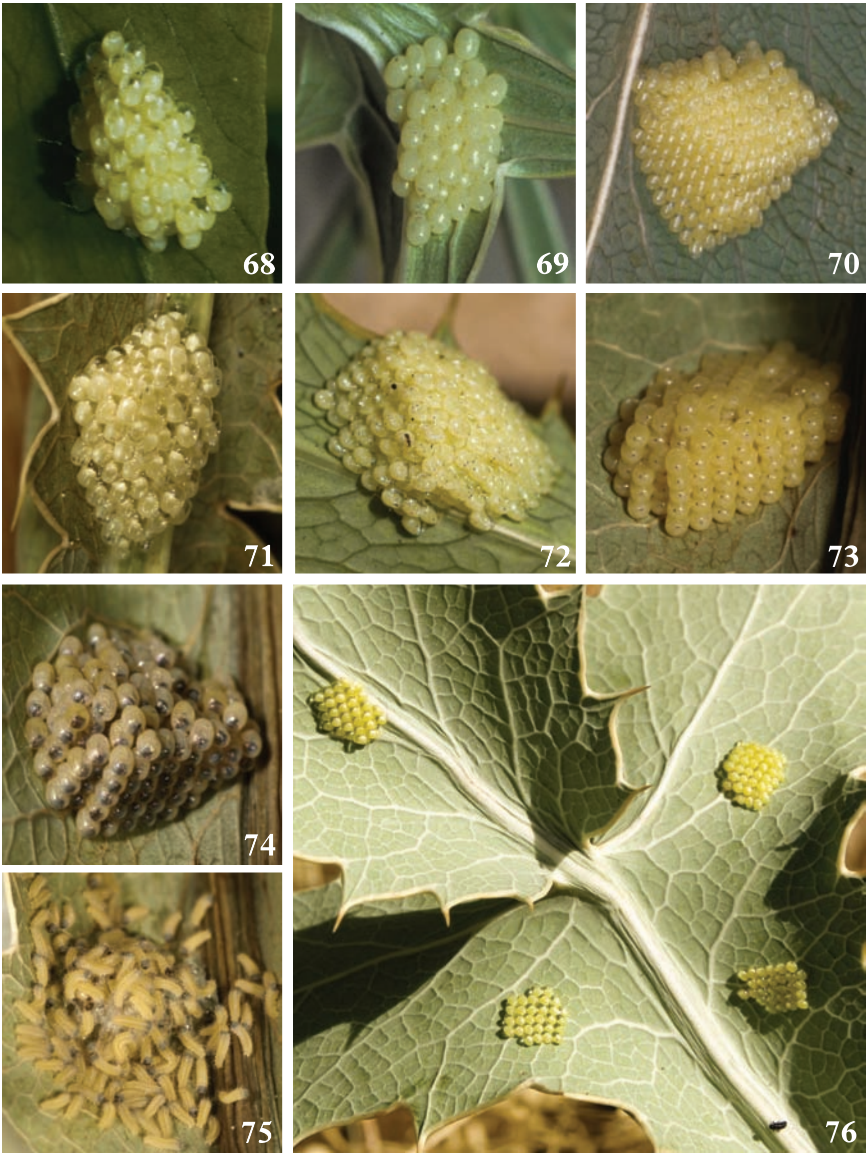
$\tan \beta = 0.55/0.8 = 0.6875$; $\beta = 34.51°$ – both base lines run in this angle.

For *Reissita simonyi*, Naumann & Edelmann (1985: 497) gave an egg size of approximately 1.1 × 1.4 mm. In this case the formula would be:

$\tan \beta = \tfrac{1}{2}\, 1.4/1.1 = 0.636363$; $\beta = 32.47°$.

Consequently, the other angles (α, γ, δ) and distances (dis) can be counted. With this formula the principle of grid formation in regular batches of Zygaeninae species is explained.

