EVOLUTION TRENDS IN TACHINID EGG MORPHOLOGY

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Tachinid egg morphology were investigated by several authors. J. Pantel (1910) divided eggs of Tachinidae into four groups: macrotype eggs, microtype eggs, membranous eggs and eggs with a stem.

The macrotype eggs, which are laid on the host’s covers, are spread in a number of genera of subfamilies Exoristinae and Phasiinae. The macrotype eggs are unincubated, have a relatively large size (more 0,4 mm), their chorion is divided into thick dorsal part and thin ventral one. The macrotype eggs usually have well-developed polygonal network on their dorsal surface, forming plastron (Hinton, 1981).

The microtype eggs usually are incubated and can be distinguished by their very small size (0,4 mm or less in length), and the characteristic shape of the chorion, which is divided into a thick and arched dorsal surface and thin and flattened (or concave) ventral one. The dorsal chorion in some species is covered by polygonal network and a system of pits, tubercules. Eggs of this sort are glued to leaves for ingestion by hosts, with adult female tachinids choosing plant species commonly fed upon by their insect hosts. Once ingested, a microtype egg hatches in the digestive system of its host and first instar larva burrows through the intestinal wall to infest the interior
of the host. Tachinids that produce microtype eggs comprise the tribe Goniini of the subfamily Exoristinae.

The membranous eggs are full incubated, they have large size (0.9-1.7 mm), relatively smooth and thin chorion; such eggs usually are laid by female outside the host, in the environment of the host (e.g. leaves, soil). Well-developed first instar larva is located inside such egg. Membranous eggs are spread among species from subfamilies Tachininae, Dexiinae, Voriinae. The eggs of membranous type forms in tachinids, which inject their eggs inside the host’s body (some Exoristinae, some Pha-siinae) too.

The eggs with a stem are characteristic of genera Senometopia Mcq. and Carcelia R.-D. (subfamily Exoristinae). The stem, which is situated on the posterior egg pole, serves for an attachment the egg on the host’s cover.

There are several points of view on the evolution of the methods of sexual reproductive strategy in Tachinidae. F.I. van Emden (1957) thinks that the laying eggs outside the host is the most primitive in Tachinidae, while the laying eggs on the host body is the most progressive in Tachinidae. Van Emden confirms his opinion by the fact that the egg-laying outside the host is spread in the family Sarcophagidae. B. Herting (1960) in his system of Tachinidae gives another opinion: the egg-laying outside the host and the infestation of the host by first-stage larva (which actively searches the host) in some groups of Tachinidae are connected with the development of ovolarvipary. According to Herting, the ovolarvipary is the most advanced form of reproduction in Tachinidae, while the laying of eggs with under-developed embryo on the host’s covers is the most primitive for Tachinidae. V.A. Richter (1992) is agreed with Herting’s point of view. V.A. Richter confirms that the laying of relatively small
number of eggs with under-developed embryo on the host’s covers is initial for Tachinidae. This method of the egg-laying is characteristic of most number of subfamily Phasiinae and non-advanced groups of subfamily Exoristinae. In more advanced genera of Exoristinae the development of ovolarvipary takes place. Ovolarviparous species of Exoristinae lay their eggs on the host or near the host. The development of microtype eggs and laying of them on the fodder-plant of the host is characteristic for one of the phyletic branch of Exoristinae - tribe Goniini. Among representatives of another subfamilies of Tachinidae (Tachininae, Dexinae and Voriinae) the ovolarvipary takes place only. V.A.Richter notes that the development of ovolarvipary is accompanied by progressive transformations of female’s reproductive system.

I have studied egg morphology of Tachinidae from 97 genera with scanning electron microscope. My investigation confirms the latter point of view.

1. MACROTYPE EGGS

1.1. Subfamily Exoristinae

Macrotypes eggs from tribes Exoristini and Winthemiini were studied by several authors. Eggs of genus *Exorista* Mg. were described by Rohdendorf (1935) and Herting (1960). Eggs of genera *Phorocera* R.-D. and *Euphorocera* Tns. were investigated by Herting (1963), Wood (1972), Danks (1974). Eggs from tribe Winthemiini (genera *Winthemia* R.-D., *Nemorilla* Rd.) were described by Thompson (1926, 1963 a), Reinhard (1931), De Loach, Rabb (1971), Danks (1974). The structure of exochorion and aeropylar cripts using scanning electron microscope were investigated by me too (Gaponov, 1996 a).

