EMBRYONIC DEVELOPMENT OF THE MITE SPINTURNIX VESPERTILIONES (PARASITIFORMES : SPINTURNICIDAE)

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EMBRYOGENESIS
EMBRYONIZATION
OF ONTOGENESIS
PARASITE
SPINTURNICIDAE

ABSTRACT : The paper presents data concerning the progress of embryogenesis of the parasitic mte *S. vespertiliones*. The adaptation to the specific conditions of parasitism resulted in considerable alterations in the entire process of the embryonic period of ontogenesis. First of all, this led to the loss of vitellus ovi by the eggs (alecithal eggs), simultaneous *adenotrophic* development of a large number of embryos (up to 10), considerable embryonization in the early stages of ontogenesis — up to the protonymph. This results in the absence of an embryonized haxapod larva, progressive growth of the size of embryos in the process of their development, changes occurring in the course of blastulation (steroblastula) and gastrulation, as well as some peculiarities of the formation of the generative elements and the digestive system. The following stages of embryogenic development were singled out : cleavage ; formation of embryonic layers ; protolarval morphogenesis ; larval morphogenesis ; and protonymphal morphogenesis. However, all these considerable changes, occurring in the course of embryonic ontogenesis, cannot be regarded as an indicator of basic differences between the mites Spinturnicidae and the rest of the cohort, because these changes testify only of the advanced specialization of representatives of this family.

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RÉSUMÉ : Cet article présente des données qui concernent la marche de l'embryogenèse du parasite *S. vespertiliones*. L'adaptation à des conditions spécifiques de parasitisme a eu pour résultat des altérations considérables de tout le processus de la période embryonnaire de l'ontogenèse. En tout premier lieu, cela a mené à la perte des grains de vitellus par les œufs (œufs alecithes), au développement adenotrophique simultané d'un grand nombre d'embryons (jusqu'à 10), à une embryonisation considérable aux premiers stades de l'ontogenèse — jusqu'à la protonymphe. Il s'en suit l'absence de la larve hexapode embryonisée, l'accroissement progressif de la taille des embryons dans le processus de leur développement, des changements qui apparaissent au cours de la blastulation (steroblatula) et de la gastrulation, aussi bien que quelques particularités de la formation des éléments générateurs et du système digestif. Les stades suivants du développement de l'embryon ont éyé singularisés : clivage ; formation des couches embryonnaires ; morphogenèse protolarvaire ; morphogenèse larvaire ; et morphogenèse protonymphaire. Toutefois, tous ces changements considérables, qui se produisent au cours de l'ontogenèse embryonnaire, ne peuvent pas être considérés comme indiquant des différences de base entre les Spinturnicidae et le reste de la cohorte, parce que ces changements témoignent seulement d'une spécialisation avancée des représentants de cette famille.

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Introduction

The family of Spinturnicidae is represented by a specialized group of Cheiroptera parasites inhabiting their wings' webs. In terms of outward appearance, while ranked by E. Lindquist within the Dermanyssoidea group (1979), this group differs from the majority of typical representatives of the Gamasina cohort. Morphological studies dealing with this group are relatively few. Studies that have so far been undertaken in this area focus on the feeding apparatus (Kozlovski, 1955), some details of the outward morphology (Deunff, 1977 ; 1982), the skeletal-muscular system (Akimov, Yastrebtsov, 1987), and some aspects of the final stages of embryogenesis (Zukovski, 1966). Even this information, however fragmentary, indicates the clear-cut trend of this particular group towards both external and internal specialization in parasitism under specific conditions. With this in mind, it would be all the more interesting to get insight into the impact of the specialization on the course of individual development and, above all, on the embryonic ontogenesis. The present paper is an attempt to examine these processes regarded as part of the specialization towards parasitism.