Telouet vic., 2,000–2,100 m, 11.vi.1990). 60, *Z. algira ifranica* (Morocco: Moyen Atlas, Ifrane vic., 22.vi.1990). 61, *Z. alluaudi lamprotes* (ex Morocco: Grand Atlas, Tizi n'Test N., vic. Idni, 1,700–1,800 m, 19.x. 2008). 62, *Z. mana* (Georgia: Borjomi W., Abastumani N., Zekari Pass S., 1,500–1,600 m, 22.vii.2009. 63, 64, *Z. angelicae elegans* (Germany: Baden-Württemberg, Schwäbische Alb, Bad Urach vic., 17.vii.1992). 65, *Z. transalpina astragali* (Germany: Baden-Württemberg, Kaiserstuhl, Badberg, 9.vi.1993). 66, *Z. loyselis ungemachi* (ex Morocco: Moyen Atlas, El Hajeb 14 km SE., 1,350 m). 67, *Z. cambysea* (Iran: Prov. Kordestan, Sanandaj NW., Saqqez-Baneh (pass), 1,950–2,100, 27.vi.2009).



Figs 68–76. Different shapes of egg batches within the Zygaeninae; batches of several layers. 68, *Z. centaureae* (ex Russia: Volga reg., Polivna, 30.iv.2001). 69, *Z. huguenini* (Kirgistan: 18 km N. Ala Buka, 1,500–1,600 m, 23.vii. 1993, *photo* C. M. Naumann). 70, *Z. seitzi tenhageni* (Iran: Prov. Esfahan, Semirom vic., Kuh-e Behrouz, 2,800–2,900 m, ex CV 000514,1). 71, *Z. turkmenica isfahanica* (ex Iran: Prov. Esfahan, Meymeh 20 km N., 2,100 m, 12.v.2009 ex CV 090507). 72, *Z. turkmenica isfahanica* (Iran: Prov. Esfahan, Meymeh 20 km

However, it goes without saying that this ideal form is variable and a perfect mathematical grid, as described above, is not to be found in nature. Females do not often obtain the exact half way length of 'egg 1' when laying 'egg 2' or 'egg 3' (Figs 101, 102). If this happens in the beginning the symmetrical rhombus can become contorted; the possible variation, however, is only within a narrow band and a rhomboid grid remains in any case. Obviously some species do not always lay their eggs in direct contact so that gaps remain and no hexagonally formed eggs are produced while a grid as described will not be formed. It strikes one that this is typical for several non-Palaearctic Zygaeninae (Figs 42–48), but it also occurs in *Z. loti* (Fig. 53), *Z. armena* Eversmann, 1851 (Fig. 52) and other species of subgenus *Zygaena* (Figs 62–65) and also in *Z. loyselis* (Fig. 66).