Eggs of tachinid flies (of Exoristini tribe) have a concave or flatten surface of the chorion, which is used for attaching to the hosts body. The same is true about the
eggs of Winthemiini. The upper surface of the chorion is thickened, convex; it protects the egg from the influence of environmental factors. The surface of the chorion has a polygonal network as well as meshwork of tubercules, folds and apertures, together forming the plastron. Macrotype eggs of genera *Exorista* Mgr., *Phorocera* R.-D., *Parasetigena* B.B. and *Bessa* R.-D. have two aeropylar zones located on the poles of the egg. The aeropylar area on the anterior egg pole has a belt (*Exorista*) or a plate with cripts (*Parasetigena, Phorocera, Bessa*); the aeropilar area of the posterior pole is represented by a compact zone of respiratory cripts. An egg of *Phorinia* R.-D. has one aeropylar zone on the anterior egg pole. Aeropylar cripts are of a spiral, net-like, or of a cellular-like facilitating the filtration of the air coming in under the chorion. Eggs of Exoristini have a hatching line represented by a transversal belt (*Exorista*) or ridge-like lid (*Bessa and Phorinia*) or an operculum lid with a conic structure (*Parasetigena and Phorocera*). Macrotype eggs of Winthemiini (genus *Winthemia* R.-D.) have an aeropylar zone shaped like a transversal belt made of respiratory cripts in the front third of the egg.

The belt with cripts forms the hatching line. The egg of *Nemorilla* Rd. species there are, typically, two aeropylar areas represented by plates on the sides of the egg on its anterior pole. The posterior pole of eggs of *Nemorilla* and *Winthemia* has no cripts.

Riany, 1985), Carcelia R.-D. (Baer, 1920) and few others. The thin detailed of egg structure for 9 genera of Blondeliini (Gaponov, 1994a) and 4 genera of Eryciini (Gaponov, 1994b) were described.

The tribae Eryciini and Blondeliini show evidence of an evolutionary transformation of the reproductive biology. Among Eryciini Aplomyia R.-D. has unincubated macrotype eggs with well-developed plastron surface (there are polygonal network, hills, tubes, pits of a plastron), but an aeropylar area is missing. Senometopia Mcq., Thelymyia B.B., Epicampocera Mcq., Phryxe R.-D., and Carcelia R.-D. have incubated eggs. Eggs of Epicampocera, Phryxe, Senometopia with well-developed polygonal network and plastron pits; their eggs with aeropylar zones (one zone on the anterior egg pole in Phryxe, two ones on the eggs poles in Epicampocera, reduced cripts in the central part of the chorion in Senometopia). Egg of Thelymyia has not a polygonal network; a plastron surface is partially reduced; the aeropylar area is represented by small cripts on the anterior egg pole. Egg of Carcelia is membranous, without polygonal network, but with the stem for attachment on the host covers. Among Blondeliini Meigenia R.-D., Zaira R.-D., Istochaeta Rd. lay their eggs on a host’s covers, which is known as the most primitive method of sexual production in Tachinidae. Medina palm off their macrotype eggs under a host’s (beetle’s) elitrae. Oswaldia R.-D. lay fully incubated eggs on a host’s body. The structural peculiarities of their eggs of Lecanipa Rd. and Ligeria R.-D. allow to assume that the former attach their macrotype eggs on a host’s covers, while the latter, probably, thrust their membranous eggs under the protruding parts of a host’s body. The evolutionary development of the ways of egg laying is reflected in the evolutionary transformation of the eggs. Lecanipa and Istochara have typically macrotype eggs with a low degree of incubation, well-
developed polygonal network and other plastron structure and aeropyle. The eggs of *Meigenia, Medina, Zaira* have a relatively thin chorion without a polygonal network; their plastron surface is partially reduced, but the aeropylar area is still preserved. *Zaira* has fully incubated eggs as well as *Oswaldia*, but the eggs of this genus posses a polygonal network, fully developed plastron surface and aeropyle. The eggs of *Zaira* and *Oswaldia* occupy an intermediate position between macrotype and membranous eggs. *Blondelia* and *Compsilura* inject their eggs into a host's body. These eggs are membranous with a thin chorion and no aeropylar area. Their plastron surface is reduced. Generally, there is a tendency towards reduction of a plastron surface and prolongation of incubation in the reproductive system of females.