Materials and methods

Female mites *S. vespertiliones* were used, assembled on the wings' webs of great bats (*Nyctalis noctula*). The mites were fixed in Buen-Dubosque-Brazil solution, which was poured in paraffin blocks. 4-6 μm thick sections were stained with hematoxylin according to the Meyer-Erlich method, and then additionally with eosine. To finalize the topographies of certain structures, embryos, isolated from female mites, were stained with picroindigocarmine by the method of Roskin (Roskin, Levinson, 1957), with subsequent plastic and graphic reconstruction.

Results

Simultaneously, up to ten embryos undergo development within the cavity of the bodies of female mites *S. vespertiliones*, causing considerable deformation of internal organs, above all the digestive and excretory systems which become shifted towards the peripheral part of idiosoma. Embryos are observed at different stages of the embryonic ontogenesis, which enables reconstruction of the entire course of development using a section of just one female mite (Pl. I : 1, 2).

The reproductive system of pubescent females *S. vespertiliones* considerably differs from the classical pattern of the reproductive system of Gamasina, with all its distinctive compartments. The central part of the ovary is located in the idiosoma dorsomedially at the level of the walking legs III. The lyriform organs, the seminal receptacle and a substantial part of the oviducal system are reduced. The central part of the ovary contains comparatively small oocytes (15 μm in diameter). Skipping the stage of vitellogenesis, the oocytes immediately enter the process of cleavage in the ovary. We have observed neither processes of fertilization, nor sperm cells capable of effecting fertilization. Besides oocytes, the ovary contains spindle-shaped cells with a large nucleus. With the ongoing process of cleavage, the size of oocytes progressively increases and can characterize a certain stage of their development. The beginning of cleavage can be described as a total asynchronous process (Pl. I : 3-7). The sizes reached after the first, second and third segmentations are 20, 29 and 34 μm, respectively. After 5-6 segmentations the cell which undergoes cleavage finds itself within a cavity whose walls consist of accessory cells and their derivatives. All subsequent processes of the embryogenesis occur inside the somatic cavity of the body. The developing embryos gradually move along the dorsal surface, anteriad, and then along the ventral surface, posteriad, in helical fashion. The most developed embryos are located in the posterior part of the opisthosoma. Following 7-8 segmentations, isolation of a blastoderm takes place, resulting in formation of a compact steroblatula. An early steroblastula reaches 50 μm in diameter (Pl. I : 6, 7). The subsequent segmentation of blastoderm cells is of unsteady character. The blastula assumes an oval shape, and a certain part of the cells formed as a result of the segmentation, immigrates to an