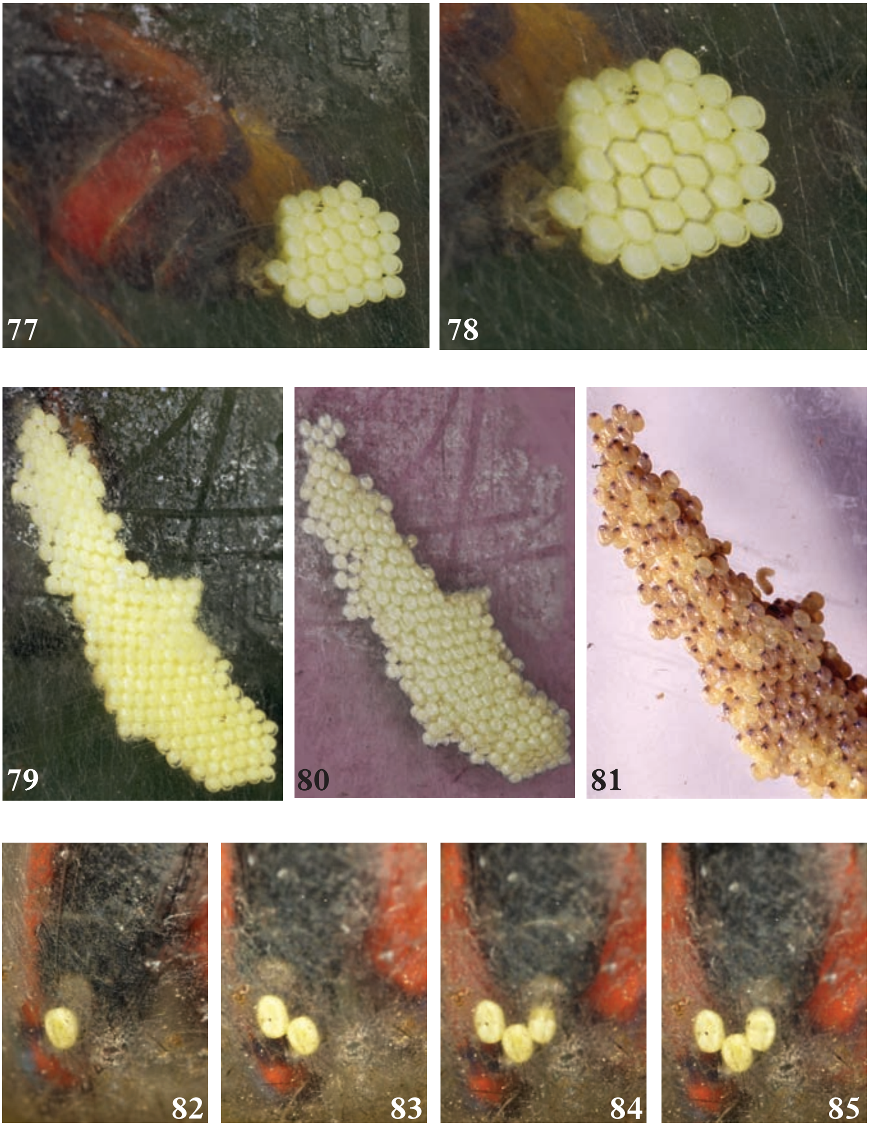
Deviations and differences occur because of the heterogeneity of the surface of the substrate, inconsistent pressure on the eggs and subsequent differences in the shape. Moreover, individual behaviour varies and breaks by the female or disturbances to her can occur, i.e. abiotic factors (temperature, wind, exposition etc.) may also influence the female during ovipositing. The fact that females of species which 'normally' lay regular batches can lay irregular batches or even single eggs when the copula was not successful shows clearly that the existence of a spermatophore, possibly the supply of nutrients, or physical inner pressure, and also the sufficient absorption of nectar and humidity play decisive roles for the accuracy of oviposition.

The females can vary the contour of the batch very early by starting a diagonal row not at the expected point but one egg later. This changes the external shape of the batch but not the grid. Even when a female makes a mistake, often it can recompense such an irregularity with another egg (Figs 96, 97, after egg 39). With the growth of the batch, irregularities occur more often and sometimes even two rows on the same side were laid without changing to the other side.

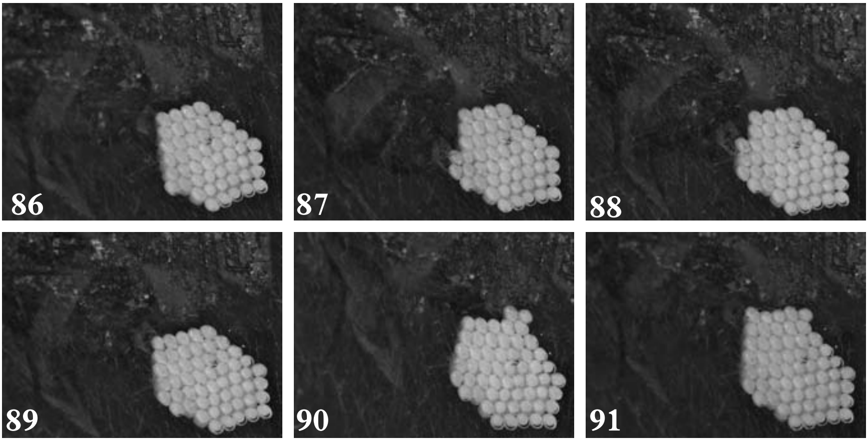
One has to keep in mind that we only consecutively numbered the eggs as in a mono-layered batch although our subject of observations (*Z. tamara*) is a species that lays multiple-layered batches. Consequently, the above-mentioned numbers only refer to the basal layer.