In tribe Ethillini (Tschorsnig, 1988) the development of an operculum for the hatching of first stage larva takes place; egg surface with polygonal networks.

Thus, the surface of macrotype eggs is a combination of holes or tubercules, usually with a polygonal network. Initially the egg surface of macrooviparous Exoristinae probably has a relatively good-developed polygonal network with a systems of regular pits as it is take place in eggs of many non-tachinoid Diptera and in insects most primitive then Diptera. I think that egg surface of *Exorista, Phorinia, Paprasetigena, Phorocera* (e.g. tribe Exoristini) is correspond to such initial hypothetical surface of eggs of Tachinidae. In a process of evolution the egg surface of Exoristinae tries two general trends. In several genera, for example in *Ethilla, Oswaldia, Lecanipa*, probably *Bessa*, the further development of polygonal ridges and a complication of a bottom of polygonal cells (as well as channels inside the chorion) took place. In another group of genera, for example in *Phryxe, Carcelia, Lydella, Drino, Zaira, Medina, Meigenia*, the process of reduction of plastron sur
face (a polygonal network and a system of pits, tuberclus and perforations) was a
goal trends in the surface transformation. Chorion of the eggs of this group of genera
became thin.

The aeropylar area is located on the anterior egg pole in the form of a belt or
a plate with cripts. Eggs of a number of genera of macrooviparian exoristins have
two aeropylar zones situated on the poles. The eggs are unincubated in the
reproductive system of females; they develop on the host’s covers. The range of
hosts is varied.

Within the subfamily (e.g. in tribae Blondeliini, Eryciini) there form eggs of a
transitory type, which combine features of macrotype and membranous eggs. The
eggs of this group have a high degree of incubation in the reproductive system of
females; their chorion is not divided into the upper and lower parts; the covers are
thin; the cripts are small; the polygonal network is absent. At the same time, in a
few genera of this group eggs preserve an aeropylar area and a polygonal network.

1.2. Subfamily Phasiinae

Macrotype eggs of Phasiinae were investigated by Dupuis (1963), Victorov

Macrotype eggs of Phasiinae are not incubated; their surface is either like net
or like an ampulæ; the polygonal network is usually absent. The aeropylar zone is
represented by a single big respiratory centre of a cellular structure on the anterior
egg pole. Macrooviparian phasiins lay their eggs on the cover of bugs, the only
hosts for Phasiinae (except tribe Strongygæstrini). The character of egg-laying and
the specific range of hosts in phassins leads to stabilization of egg’s characteristics.
When some phasiins transit to inserting their eggs under the host’s covers (e.g.
Elomyia) there form eggs of transitional type (the surface of their chorion becomes
thinner; the plastron structures are reduced, while the aeropylar zone is located on
the appendix, sticking out from under the host’s covers. Analysis of the exochorion
structure of eggs of Slyogymnomyia nitens, Strongygaster globula, Elomyia
lateralis, Cylindromyia brassicaria allowed to make the following conclusions.
While laying their macrotype eggs on the covers of the host phasiins retain their
initial morphological characteristics: development of an ampule-shaped or net-like
plastron surface; stabilization of the aeropylar zone as a single respiratory centre
with a netlike structure inside. At the same time, eggs of the phasiins with this type
of egg-laying investigated earlier (genera Heliozeta, Clytiomyia, Cistogaster,
Ectophasia, Subclytia, Gymnosoma) are devoid of the polygonal network
(Gaponov, 1991, 1992). This has been noted in several of papers on genus
Gymnosoma (Dupuis, 1963; Viktorov, 1967; Khitzova, Golub, 1972). Eggs of
Slyogymnomyia nitens, on the other hand, have a developed polygonal network.