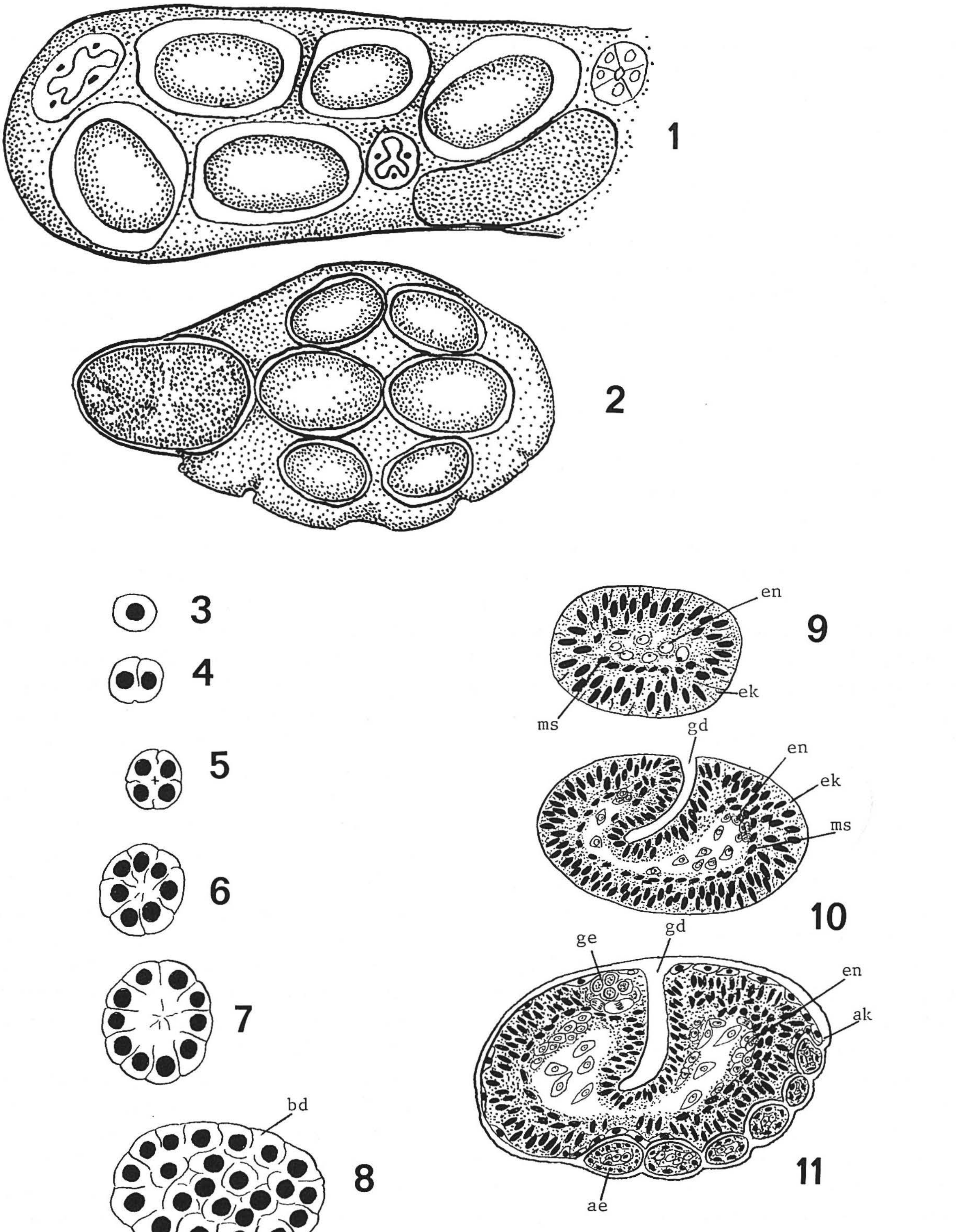
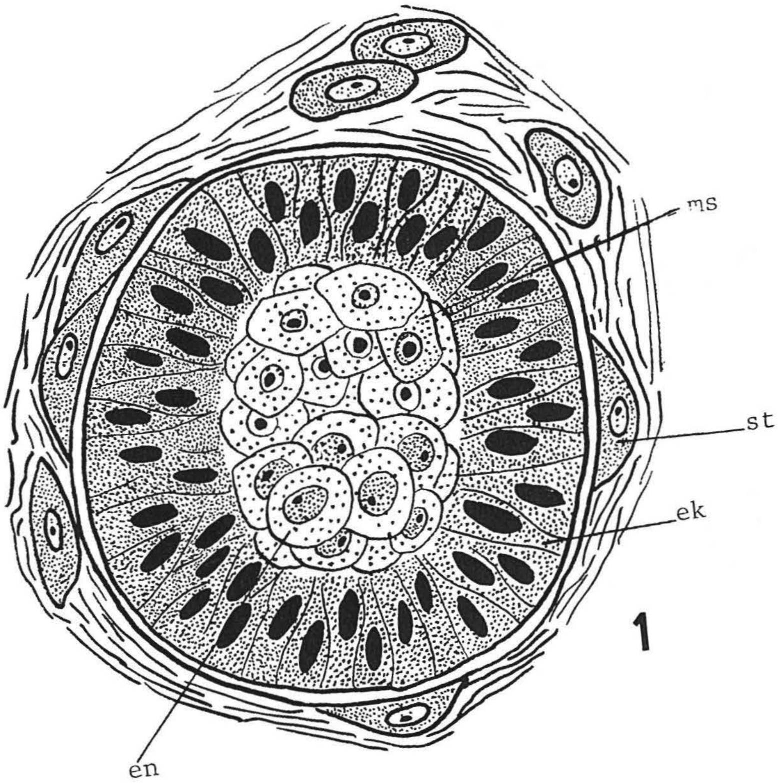


PLATE I : Stage sequence of embryogenesis.