Interestingly, in batches of several layers, the latter are not laid one after the other as one might expect at first sight. After having laid the first six eggs, the female began depositing eggs on top of this basal layer, thus producing the second layer. Consequently the mentioned number of each egg in the example described above is not in the order that it was oviposited but in the order that it was arranged in the basal layer. Batch formation of several layers is figured in Figs 6 and 14–16.

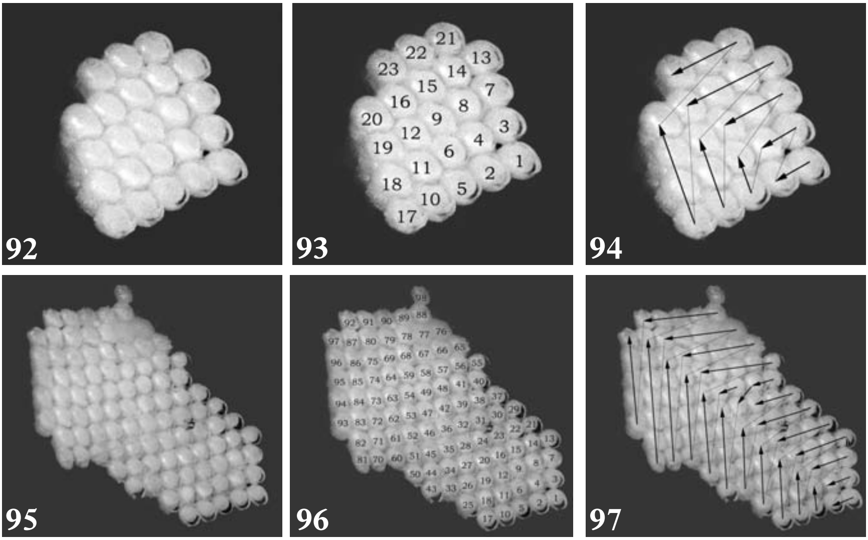
N., 2,100 m, 19.vi. 2009. 73–75, *Z.* hybr. *isfhanocturzina* (CV 090509: *Z. turkmenica isfahanica* (Meymeh, leg. ovo) × hybr. *nocturzina* (ex CV 070521,2). 76, *Z. seitzi* (Iran, Prov. Chaharmahal-va-Bakhtiyari, Borujen S., Dorahun 6 km S., 1,800 2,100 m, 15.vi.2009); four batches of eggs were deposited on the underside of one leaf of *Eryngium billardieri* – two batches were double layered, two were single layered.