With the transit of some phasiins from the laying of macrotype eggs on the
host to the slipping of them under the host’s covers, formation of the transitory type
of eggs is observed. In eggs of Elomyia these peculiarities of egg-laying caused the
development of a protuberrance with an aeropylar zone. The main part of the egg
turns out to be sheltered by the host’s covers; the polygonal network is absent; the
plastron surface is greatly reduced (Gaponov, 1996 b).

Eggs of Strongygaster are macrotype, but considerably incubated; they differ
from the typically phasioidal ones in that they have a polygonal network, and their
aeropylar zone is not concentrated in one centre, though the aeropylar cripts retain a
cellular structure as in other macrooviparian phasiins. Structural peculiarities of the
eggs of this type of phasiins can be accounted for by the isolation of Strongydastrini
from the general phyletic branch of phasiins (Shima, 1989) which is connected with parasitism in ants, not in bugs.

2. MICROTYPE EGGS

The eggs of this type are incubated in the reproductive system of females, in which a sack-shaped uterus is developed.

A description of the size, shape, colour and chorion structure of microtype tachinid eggs has been published for *Ceromasia auricaudata* Tns. (Coppel and Maw, 1954), *Gonia* spp. (Strickland, 1923), *Sturmia bella* Mg. (Mellini, 1956; Thompson, 1963 b), *Elodia morio* Fll. (Kahrer, 1987), *Pseudogonia rufifrons* Wied. (Baronio and Campadelli, 1979, as *Gonia cinerascens* Rd.) and for some others. Salkeld (1980) investigated 21 North American species of Goniini using scanning microscope and he stated that the micropilar area of such eggs is situated ventrally and subapically, and that the aerea of cripts on the anterior egg pole is not micropylar structure but rather an aeropylar zone with a respiratory function; Salkeld described the outer and inner structure of microtype eggs. I was investigated microtype eggs of 19 genera from Palearctic (Gaponov 1996 c) with the description of their chorion structure, aeropylar areas, plastron surface.

I noted that some morphological features of microtype eggs reflect cenogenesis. The term cenogenesis refers to the appearance in the embryo of some adaptive structures that are not preserved in the mature adult organism. Cenogenetic features are acquired over time by evolution of adaptation in pre-adult stages, in response to conditions faced during embryonic and larval development.

The surface of microtype eggs of Goniini, which are laid on the host's fodder plant, is covered with a system of holes, tubercules, pits, hills, apertures, and in
some species a polygonal reticulation, forming the plastron surface. This diverse array of chorion structures is adapted for both atmospheric and aquatic respiration. The polygonal network enlarges the air space in the inner parts of the egg shell. The inner layer is perhaps important for maintaining optimal temperature and humidity levels inside the egg (air being a good insulator). The ventral chorion is porous and concave or flattened. The primary function of the ventral chorion is to ensure the secure attachment of an egg to the surface of a leaf. The junction seam joining the dorsal and ventral chorions rests on the plant surface and protects the thin ventral surface of the egg. The diameter of the surface apertures may probably vary within certain limits.

Microtype eggs are usually melanized, and such melanization influences the response of an egg to sun energy. Melanized structures probably absorb or reflect heat, thereby supporting the environmental stability of the inner part of the egg.

The microtype eggs can be divided into types based on the structure of the dorsal chorion. Eggs of the first group are characterized by a polygonal network on the dorsal surface (e.g. *Masicera* Mcq., *Sturmia* R.-D., *Blepharipa* Rd., *Phryno* R.-D., *Ceromasia* Rd., *Frontina* Mg., *Eumea* R.-D., *Bothria* Rd., *Zenillia* R.-D. etc.). Egg's surface of these genera has been complicating in the process of evolution. The second type of dorsal chorion is characterized by the absence of a polygonal network (e.g. *Pales* R.-D., *Gonia* Mg., *Gaedia* Mg., *Pseudogonia* B.B., *Clemelis* R.-D., *Spallanzania* R.-D., *Prosopoea* Rd. etc). Probably, the reduction of a polygonal network on the egg surface of these group of genera is another trend.