1. — Positions of embryos in the idiosoma of a female mite (sagittal section) ; 2. — Positions of embryos in the idiosoma of a female mite (frontal section) ; 3. — II — stages of embryogenesis. ae — germs of extremities ; ak — cephalic bladebone ; bd — blastoderm ; ek — ektoderm ; en — entoderm ; ge — genital germ ; gd — dorsal groove ; ms — mesoderm.

area under the blastoderm. The formation of germinal layers begins after the embryo size reaches 70 × 45 μ (Pl. I : 8 ; II : 1, 2). The cells located under the blastoderm undergo differentiation, thus forming entoderm and mesoderm (Pl. II : 1, 2). No clear-cut topographic localization of these processes can be traced. Blastoderm cells assume the character of stratified epithelium with readily stained nuclei and poorly discernible boundaries. The diameter of the nuclei reaches 5 μ. Nesodermal cells are large, the cytoplasm is actively stained, while entodermal cells are somewhat smaller and have a less readily stained cytoplasm but a larger nucleus. Entodermal cells gradually concentrate largely on the anterior and posterior poles of the embryo. In the process of growth, the embryo central part develops a cavity containing solitary entodermal cells, whereas mesodermal cells are located directly under ectoderm and are absent only on a small area of the dorsal surface, where, after the embryo reaches the size of 140 × 80 μ, there occurs a deep invagination of ectoderm with formation of a dorsal groove (Pl. I : 10). At the base of the dorsal groove, in its posterior part, a primary reproductive germ is generated at the expense of the cells of mesodermal origin of which size reaches 30 μm and which are characterized by a high rate of segmentation. The differentiation of somites starts after the size of the embryo reaches 180 μ. Initially, the ventral stripe divides into four parts which are outwardly marked with invaginations of ectoderm. Subsequently, the anterior part divides into two somites. The two posterior parts also undergo segmentation. The most posterior part, representing the opisthosoma, bears no traces of segmentation (Pl. I : 11). The processes of final differentiation of somites come to an end when the embryo size reaches 220 μm. The subsequent development is accompanied with the formation of germs of some organs : the synganglion is the first to be produced at the expense of the immigration of ectodermal cells of the embryo anterior part. The germ of the synganglion rapidly spreads out, differentiating into a cortical layer and a neuropil, and occupying nearly a half of the entire volume of the idiosoma. No blastokinesis processes were observed, and after the formation of the synganglion the dorsal stripe disappears. The formation of the middle intestine is accompanied by the immigration of entodermal cells and their epithelization. At first, a sacciform germ of the stomach is formed directly behind the synganglion, followed by the rectal sack with processes of the Malpighian tubes. The germs of all these parts of the digestive and excretory systems are virtually devoid of cavities, each representing an ordered aggregation of cells. The formation of the anterior and posterior intestines occurs much later. The salivary glands emerge on the anterodorsal surface of the embryo, directly above the synganglion. The origin of this germ is yet to be elucidated, but it is clear its differentiation takes place in the milieu of mesodermal cellular elements. The embryo ectoderm becomes flat, acquiring all the features characteristic of superficial epithelium, which forms a cuticle on the surface. Simultaneously with the development of systems of organs, there occurs the differentiation of extremities. The cephalic lobe takes up an anterodorsal position (Pl. I : 11), the chelicerae — outgrowths of the first segment — become separated, while their base submerges into the surrounding ectoderm. The second segment forms two germs. The first pair is represented by small tubercles, while the second one has a much larger size. The first pair gradually merge together, and at subsequent stages the place of accretion is marked only with small crypts on the dorsal surface (Pl. III : 1, 2). The second pair of the outgrowth of this segment become separated, shaping into terminal segment-like formation of pedipalps, while their base is laterally overgrown with the bases of chelicerae which accrete with the cephalic lobe, forming the dorsal surface of the gnathosoma (Pl. III : 1, 2). The development of extremities III-IV of the segment is uniform. They elongate, and strangulations appear on the surface, which correspond to the future segment-like formations. By the time the embryo enters the external medium all the four pairs of legs have a full-grown ambulacrum, developed muscles and articulated outgrowths. Of speial interest is the process of formation of the endoskeletal structure — endosternite, which forms from mesodermal cells simultaneously with the musles (Pl. III : 4). The endosternite germ form behind the