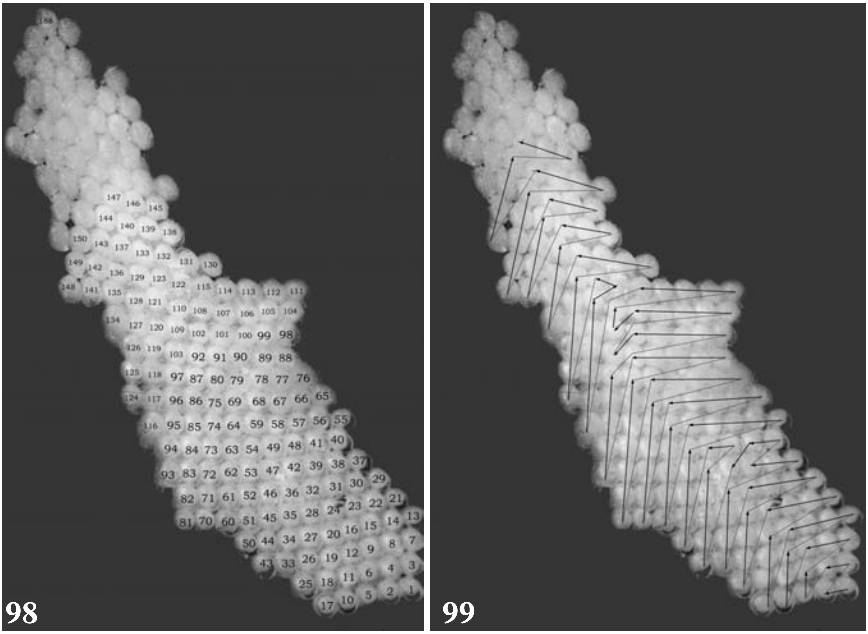
Figs 77–85. Producing basal layer. 77–81, *Z.* hybr. *albormara* (CV 080429,2) ovipositing; note the hexagonal contour surrounding the eggs (marked in Fig. 78), the accurate grid at the beginning and the enormous size at the end. The larvae are emerging at the 'mother pole' (77–79 view from underside, 80–81 view from above). 82–85, *Z. alluaudi lamprotes* female starting to oviposit (Morocco: Haut Atlas, Tizi n'Test N., vic. Idni, 1,700–1,800 m); eggs 1, 2 and 3 forming typical V-shape.



Figs 86–91. Producing rows in egg batches. The female of *Z.* hybr. *albormara* (data as in Fig. 77) starts from the periphery and goes to the centre: having reached the 'peak', she then changes to the periphery of the other side to start a new row. The growth in rows, the rhomboid contour and the grid of the basic layer are well visible.



Figs 92–97. Structure of basal layer (data as in Fig. 77). In Figs 93 and 96, the eggs are numbered in the sequence that they were deposited in the basal layer; the arrows show the rows as connecting eggs were laid. Grey lines indicate the movements of the abdomen to start a new row.

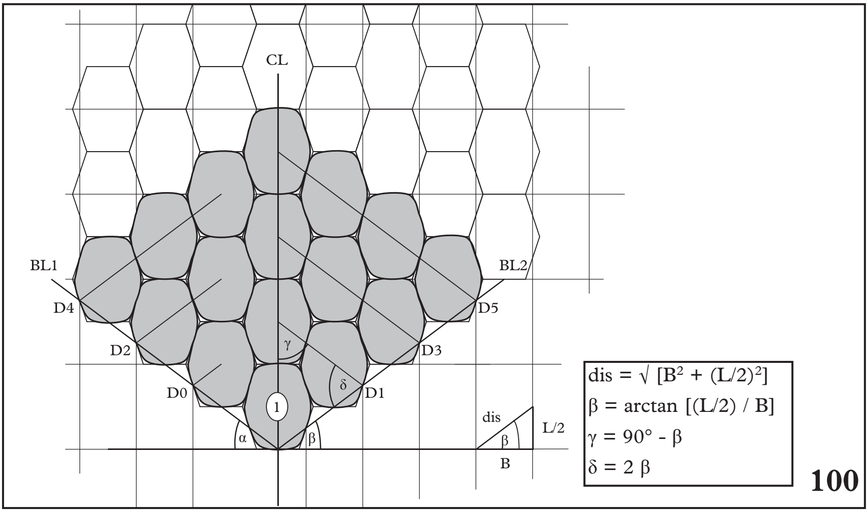


Figs 98, 99. Complete structure of basal layer (data as in Fig. 77) consisting of 188 eggs. The whole batch was laid within 237 minutes and consisted of 532 eggs; yet every 27 seconds an egg was deposited.