As a rule there is an aeropylar zone which in the process of evolution tends to get stabilized in its position on the anterior pole of an egg while its cripts concentrate in
one respiratory centre shaped like a plate. Thus, the system of aeropylar cripts is
not condensed into a single centre in Gaedia, but it is situated in the anterior third of
the egg. The eggs of Gonia, Pseudogonia, Spallanzania, Pales, Elodia, Clemelis
are characterized by the concentration of aeropylar cripts into a single centre, repre-
sented by a raised or non-arised plate. The enlargement of openings on the egg
surface and the reduction of respiratory cripts occur together in the tachinid genera
Erycilla, Bothria, Prosopea. In Phryno and Prosopea the aeropylar structure is ab-
sent, but its function is taken over by the large openings and pits on the surface of
the dorsal chorion. The enlargement of respiratory cripts and their consolidation at
the apex of anterior egg pole within a distinct aeropylar area takes place in the eggs
of Ceromasia, Frontina, Masicera, Sturmia, Blepharipa (Gaponov, 1996 c).

In summary, it is my view that the evolutionary transformations of microtype
tachinid eggs are characterized by a concentration and enlargement of the aeropylar
cripts and by the separation of a single aeropylar centre. It seems that aeropylar
cripts originated through a consolidation of pits and openings of the chorion plas-
tron surface and their migration to the anterior egg pole (the process of oligomeriza-
tion); it is concerned to aeropylar area of macrotype eggs too.

The appearance of microtype eggs in one of the phylogenetic branches of the
Tachinidae, and the spread of these eggs by females on the surface of leaves in the
habitats of hosts, is a prime example of adaptive evolution in tachinid eggs. This type
of egg production is evolutionary advanced, and among other advantages it allows for
the infestation of night feeding hosts.
3. MEMBRANOUS EGGS

Membranous eggs are typically spread in subfamilies Tachininae, Dexiinae, Voriinae, representatives of which are ovolarviparous. Also the eggs of this type are characteristic of some Exoristinae and some Phasiinae.

Summary of structure of several eggs of this type are given by Ferrar (1987).

Membranous eggs of Tachininae, Dexiinae are incubated in the spiral uterus of a female (apomorphic condition).

Among Tachininae typical membranous eggs with transparent thin homogeneous chorion without both polygonal network, and aeropylar area there is in tribes Tachinini (Tachina, Nowickia, Mikia, Peleteria), Nemoraeini (Nemoraea), Linnaemyiini (Linnaemyia, Lydina), Ernestiini (Eurythia R.-D., Hyalurhus, Gymnochaeta, Zophomyia), Pelatachinini (Pelatachyna), Triarthriini (Triarthria), Leskiini (Leskia, Bithia, Aphria), Minthoini (Minto), Microphthalmini.

In some cases (for example, in Hyalurhus, Nemoraea, Tachina, Macquartia, Aphria) the hatching of the membranous tachinins eggs can be realized with the help of a transversal seam on the posterior egg pole. Eggs of this type are laying by female outside the host, and first instar larvae are hatched quickly from the eggs and search for the host.

However, the structure of exochorion of some representatives of Tachininae may be diverse. A number of genera of the subfamily Tachininae have eggs of a transitional type, e.g. Macroprosopa B.B., Actia R.-D., Lypha R.-D., Siphona Mg., Bracteola Richter.

These eggs are considerably incubated; their chorion thin, but it preserves a polygonal network and an aeropylar area with cripts on the anterior egg pole.
(Gaponov, 1993). Their features of membranous and macrotype eggs are combined. For example, exochorion of the eggs of *Lypha* and *Bracteola* with a polygonal network. Probably, first instar larvae exits after relatively long period, and such eggs pass a partial additional incubation in an environment. Eggs of *Actia* with both unclear polygonal network, and an aeropylar area. Probably, in these cases eggs are laying on the host covers. The egg of *Macroprosopa* rather macrotype. The chorion is divided into upper and lower chorions, covered by well-developed polygonal network; on the anterior egg pole there is a typical aeropylar area with cripts.