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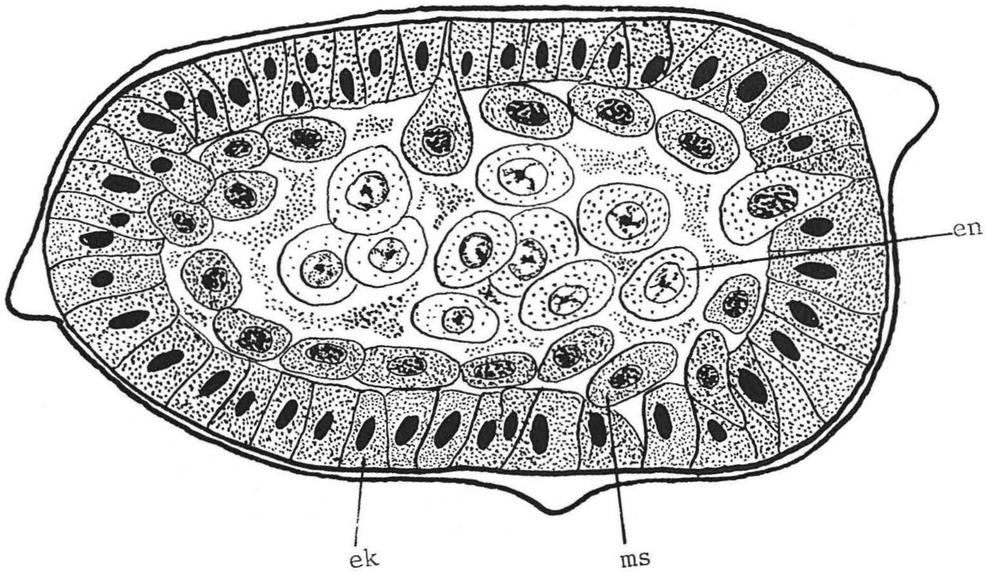
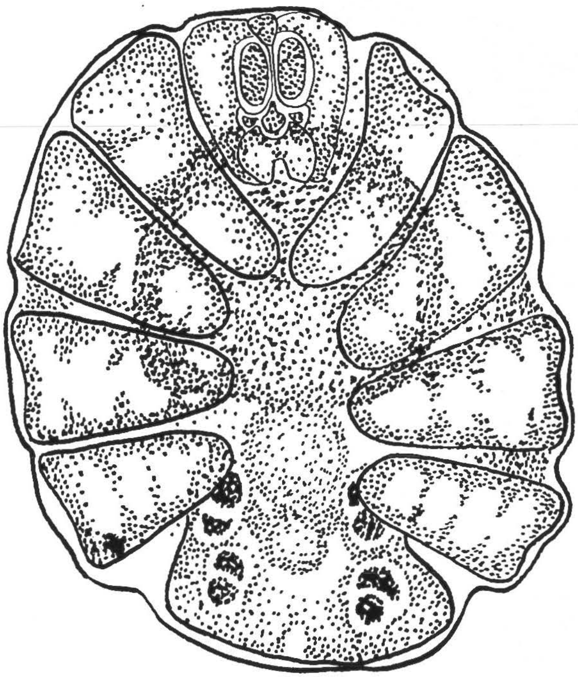


PLATE II : Formation of embryonic layers.
1. — early gastrulation ; 2. — late gastrulation. Designations — same as Fig. I (st — satellite cells).