Observations on egg development

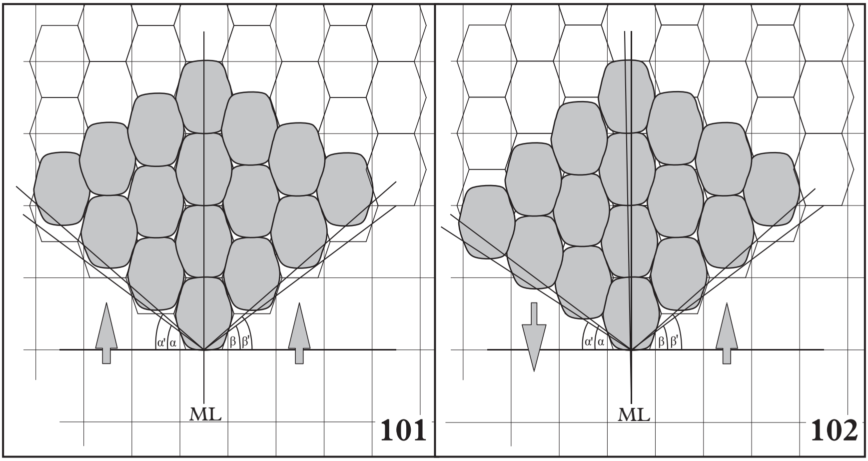
The eggshell (chorion) of insects not only consists of chitin-like substances (chorionin) but also contains energy-rich lipoproteins. The shells of eggs of *Zygaena* species are very thin, subject to deformation when the eggs are freshly laid and always translucent. Therefore the progress of development inside the egg can be easily observed at any time and unfertile (undeveloped) eggs can be counted. Egg development has been described for *Apoda limacodes* (Hufnagel, 1766) (Limacodidae, Zygaenoidea) by Lussi (1994: 239).

Freshly laid eggs contain one part consisting of an opaque, milk-like liquid (Figs 3, 4), which in a short time develops into two well-differentiated and well-separated liquid parts that vary in amount (e.g. Figs 21, 35, 40, 43, 52). In *Z. tamara* we noted that the yolk sack (distinctive as a cloudy, opaque liquid that is sometimes more yellowish) occupies *ca* 70% of the volume of the egg, while a more watery, clear part comprises *ca* 30%. The transparent watery section is lighter and therefore is always positioned at the upper part while the opaque part with a higher specific weight is formed at the lower part of the egg, i.e. their positions are simply according to the gravity. A crescent-like surface separates the yolk sack from the watery part in the beginning and usually