In the representatives of subfamily Dexiinae (for example, *Dexia* Mg., *Ptrosena* Le Peletier et Serville, *Zeuxia* Mg. and all others), the first instar larvae are planidium-shaped and may get out of the egg shells already at the stage of egg-laying. Their chorion is thin and membranous. In all Dexiinae eggs without any network, plastron surface or aeropylar area. The hatching of the first instar larvae takes place in the moment of the egg-laying.

Tachinid flies from the subfamily Voriinae lay membranous full incubated eggs on the host cover. Their chorion is thin but with irregular pits or small «drops» which represent themselves a remainders of a plastron surface (*Peteina* Mg., *Eriotrichix* Mg., *Voria* R.-D., *Phyllomyia* Mg., *Athrycia* R.-D.). Probably there is bad-developed channels with air inside their chorion. Aeropylar area is absent.

A number of Exoristinae (*Blondelia, Compsilura*) and Phasiinae (e.g. Cylindromyiini, Leucostomini) inject their membranous eggs into the body of the host. Genera of this group have membranous eggs with reduced plastron surface without an aeropylar area, but usually with a longitudinal seam of opening the egg. Part of the phasiins, including *Cylindromyia*, transit to the injecting of membranous
eggs into the host’s body. The chorion of such eggs is thin, with some fragments of the plastron surface. There is a longitudinal seam of hatching (Gaponov, 1996 b).

In general, the process of a reduction of a polygonal network, plastron surface and aeropylar area is characteristic of membranous eggs.

Thus, ontogenesis of Diptera as well as of any other insects goes through a number of stages. Since any kind of adaptation is a result of evolution and every stage of ontogenesis, including the egg stage, is adapted to some specific environmental conditions, each stage of ontogenesis evolved more or less independently of others. Development of provisory devices (cenogenetical adaptations) such as chorion, amnion, allantois and their improvement was one evolutionary way of ontogenesis at the egg stage. Another was shortening and simplification of the stage, leading to the end of elimination at this phase of ontogenesis.

Thus, development of embrionic egg shells as a manifestation of specialized embryoadaptations provides protection and, as a result stability for the early stages of ontogenesis. Embryonization in the evolution of macrooviparian and microoviparian Tachinidae allows further evolutionary improvement and simplification of those processes of individual development which eventually lead to puberty. Evolution of the egg stage in Tachinidae (probably, in whole Superfamily Tachinoidea (families Tachinidae, Calliphoridae, Rhinophoridae and Sarcophagidae) is caused by philembriogenesis of which I have observed three modes, namely, anaboly, deviation and reduction through rudimentation.

Anaboly consists in the addition of new stages to those which existed in the ancestors; it is conducive to further development of the organs already possessed by the ancestors. Thus more primitive Diptera have a three-layer chorion - in Tachini
dae it undergoes the following changes oligomerization of plastron elements and aeropylar cripts, development of different kinds of plastron surface, modification of interior cavities, appearance of the aeropylar zone. Owing to anaboly the previous stage in the development of organs, chorion in particular, becomes a palingenetic recapitulation, which results in specialization of development.

In my opinion, development of microtype eggs in Tachinidae (tribe Goniini) is connected with deviation as a restructuring of the stage which existed in their ancestors (macrooviparian Exoristini).

Reduction take place in the evolution of eggs in Tachinidae through rudimentation, i.e. a slow disappearance of the structures, which lose their function and become useless. As ovolarvipary or larvipary develops, eggs lose plastron structures; rudimentation of the aeropylar cripts is manifest (Gaponov, 1996 d).

Shortening and simplification of the metamorphose in the egg of ovolarviparian Tachinidae account for the reduction of provisory devices resulting in partial embryonization. The latter serves as a prerequisite of subsequent lengthening of postembryonic stage and development of new devices.

The variety of adult and larval features in Tachinidae and the similarity of some of these features with of tachinids from different groups can be explained by evolutionary parallelism (homoplasy) that is very widespread in the family Tachinidae (Richter, 1987). This confirms N.I.Vavilov’s (1935) opinion that the greatest parallelisms take place within a group of related genera or within the limits of a single family. Comparison of eggs of different groups of tachinid flies (especially of the eggs of transitional forms) allows to establish the unity origin of different
representatives of the family. In the egg structure of different groups of tachinids morphological parallelisms are widespread.

REFERENCES