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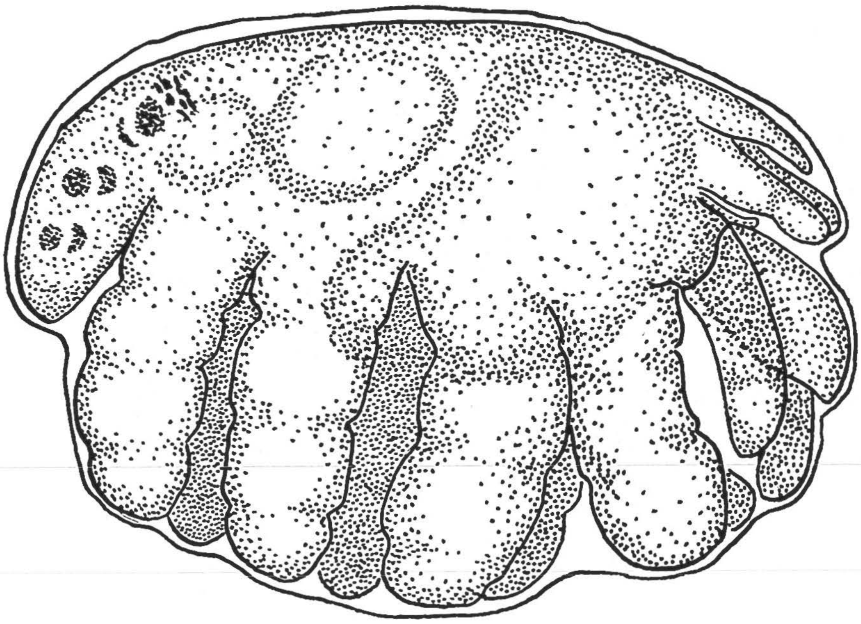

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PLATE III : Embryos at late stages of embryogenesis.

synganglion in the proximity of the ventral surface of the embryo, emerging from the swarm of mesodermal cells. From the very same swarm of cells differentiate the cells which subsequently form muscle fibers of external muscles of the lower extremities.

The development of an embryo is accompanied by considerable alterations in the generative system, which moves into the opisthosoma. Out of the oogoniums, undergoing the process of prolific reproduction, moves out a group of rapidly growing cells. There are normally no more than eight such cells within an embryo idiosoma, of which four are located in the posterior part of the opisthosoma, while the remaining two pairs occupy a lateral position — at the base of the legs IV (Pl. IV : 1, 2). Having, as a rule, two nuclei each, these cells are surrounded by a number of satellite cells which are of the same origin. A fullgrown embryo (670 × 500 μm) is located in the posterior part of the idiosoma, with its prosoma taking up the entire volume of the female opisthosoma. Such an embryo has a well-developed gnathosoma, lower extremities and germs of all the main systems of organs (Pl. III : 5). An embryo going out into the external medium was not observed. The assumption that this process may be effected in a way typical for Gamasina, i.e. via the genital orifice, is unlikely because the extension of membranes and intercoxal distances are much smaller as compared with the size of an embryo.

Discussion

As shown by comparative studies of the mites Spinturnicidae and other Gamasina (Steding, 1923; Warren, 1940, 1941; Zukovski, 1965, 1966; Akimov, Yastrebtsov, 1988), the group of mites in hand displays considerable distinctions during the embryogenesis. This immediately leaps to the eye despite the fact that data concerning other representative of the cohort are rather fragmentary and apparently fail to embrace all possible ways of development of these processes. The most significant distinction lies in the fact that Spinturnicidae show an early maturation of oocytes and the absence of the processes of vitellogenesis, i.e. they belong to the alecithal type. This accounts for complete cleavage (at the initial stages), formation of a steroblastula, simultaneous development of a large number of embryos whose development is of the hemocell nature uncharacteristic of Gamasina. Considerable changes occurring in the course of embryonal development, which are connected with the secondary transition to alecithal eggs, are characteristic of certain web-winged parasites (Ivanova-Karas, 1948, 1950, 1954), though their embryogenesis follows a different pattern.