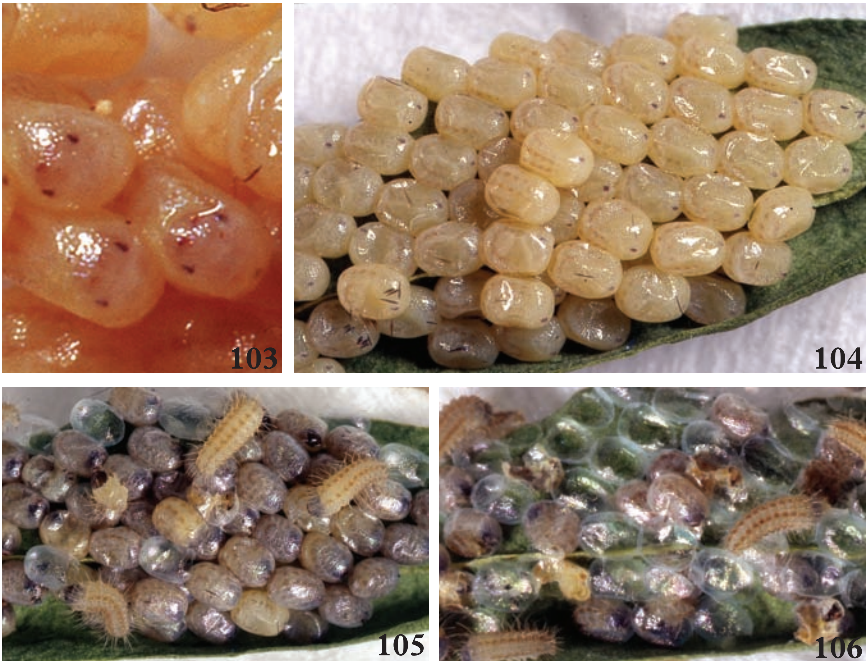


CL = central line, with starting point (1) of ovipositing
BL1, BL2 = base lines
D1, D2 … = diagonal rows; as the eggs are laid, starting from base lines
α, β = angle determining BL1 and BL2 (and parallel lines) (eggs are not laid in this order)
δ = angle determining diagonal rows (as the eggs are laid)
γ = angle between CL and diagonal rows
dis = distance between two neighbouring egg centres along the diagonal rows and lines
L = length of ovum; **B** = breadth of ovum

rows = as the eggs are laid (e.g. D1, D2, D3…)
lines = optically not to separate by rows; however the eggs are not laid in this order
(e.g. CL and parallel lines, BL1, BL2 and parallel lines)



Figs 100–102. Trigonometric structures of basal layer (for explanations see text and legend below Fig. 100). 101, 102, changes in symmetry when 'starting eggs' do not build a perfect V-shape.



Figs 103–106. Egg development and hatching of larvae. Figs 103, 104 show developed features of the embryo: two-dot-stage (head) and pigmentation on the dorsum, while in Fig. 105 the larvae are hatching by opening a hole at the micropylar pole or sideways close to the micropyle. All larvae hatch at the same side. Part of the eggs-shells was eaten and cannibalistic attacks occurred (Fig. 106); visible at the opened egg-shells with traces of the remains of siblings.

divides vertically, with a slight convex shape. As the majority of eggs were not laid in a perfect plane, one could get the impression that one pole always becomes translucent. However, experience gained from turning freshly laid eggs and the observation of a female of *Z. haematina* (Figs 14–16) that was photographed in the wild laying eggs that were placed almost in a fairly level plane showed us that simply the gravity and the different specific weights of the two parts are responsible for such a division. Zooming into the photo (Fig. 16) in the laboratory showed that the light, translucent part could even be positioned at the upper side which is not one of the poles but the lateral side of the ovum.

The micropylar region is always situated at the anterior pole (proximal to the tip of the mother's abdomen) of the egg; and here at this end of the egg the head of the larva becomes visible at the end of the embryonic development. All observed larvae emerged at this proximal (anterior) part of the egg (Figs 5, 74, 104, 105).

In burnet moths, the spermatozoa, probably always more than one, penetrate the ovum via the micropyle while the egg is located in the infundibulum on its way to the oviductus communis, where subsequently the two sebaceous glands coat it with a film-like adhesive. This coating is supposed to have several functions: of these, one is adhesion to the substrate, another is that it contains a poisonous secretion as a protection against parasitoids or predators, a third might be closure of the open ooporus. Subsequently the parental gametes unite to form a diploid zygote inside the yolk sack and embryogenesis begins; however, visible changes in the two-phased plasma during the first three days are poor. The transparent section becomes reduced in size (to *ca* 10–20%), while the opaque section expands (to *ca* 80–90 %) and slight structural changes inside this section occur, such as the appearance of a bubble-like formation of the lighter and darker materials. Often a light, watery, lens-like structure surrounded by the opaque section at the centre, and sometimes some slight movements, can be observed.

After 5–9 days, depending on the species and weather conditions during that period, the eggs change colour and the first structures inside become visible. There are differences in the speed of development between the different species and even within the single batches (Fig. 81, 105); as a consequence, not all larvae emerge at the same time. The sclerotization starts with a 'two-dot stage' (Figs 73, 103, 104) that was observed in all species. These two darkened dots are located at the proximal end of the egg at the position where later the stemmata (ocelli) are located. The mandibles, clypeus and head capsule, together with two slightly darkened dorsal bands across the thorax and abdomen, become visible one or two days before hatching and finally the setae are observable. At this stage the developing eggs were inspected twice or even several times a day.

The larva inside the egg moves by turning its head, the mandibles open and close and typical movements of eating are clearly visible. When the yolk sack inside the egg has been completely eaten the embryo is fully developed (Figs 74). Now the egg is blown up and the larva begins to open the shell by 'licking' and eating it at the anterior part (that, which was the proximal pole to the female when the egg was laid). Normally the immediate pole is not opened, but an area beside it, predominantly laterally, so that it is the direct way out of the shell without any drawbacks because of neighbouring eggs or substrate.

Under natural central European conditions, the egg development from oviposition to hatching of the larvae lasts in late spring (May) from 8–12 days. There are specific differences. While *Z. filipendulae* and *Z. loti* emerged after 8 days, *Z. tamara*, *Z. nocturna*, *Z.* (?) *tamara* subsp. [from Alborz range, Iran] needed 9–10 days. As one would expect, the speed of development (probably of all ontogenetic stages) is dependent on the ambient temperature and may vary in nature by up to more than three days.

Under artificial conditions the duration of the egg stage can be extended twofold without notable losses. A female of *Z. dorycnii araratica* from Georgia (CV 090522) laid seven batches of eggs between 23–28 May 2009. Two batches (69 and 25 eggs) were laid on 24 May of which the first was kept under 'normal' conditions (19–21°C) while the second was kept comparatively cool

(12°C). The first batch, consisting of 69 eggs, showed fully developed embryos on 31 May when the larvae started to hatch. On the same date the other batch was brought from 12°C into 'normal' conditions. No development was visible at this time; it was apparently interrupted, as the larvae needed 7 more days to hatch, thus extending the egg phase to 15 days in comparison to the first batch, the eggs of which hatched after 8 days.

A female of *Z. fredi* (CV 090714; originating from Iran, prov. Hamadan, Kuh-e Garin, Nahavand SW., Gardaneh-ye Gema Siab, 2,850 m) laid several eggs along a stem of *Bupleurum falcatum* L. on 15.vii.2009. As there was no chance for feeding during a 10-day trip to Georgia, the eggs were put in the fridge where they remained from 15–26 July; 11 days later, no development was recognizable. After taking them out and placing them in room conditions, their development needed seven further days before hatching (2.viii.2009, ab ovo), thus extending the egg stage to 18 days, while in Iran (25–35°C) only six or seven days are necessary for the entire development. It is noteworthy that all eggs exhibited normal development and the percentage of hatching did not vary from those of batches under normal conditions.

Surprisingly, in five large batches, each of which consisted of more than 300 eggs and for which the females needed more than three hours for oviposition, the eggs that were laid at the end of the oviposition period were the first to emerge, although their insemination was obviously later and abiotic conditions were identical. One explanation might be that there was a higher provision of nutrients in the yolk sack at the end of oviposition.

Acknowledgements

We thank our friends and colleagues for various help and fruitful discussions, viz. Mr Günter Ebert, Prof. Dr Dr Konstantin A. Efetov, Ms Petra Dieker, Mr Ingmar Harry, Mrs Rine Schneijderberg, Mr Jochen Schünemann, Dr Jörg-Uwe Meineke, Dr W. Gerald Tremewan and Dr Robert Trusch. Livestock that was used during these investigations was generously provided by Prof. Dr Günther Buntebarth (*Z. dorycnii*), Mr Marc Nicolle (*Z. tremewani*), Dr Chiharu Koshio and Mr Kiyoshi Horie (*Z. niphona*, *Illiberis rotundifolia*) and Mr Thomas Keil (*Z. viciae* and *Z. fredi* from Armenia). Without the availability of the enormous collection of transparencies depicting Afrotropical and Oriental Zygaeninae that were photographed by the late Prof. Dr Clas M. Naumann, this general overview on egg batches would not have been possible.

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