Embryonization of the initial stages of ontogenesis is characteristic of many mites, representing one of the trends in their evolution (Zakhvatkin, 1953; Vainshtein, 1977; Sitnikova, 1978).

In the majority of cases, however, it is connected with the accumulation of an amount of nutrients which is sufficient for such a development. In contrast, the embryonization in Spinturnicidae, up to the protonymph stage, is connected with the loss of vitellus ovi and the possibility of exotrophic nutrition at the expense of the female. This also accounts for the progressive increase in size occurring in the course of development, which can be regarded as an indicator of this or that phase of embryogenesis. In general, several stages may be singled out in the embryonic development of Spinturnicidae : 1. *Cleavage* — occurs in the ovary and is characterized by the increase in size from 20 to 50 μm (Pl. I : 3-7). 2. *Formation of embryonic layers* — initial stages take place in the ovary, while the subsequent ones occur in the cavity of the body; characteristic of this stage is the formation of the steroblastula and the immigration-type gastrulation; the size varies from 50 to 130 μm; the stage ends with the formation of the dorsal groove. 3. *Praelarval morphogenesis* — this stage is characterized by the formation of a germ of generative organs; synganglion, somites and germs of six pairs of extremities; it ends after the dissappearence of the dorsal groove and the formation of a cuticle; the size varies from 130 to 250 μm (Pl. I : 10. 11). 4 *Larval morphogenesis* — there occurs the formation of germs of the middle intestine, the Malpighian tubes and salivary glands; differentiation of the gnathosoma and segments of extremities takes

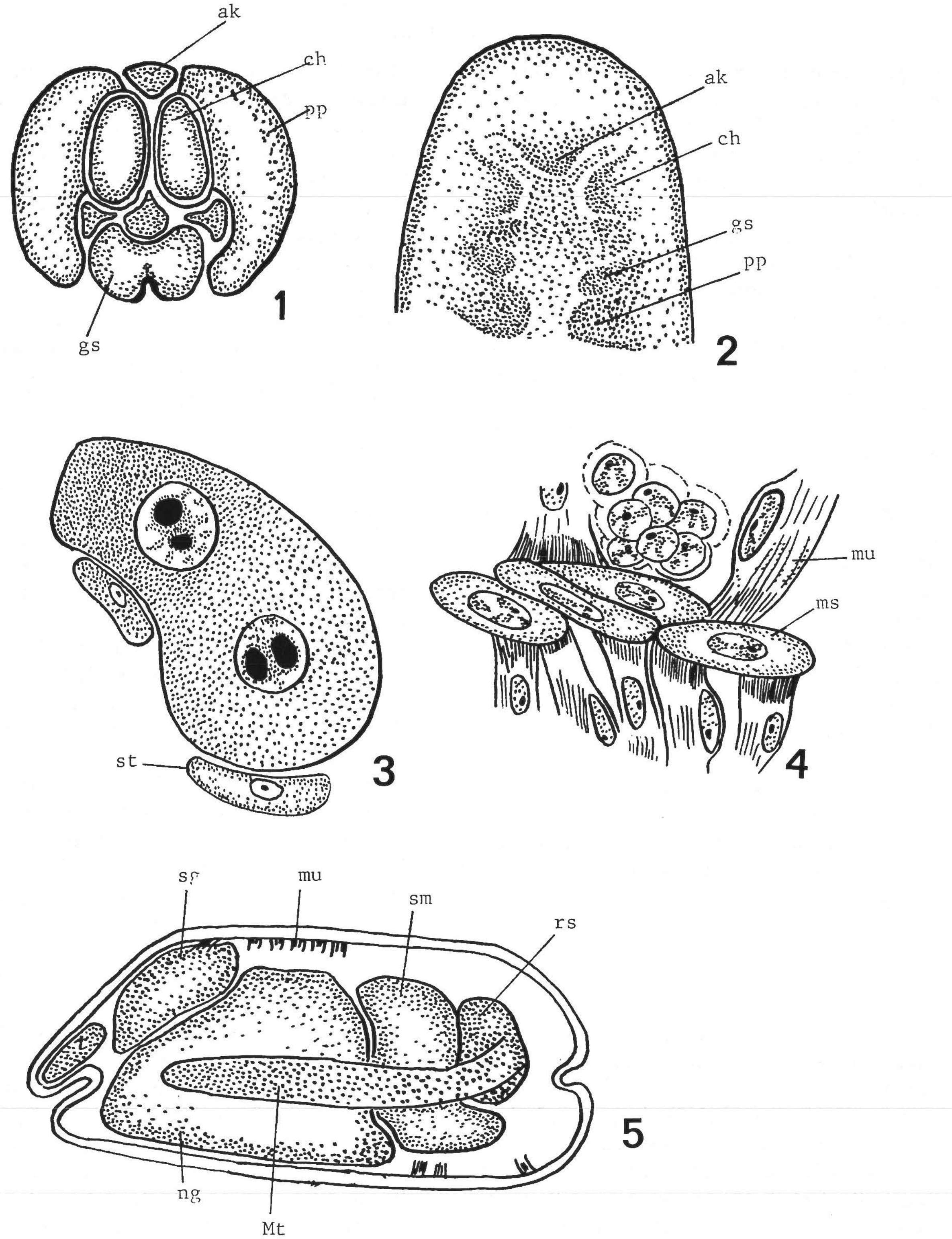

PLATE IV : Development of organs.

1. — feeding apparatus (cross section) at the stage of larval morphogenesis ; 2. — anterior part of the body during praelarval morphogenesis ; 3. — an oocyte during larval morphogenesis ; 4. — formation of endosternite ; 5. — arrangement of organs during larval morphogenesis. ak — cephalic bladebone ; ch — chelicerae ; gs — hypostome ; ms — mesoderm cells ; mt — Malpighian tubes ; mu — muscles ; ng — synganglion ; pp — pedipalps ; rs — rectal bladder ; sg — salivary glands ; st — satellite cells ; sm — " stomach ".

place ; eight oocytal cells are formed ; the size varies from 250 to 300 μm (Pl. III : 1, 2). 5. *Protonymphal morphogenesis* — anterior and posterior intestines are formed, as well as the endosternite ; differentiation of muscular complexes, ambulacrums and setae takes place ; neurosecretory cells differentiate in the synganglion ; the size increases from 300 to 670 μm (Pl. IV : 5).

The advanced embryonization results in the lack of the stage described as a hexapodal larva. This salient feature in the development of Spinturnicidae was indicated by Zukovski (Zukovski, 1966). In Spinturnicidae all the four pairs of legs develop simultaneously, and no reductional processes have been observed connected with the IV pair of walking legs. The formation of the middle intestine is also a feature of interest. In most parasitic mites, the formation of the middle intestine is connected with vitellus ovi becoming overgrown with entoderm and, in some cases, vitellophages are involved in these processes (Wagner, 1982 ; Hefezur, 1983). Due to the absence of vitellus ovi, the formation of the germ of the middle intestine occurs in a different way. The formation of this compartment of the intestine is accompanied by the migration of entoderm cells, including the free cells corresponding to vitellophages, to the prosoma which accumulates a swarm of such cells with no lumen. The lumen appears at later stages at the expense of the epithelization and differentiation of cells of this germ.

Thus, the specialization of Spinturnicidae to parasitism in specific conditions led to a substantial alteration of the entire process of embryogenesis. This manifested itself above all in the loss of vitellus ovi by eggs, simultaneous hemocell development of a large number of embryos, and considerable embryonization of the early stages of the ontogenesis (up to the protonymph). This results in the absence of an embryonized hexapodal larva, the progressive increase in size of the embryo in the process of its development, the alteration of the course of blastulation and gastrulation, as well as some peculiarities of the formation of generative elements and the digestive system, and a substantial reduction of elements of the reproductive system in adult females. However, all these substantial changes occurring during the embryogenic ontogenesis, cannot be regarded as an indicator of basic differences between Spinturnicidae and representatives of the rest of the cohort, since they indicate only non-advanced specialization of representatives of this family.

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